

The role of habitat area and edge in fragmented landscapes: definitively distinct or inevitably intertwined?¹

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Abstract: Over the past few decades, much research has focussed on the effects of habitat area (i.e., patch size) and edges in fragmented landscapes. We review and synthesize the literature on area and edge effects to identify whether the ecological processes influenced by patch size and edge are distinct, to summarize evidence for the relative effect of each, and to discuss how estimating their independent effects may be accomplished in field studies. Area and edge directly influence ecological processes in distinct ways, yet indirect effects can be similar, making it difficult to isolate the effects of area and edge in nature. Many studies investigating both area and edge have been confounded in their design and (or) analysis (i.e., studies did not control for one potential effect while testing for the other). Nonconfounded studies have more frequently shown support for edge effects, and comparisons between nonconfounded and confounded studies suggest that some observed area effects could be explained by edge effects. We argue that by focussing on the fundamental processes directly influenced by area and edge, and by developing more rigorous study designs and analyses that isolate their relative influence, greater insight can be gained in future investigations on habitat loss and fragmentation.

Résumé : Au cours des quelques dernières décennies, beaucoup de travaux se sont intéressés aux effets de la surface de l'habitat (c'est-à-dire la taille des taches) et des lisières dans les paysages fragmentés. Nous passons en revue et résumons la littérature sur les effets de la surface et des lisières afin de déterminer si les processus écologiques influencés par la surface et les lisières sont différents, de résumer l'information sur les effets relatifs de chacune de ces variables et d'examiner comment estimer leurs effets respectifs dans des études de terrain. La surface et les lisières affectent directement les processus écologiques de façon distincte, mais leurs effets indirects peuvent être semblables, ce qui rend la distinction entre les effets de la surface et ceux des lisières difficile en nature. Plusieurs études qui considèrent la surface et les lisières confondent les deux variables à cause de leurs plans d'expérience et (ou) d'analyse (c'est-à-dire elles ne tiennent pas compte d'un effet potentiel en testant l'autre). Plus fréquemment, les études qui ne confondent pas les deux variables ont découvert des indications de l'existence d'un effet des lisières; de plus, une comparaison d'études avec ou sans variables confondues indique qu'une partie des effets attribués à la surface peut s'expliquer par les effets des lisières. Nous croyons qu'en se concentrant sur les processus fondamentaux influencés directement par la surface et les lisières et en mettant au point des plans d'expérience et d'analyse plus rigoureux pour isoler les effets relatifs de chacune des deux variables, il sera possible d'obtenir de meilleures perspectives dans les recherches futures sur la perte et la fragmentation des habitats.

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Introduction

Landscapes are composed of a patchwork of habitats that vary in size, shape, and location. Ongoing habitat loss continues to influence landscape structure, with habitat loss

generally leading to increased fragmentation of habitats (or the breaking apart of habitat, independent of loss; Wiens 1995; Fahrig 2003), whereby patches decline in size, increase in isolation, and increase in the proportion of edge

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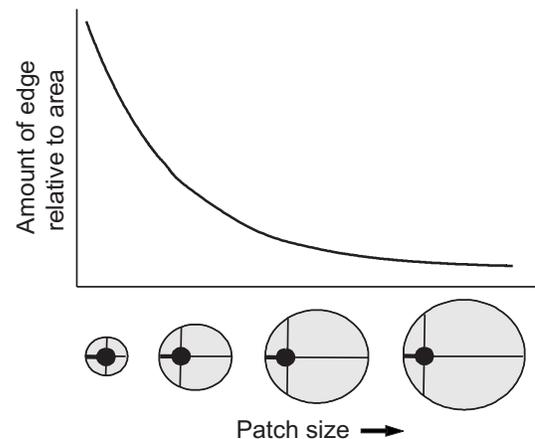
habitat. Because habitat loss is often implicated as the most important threat to biodiversity (e.g., Wilcove et al. 1998), understanding how habitat loss and fragmentation influence ecological patterns and processes has been (Gates and Gysel 1978; Ambuel and Temple 1983), and continues to be (Tscharntke and Brandl 2004; Ewers and Didham 2006), a central focus of landscape ecology, population and community ecology, and conservation biology.

Both habitat area and isolation have long been considered important in affecting ecological patterns and processes. For instance, the equilibrium theory of island biogeography (ETIB hereinafter) and metapopulation theory incorporate area and isolation to explain variation in community structure and population dynamics, respectively (MacArthur and Wilson 1967; Levins 1969; Hanski 1998). These theories have also been applied to understand habitat loss and fragmentation, but with limited success (Doak and Mills 1994; Wiens 1995; Gascon and Lovejoy 1998; Laurance et al. 2002). One explanation for this limited success is that the boundaries of habitat fragments — habitat edges — can also profoundly influence ecological patterns and processes (Gascon and Lovejoy 1998). In fact, a survey of recent experiments on habitat fragmentation suggested that habitat edges are the primary drivers for the influence of fragmentation (Harrison and Bruna 1999).

Over the past three decades, a great deal of research has focussed on the influence of habitat edges and area on a wide diversity of patterns and processes in fragmented landscapes. Much of this research has been driven by concern for recent population declines of many species (e.g., Herkert 1994), improved technology that allows rapid assessment at broad spatial scales (e.g., Alencar et al. 2004), and an increasing awareness that space can have novel effects on a variety of ecological and evolutionary processes (e.g., Kareiva 1990). Yet, attempts to provide conceptual and predictive frameworks to guide our understanding of the unique roles of habitat area and edge have been rare (but see Ries and Sisk 2004).

While both habitat area and edge may influence individuals, populations, and communities, understanding the relative role of these landscape characteristics is crucial for implementing sound conservation strategies. Because habitat area and edge reflect different aspects of landscape structure — landscape composition and configuration, respectively (McGarigal and Marks 1995) — the importance of each suggests different foci for conservation efforts. Furthermore, when habitat edges are implicated in the effects of fragmentation, the type of edge often influences observed outcomes (Sisk et al. 1997; Chalfoun et al. 2002a; Fletcher and Koford 2003; López-Barrera et al. 2006), suggesting that managers and conservationists may need to focus on specific attributes that surround remaining fragments. Habitat area and edge in landscapes nonetheless tend to covary in their amount (Fig. 1), and many studies have not been able to isolate the unique contributions of each element (Parker et al. 2005). Another complication is that effects from habitat edges may explain observed area effects (Bowers et al. 1996; Laurance et al. 1998; Fletcher 2005), making it difficult to interpret if purported area effects are actually a manifestation of edge effects. These problems are exacerbated when considering the cumulative influence of multiple edges within fragments (Fig. 1), as opposed to

Fig. 1. The interplay of patch size and edge. As patch size decreases, the relative amount of edge increases. In addition, the influence of multiple (all surrounding) edges is exacerbated in smaller patches. This pattern is shown by the point in each patch of increasing size, which all have the same nearest distance to edge (marked by the thick lines to the left of the solid circles). However, as patch size increases, the cumulative distance to all edges also necessarily increases (illustrated in the four cardinal directions), and typically does so in an exponential manner.



only the influence of the nearest edge (Malcolm 1994; Fletcher 2005).

Our objective is to examine the effects of both area and edge to better understand their unique contributions to habitat fragmentation. We first synthesize separate conceptual frameworks for the mechanisms that underlie area and edge effects. We then examine the literature where both edge and area effects were measured within the same investigation to determine their relative contribution to fragmentation dynamics. We conclude by discussing how future field studies should be designed to limit the potential confounding issues that arise when investigating the role of area and edge in fragmented landscapes. For the purposes of this article, “patch size effects” are changes in ecological responses (per unit area) as a function of patch area per se, and thus independent of other potential causes, such as those arising from changes in the relative amount of edge. Alternatively, we use “area effects” as a broader term that describes changes in ecological responses with habitat area, which may or may not be independent of other potential causes (a definition implicitly used in the literature), such that patch size effects are a subset of area effects. We do not include studies that examine total habitat area within a landscape because issues of scale and landscape context make inferences on the effective area available to organisms difficult to interpret. “Edge effects” are changes in ecological responses that vary with distance from edge (Ries et al. 2004). Interpreting the unique roles of patch size and edge will improve our understanding of habitat fragmentation and help to refine conservation strategies aimed at mitigating the effects of habitat loss and fragmentation.

Conceptual frameworks for edge and area effects

Investigations on habitat area and edge have largely been

conducted separately, with relatively few attempts to explicitly compare the influence of both landscape elements. Investigations on habitat area have centered on either the ETIB or metapopulation theory and determining their applicability in fragmented landscapes (e.g., Hanski 1998; Ricketts 2001; Brotons et al. 2003). Researchers have proposed several mechanisms for the influence of habitat area (MacArthur and Wilson 1967; Root 1973; Gilpin and Diamond 1976; Ambuel and Temple 1983; Matter 1997; Fletcher 2006), yet there is much overlap in the description and interpretation of these mechanisms (see Brotons et al. 2003), with no current framework that describes and links fundamental mechanisms for area effects. Similarly, a large literature has provided a suite of potential mechanisms underlying edge effects (Wiens et al. 1985; Murcia 1995; McCollin 1998; Fagan et al. 1999; Cadenasso et al. 2003). Ries et al. (2004) recently synthesized the proposed mechanisms for edge effects into a unified conceptual framework, focussing on how habitat edges influence the distribution and abundance of organisms. Below, we briefly review their framework and apply a similar approach to understand how area influences ecological patterns and processes, highlighting empirical examples that find evidence for such mechanisms.

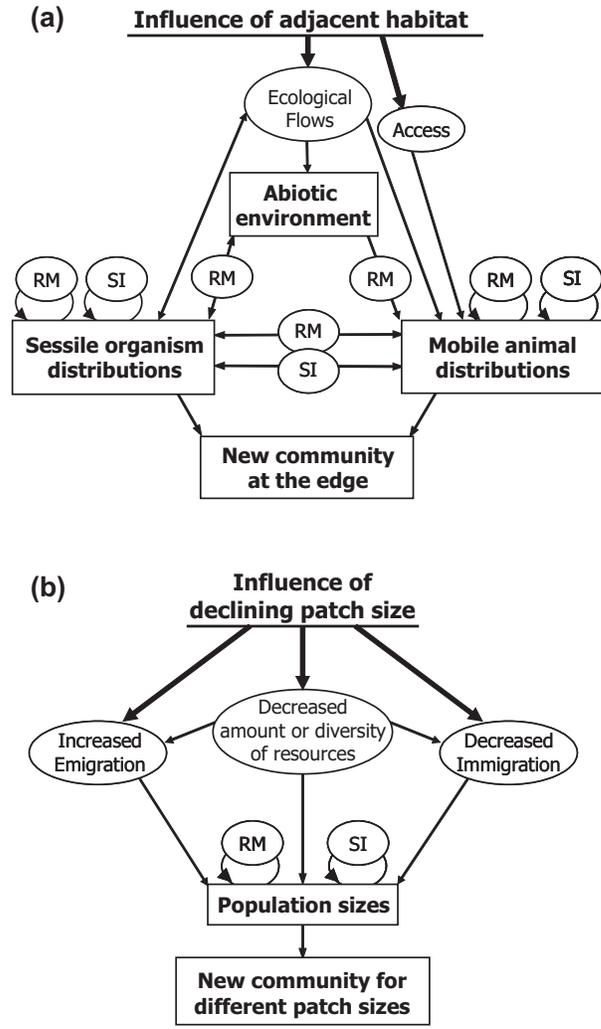
Mechanisms of edge effects

Habitat edges fundamentally influence ecological processes in two direct ways: (1) by altering the flows of energy, materials, and (or) organisms and (2) by providing access to spatially separated resources (Ries et al. 2004). These two direct effects can lead to indirect effects through resource mapping and species interactions (Fig. 2a), all of which may lead to changes in populations and community structure near edges (Fagan et al. 1999; Ries et al. 2004). Resource mapping occurs when an organism’s distribution reflects (“maps” onto) that of its resources (see Ries et al. 2004). Changes in species interactions include variation in predator-prey interactions (Ries and Fagan 2003), competition (Suarez et al. 1998), or facilitation (Jules and Rathcke 1999) near edges. These direct and indirect effects capture most dynamics that occur near edges (McCollin 1998; Fagan et al. 1999; Ries et al. 2004). Much of the observed variation in dynamics near edges can be explained by the edge type investigated, where the type of habitat surrounding fragments has the potential to influence each of the aforementioned mechanisms (Ries and Sisk 2004; Ries et al. 2004).

The flow of materials and organisms can be influenced by edges, where habitat boundaries can amplify, attenuate, or reflect flows into and out of adjacent patches (Strayer et al. 2003). In turn, variation in ecological flows can lead to abundance and (or) diversity gradients near edges, which can be influenced by edge contrast (Stamps et al. 1987), the surrounding matrix (Ricketts 2001; Chalfoun et al. 2002a), and species’ life histories (Henle et al. 2004). Ecological flows are predicted to cause declines in abundance near edges within preferred habitat, but increases in abundance within the adjacent habitat caused by “spillover” (Ries and Sisk 2004). There are numerous examples of edges influencing ecological flows, including energy flows that impact microclimate (Chen et al. 1995), seed dispersal (Cadenasso

Fig. 2. Conceptual frameworks that identify different process-based pathways by which the distribution of organisms are influenced by habitat edge and patch size, where thick arrows denote direct effects of edge and patch size and arrows denote indirect effects.

(a) Habitat edges directly influence the ecological flow or movement of materials, energy, and organisms, as well as directly providing access to spatially separated resources for mobile organisms. These issues indirectly influence resource mapping (RM) and species interactions (SI). (Modified from Ries et al. 2004, reproduced with permission of Annu. Rev. Ecol. Evol. Syst., vol. 35, p. 496, © 2004 Annual Reviews.) (b) Declines in patch size from habitat loss and fragmentation directly result in a reduction of the amount and (or) diversity of available resources. Declining patch size also alters the likelihood of movement into and out of patches by dispersing individuals, with most theory assuming that declining patch size increases emigration and decreases immigration rates. Emigration and immigration can be directly influenced by changes in patch geometry within landscapes (e.g., the “target” effect) or indirectly through changes in resource concentration. These issues are predicted to generally decrease population size and increase local extinction risk of organisms, which have indirect effects on resource mapping and species interactions. Indirect effects of resource mapping and species interactions can be variable, however, leading to potentially complex effects on resulting population and community dynamics. See text for details.



and Pickett 2001), and animal movement, with butterfly movement particularly well studied (Haddad 1999; Ries and Debinski 2001; Schultz and Crone 2001; Schtickzelle and Baguette 2003). A rigorous example highlighting the consequences of ecological flows comes from a recent experiment by Levey et al. (2005), who demonstrated that the effects of corridors on seed dispersal by birds could best be explained by edge effects: individuals encountering edges tended to reflect back into the focal patch, which in turn led to extensive use of corridors.

Mobile organisms, as opposed to sessile ones (Fig. 2a), near edges may also gain access to resources from adjacent habitats (Rand et al. 2006). If organisms gain access to such spatially separated resources, an increase in the density of individuals is predicted near edges. In a classic example, aspen experienced the heaviest outbreaks of a leaf-mining insect (*Phyllonorycter salicifoliella* (Chambers, 1875)) near stands of coniferous trees, which *P. salicifoliella* used as overwintering sites (Martin 1956).

Changes in ecological flows often result in distinct resource gradients near edges, which influence the distribution of the plants and animals that map onto changes in those resources. Such resource mapping can occur via plants and animals mapping onto gradients in abiotic or plant resources, or via animals mapping onto other animal resources (Ries et al. 2004). For example, foraging behaviors of white-footed mice (*Peromyscus leucopus* (Rafinesque, 1818)) in forest fragments of Ohio suggested that increased food availability may explain elevated mouse densities near edges (Wilder and Meikle 2005). While resource mapping can result in either increases or decreases in abundance and diversity, knowledge of relative habitat use can allow investigators to predict responses to edges (Ries and Sisk 2004; Ries et al. 2004).

Finally, much theoretical and empirical research has centered on the indirect effect of habitat edges on species interactions (Fagan et al. 1999; McGeoch and Gaston 2000; Chalfoun et al. 2002b). For instance, many investigations have estimated whether predation on bird nests increases near edges, with highly variable results, yet much of this variability can be explained by edge type, knowledge of specific predator behavior (which is often not measured), and landscape context (Paton 1994; Hartley and Hunter 1998; Lahti 2001; Chalfoun et al. 2002a, 2002b; Stephens et al. 2004). Fewer empirical examples exist for changes in other species interactions near edges. In a rare example, Suarez et al. (1998) reported that Argentine ants (*Linepithema humile* (Mayr, 1868)) found predominantly near edges appear to outcompete the local, native ant species.

Mechanisms of area effects

To address mechanisms of area effects, we distinguish between mechanisms that generate patch size effects, as defined above, and other mechanisms that can lead to changes with area that do not occur from patch size effects. Furthermore, we differentiate between two alternatives when focusing on measures of population size and density: (1) population size changes with declining patch size, but population density remains constant, and (2) population density changes with patch size. The ETIB focussed on changes in species richness with island area based on variation in colo-

nization and extinction rates (MacArthur and Wilson 1967); an implicit assumption of this theory is that population density remains constant with area (Andren 1994; Connor et al. 2000; Brotons et al. 2003). Yet if changes in density occur (Bowers and Matter 1997; Bender et al. 1998; Connor et al. 2000), populations and communities may be strongly influenced by effects of habitat loss and fragmentation. We first outline mechanisms that generate patch size effects (Fig. 2b), focussing on how patch size influences population size, density, and community structure, and subsequently note two primary factors that can lead to area effects which are not patch size effects.

Declines in patch size with habitat loss and fragmentation fundamentally influence the abundance of organisms in two direct ways. First, as patches decrease in size, declines in the amount or diversity of resources, or both, influence population sizes of plants and animals by altering carrying capacities. Second, variation in patch size also influences the extent of emigration and (or) immigration by dispersers (Root 1973; Gilpin and Diamond 1976; Risch 1981; Lomolino 1990). Together, these direct effects can further lead to indirect changes in species interactions and resource mapping, leading to changes in community structure (Fig. 2b).

As patch size declines, the most obvious effect is a decline in the amount and (or) diversity of resources available to organisms, yet this phenomenon can have potentially novel, cascading effects through indirect pathways (Fig. 2b). Indeed, when patch size declines to very small sizes, lack of resources or insufficient space may cause patches to fall below the minimum area requirements of individuals (e.g., territory size; Stratford and Stouffer 1999). The resource concentration hypothesis (Root 1973) states that smaller areas contain a lower concentration or diversity of resources (Fig. 2b), resulting in lower densities of individuals (see also Ambuel and Temple 1983). Lower concentrations of resources can reduce density through reduced local recruitment based on declining habitat quality (Risch 1981; Matter 1997). MacArthur and Wilson (1967) also highlighted that changes in habitat heterogeneity with declining area could lead to declines in species richness. Thus, the ETIB and the resource concentration hypothesis predict that declining resources should have a negative impact on population size and (or) density, which subsequently increases extinction probability (Didham et al. 1998a, 1998b), alters species distributions, and changes community structure. Indirect effects of variation in resource mapping can further influence populations and communities when declining patch size differentially affects some resources more than others (Fig. 2b).

Immigration and emigration rates are influenced by several factors, such as edge type (Ries and Debinski 2001), population density (Matthysen 2005), and habitat quality (Pulliam 1988). Nonetheless, declining patch size is generally thought to directly decrease immigration rates because individuals moving through a landscape are less likely to encounter small patches (the "target" effect; Gilpin and Diamond 1976; Lomolino 1990), thereby reducing population size and density (Fig. 2b). Bowman et al. (2002) recently reviewed general heuristic arguments regarding immigration and concluded, however, that while immigration may often increase with patch area, leading to larger population size,

many immigration behaviors should actually contribute to a decline in density with increasing patch size. This relationship may occur because immigration rates per unit area are likely to decline owing to the negative exponential nature of patch circumference per unit area with increasing patch size (see also Hamback and Englund 2005). Conversely, individuals moving within smaller patches are more likely to encounter boundaries than those moving in larger patches (Stamps et al. 1987), thus consistently increasing emigration rates out of smaller patches (Bowman et al. 2002). For example, Cronin (2003a) found that a planthopper (*Prokelisia crocea* (Van Duzee, 1879)) exhibited higher emigration rates in small patches than in larger patches. Such variation in emigration rates is predicted to cause lower densities and community diversity in small patches (Fig. 2b).

Both emigration and immigration can also be indirectly influenced by patch size through changes in resource concentration (Fig. 2b; Root 1973), where higher concentrations of resources in large patches are thought to decrease emigration rates and increase immigration rates. For instance, some social behaviors, such as conspecific attraction (i.e., the use of conspecifics as positive proximate stimuli for selecting locations of habitat), may cause an increase in immigration and a decrease in emigration in large patches, leading to patch size effects, and, albeit weak, edge effects on density (Fletcher 2006). However, such behaviors are better explained by patch size than edge, because increasing patch size increases the opportunity for the presence of social cues, which may be used as indirect measures of resource quality.

Species interactions can be indirectly influenced by declining patch size when disproportionate changes in one species' density or behavior alter its interactions with other species (e.g., Orrock and Fletcher 2005). Both the enemies hypothesis (Root 1973; Risch 1981) and the density compensation hypothesis (MacArthur et al. 1972) have been developed to explain how species interactions are altered with declining patch size (Fig. 4); however, each focusses on different types of interactions and makes different predictions for changes in population density. The enemies hypothesis states that predators are more abundant or more effective in smaller areas of habitat (Root 1973; Risch 1981; Askins et al. 1987), thereby altering species interactions. For example, predators may forage for relatively longer periods per unit area in smaller patches because the distance to other resources is often greater than that in larger patches (Stephens and Krebs 1986). We note, however, that the original logic for the enemies hypothesis (Root 1973; Risch 1981) is specific to insect predator – herbivore interactions in monocultures and polycultures and may not apply broadly across taxa in fragmented landscapes. Furthermore, some empirical evidence suggests that predator density can actually increase with patch size (Chapin et al. 1998; Pardini 2004). Conversely, the density compensation hypothesis predicts that declining species richness with reduced area (MacArthur and Wilson 1967) will cause densities to increase owing to a decrease in interspecific competition (MacArthur et al. 1972). Other types of interactions may also be affected, such that density may increase or decline based on the specifics of each interaction.

Although some studies in fragmented landscapes have at-

tempted to test for changes in movement, resource mapping, and species interactions with patch size, surprisingly few have shown strong mechanistic support for observed area effects. Many of these investigations have attempted to understand why some bird species are area sensitive, or avoid small patches. A recent example from Japan (Kurosawa and Askins 2003) showed that many forest birds occurred at lower densities in smaller patches, and such patches also contained higher densities of predators, providing some support for the enemies hypothesis. Similarly, Herkert (1994) found that many grassland birds were sensitive to area, and that for some species, such as Henslow's Sparrow (*Ammodramus henslowii* (Audubon, 1829)) and Savannah Sparrow (*Passerculus sandwichensis* (J.F. Gmelin, 1789)), small fragments contained fewer potential resources per unit area (based on habitat structure). However, in both of these examples, and indeed in many investigations on area effects (Parker et al. 2005), investigators did not isolate whether observed area effects were patch size effects.

Finally, there are two main factors that can generate area effects, such that observed effects are not actual patch size effects. First, the proportion of edge tends to increase with declining patch size (Fig. 1). If a species responds to edges, these responses can result in changes in density (or other metrics) in patches of different sizes (Sisk et al. 1997; Fletcher 2005), and could be falsely attributed to a patch size effect. Therefore, to understand the unique roles of area and edge in fragmented landscapes, we need to not only control for edges when investigating effects of area but also to focus on the direct mechanisms responsible for edge and area effects. Second, as sampling increases, so does the likelihood of detecting an individual or a species, resulting in increases in the likelihood of occurrence or species richness with area sampled (Connor and McCoy 1979; Horn et al. 2000). This relationship has been termed the random sampling hypothesis and can explain some observed area effects (Haila et al. 1993; Andren 1994; Horn et al. 2000). Variation in sampling effort, however, should not cause changes in density or other measures that do not increase with sampling (e.g., fecundity).

Interplay of area effects, edge effects, and landscape context

These conceptual frameworks highlight the distinctiveness of direct effects of patch size and edge on ecological patterns and processes, yet both edge and patch size can have indirect effects on species interactions and resource mapping, such that observed effects can appear similar in nature. For instance, if species interactions change as a function of patch size (Fig. 2b), these interactions will also inevitably vary with distance to edge across patches (Fig. 1). Consequently, isolating whether species interactions vary from edge or patch size will often be difficult. On the other hand, the direct effects of edge and patch size are distinct (Figs. 2a, 2b), such that by testing for these potential effects, we can draw stronger inference regarding the unique roles of area and edge.

Edge and area effects also have the potential to interact. For example, Kiviniemi and Eriksson (2002) found that plant species richness in grasslands of Sweden increased near edges in small fragments but declined in large frag-

ments. Our conceptual frameworks (Figs. 2a, 2b) suggest that edge effects from variation in ecological flows could potentially have synergistic effects on patch area influencing the amount of resources, but there is no explicit empirical evidence that isolates this potential synergism. Indeed, little clear evidence currently exists for area and edge effects interacting in fragmented landscapes (Nour et al. 1993; Matthews et al. 1999; Galetti et al. 2003; Lienert and Fischer 2003; Fletcher 2005; but for a recent example see Ewers et al. 2007).

There is ongoing interest in determining when, where, and how the surrounding landscape influences populations and communities within focal areas. Landscape context influences edge effects primarily through variation in matrix quality. Matrix quality can alter changes in the movement, or flow, of materials, energy, and organisms — effects that are fundamentally linked with variation in the permeability of habitat boundaries (e.g., Collinge and Palmer 2002). While there has been interest in understanding how landscape context can influence edge effects (Donovan et al. 1997; Tewksbury et al. 1998; Chalfoun et al. 2002a), an outstanding question is whether matrix quality effects are in reality simply effects of different edge types (Fletcher and Koford 2003; Ries and Sisk 2004), or vice versa. That is, are purported matrix effects driven primarily by variation in local edge effects caused by different edge types, or are edge type effects actually generated by large-scale differences in matrix quality? Answers to this question would be extremely valuable in interpreting whether large-scale fragmentation constrains local processes or whether local processes “scale up” to generate large-scale patterns.

Landscape context may also influence area effects in that distances between habitats can alter effective population sizes when individuals use more than one patch (Diffendorfer et al. 1995). However, there are no current predictions for matrix quality altering patch size effects, based on the fundamental processes patch size influences (Fig. 2b). While matrix quality may influence the movement of organisms, thereby altering immigration probabilities, the relative “target” effect of area should not vary, all else being equal. However, matrix quality can sometimes become more important than area in driving immigration rates, such that patch size may explain less variation in movement than characteristics of the matrix (Bender and Fahrig 2005). When the surrounding matrix provides novel resources used by some individuals, densities can increase with declining patch size (Dunning et al. 1992; Norton et al. 2000; Davies et al. 2001; Estades 2001), yet such density elevation is not driven by patch size effects. Instead, such effects are more directly related to edge effects allowing access to spatially separated resources (Didham et al. 1998a).

The relative role of area and edge: empirical evidence

To explore the relative roles of habitat area and edge, we reviewed studies that simultaneously tested for both effects in fragmented landscapes within an investigation. We focussed on three key questions. First, do investigators design studies that limit the potential confounding of area and edge when addressing these effects? Second, do studies more fre-

quently find evidence for edge or area effects? Third, do investigators test for fundamental mechanisms responsible for patch size and edge effects? We also address whether results vary when comparing confounded and nonconfounded studies, and whether results vary depending on taxonomic group, the metric used, or habitat type.

Review methods

We first screened 231 articles gleaned from the *Web of Science*, using “patch size* AND edge* AND fragment*”, “habitat area* AND edge* AND fragment*”, “area effect* AND edge* AND fragment*”, and “fragment size* AND edge*” as key words (accessed 14 March 2006). We also supplemented this list with other relevant articles. From these articles, 60 tested for both the effects of area and edge. For this review, we considered habitat area to include only issues of patch size and did not consider landscape-level analyses (e.g., Belisle et al. 2001; Fletcher and Koford 2002). For edge effects, we considered studies that estimated responses at the within-patch scale, using distance to edge, and at the patch scale, using measures of patch shape (e.g., perimeter to area ratios).

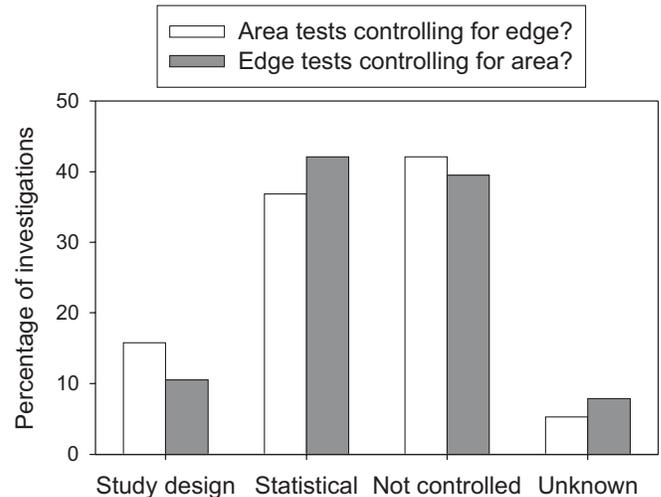
Our overarching goal was to determine if studies more commonly showed evidence for edge or area effects. As such, we focussed on within-study, pairwise comparisons that used similar methodologies to interpret the evidence for edge and area effects. Some investigations tested for both area and edge, but used different patches, different sampling units, or different species for each test (Dijak and Thompson 2000; Beier et al. 2002; Cronin 2003b); such studies were omitted. To limit biases from variation in sampling effort, we also only included studies with equal sample sizes for testing the effects of area and edge for a given response variable. We inferred sample size based on either the reported denominator degrees of freedom or on reported sampling units used for analyses. These criteria reduced the data set to 38 articles with 213 response variables measured. Our approach controlled for many issues that arise when summarizing effects across studies, as is often attempted in meta-analytic approaches (e.g., Bender et al. 1998; Connor et al. 2000). Yet we chose not to perform a formal meta-analysis for several reasons. First, we emphasize that our goal was not to estimate overall effect sizes, which would be highly variable across studies depending on the taxa and metric investigated, but instead to identify the relative support for area or edge effects within investigations. Second, formal meta-analyses primarily attempt to control for variation in sample size across studies; however, by limiting our summaries to investigations with the same sample size, we controlled for this issue directly. Finally, a formal meta-analysis would have further reduced our data set by approximately 30%. We note that using the entire data set (all 60 articles listed above) provided similar qualitative results as those presented below.

For each article, we first summarized a variety of information related to sampling design. We were interested in sampling concerns that occur when investigators test for area and edge effects (Connor and McCoy 1979; Horn et al. 2000; Mancke and Gavin 2000; Parker et al. 2005), particularly situations where area tests were confounded by potential edge effects, such that an observed area effect could not

be inferred as a patch size effect. Parker et al. (2005) recently noted that most, if not all, studies on forest bird distribution in relation to area confounded potential area effects with edge effects because large patches had samples away from edges, whereas small patches inevitably did not. In contrast, similar studies focussing on edge effects tended to avoid such issues by selecting relatively large patches for comparisons (Parker et al. 2005). Here, we distinguish studies that control for these issues statistically, via covariates (e.g., Dunford et al. 2002) or residual analysis (e.g., Winter et al. 2000), those that control via study design (e.g., Wilder and Meikle 2005), and those that make no attempts to control for the confounding nature of area and edge (e.g., Hickerson et al. 2005). Study designs that we accepted as controlling for edge effects in tests of area included designs where samples were taken at the same distances from the nearest edge in patches of different sizes. While that approach does not control for multiple edges (Fig. 1; Fletcher 2005), in practice there are few ways to do so when testing for area effects. Study designs that we accepted as controlling for area when testing for edge effects included tests for edge within a given patch size class. Based on these classifications, we then compared conclusions from nonconfounded analyses to that of confounded analyses.

We report two main results for each response variable measured in the 38 studies. The first is whether significant effects were observed for edge, area, both, or neither. When observed for both, we report which effect was stronger based on inferential statistics provided in the article (e.g., *P* values, *F* statistics, confidence intervals), which is reasonable because we only considered studies with identical sample sizes for analyses of edge and area effects for a given response variable. The second main result is whether edge and area responses were concordant or discordant. We defined concordant responses as those where edge and area effects were observed in similar directions. For example, if the density of an organism declines near an edge (a negative edge effect; Ries et al. 2004) and declines in density with decreasing patch size (a positive area effect; Bender et al. 1998), then such responses would be concordant because habitat fragmentation generally increases the proportion of edge and decreases patch size. A concordant response suggests that habitat fragmentation has consistent effects on edge and area responses of a given variable and suggests four possible scenarios: (1) area and edge effects are driven by similar indirect processes (e.g., species interactions; Figs. 2a, 2b), (2) area effects may be explained simply by edge effects (particularly in confounded studies), (3) edge effects may be explained simply by patch size effects (particularly in confounded studies), or (4) our conceptual frameworks are incomplete and edge and area responses are, in fact, driven by some shared but unknown ecological mechanism. We only considered responses discordant if opposing patterns were observed for area and edge effects. Discordant results suggest that (i) edge effects do not drive observed area effects and that (ii) observed edge and area effects are generated by distinct ecological processes. We also note that the responses could be concordant or discordant as a result of chance alone. Mixed responses, where one effect was observed but the other was not, are difficult to interpret because low sample sizes may limit documenting

Fig. 3. Summary of investigations reviewed ($n = 38$) that did and did not attempt to control for the confounding nature of edge and area. We distinguished studies that control for these issues statistically, via covariates or residual analysis, those that control via study design, and those that make no attempts to control for the confounding nature of habitat area and edge. Only studies where the same response variable was tested for both factors were included. See text for details.



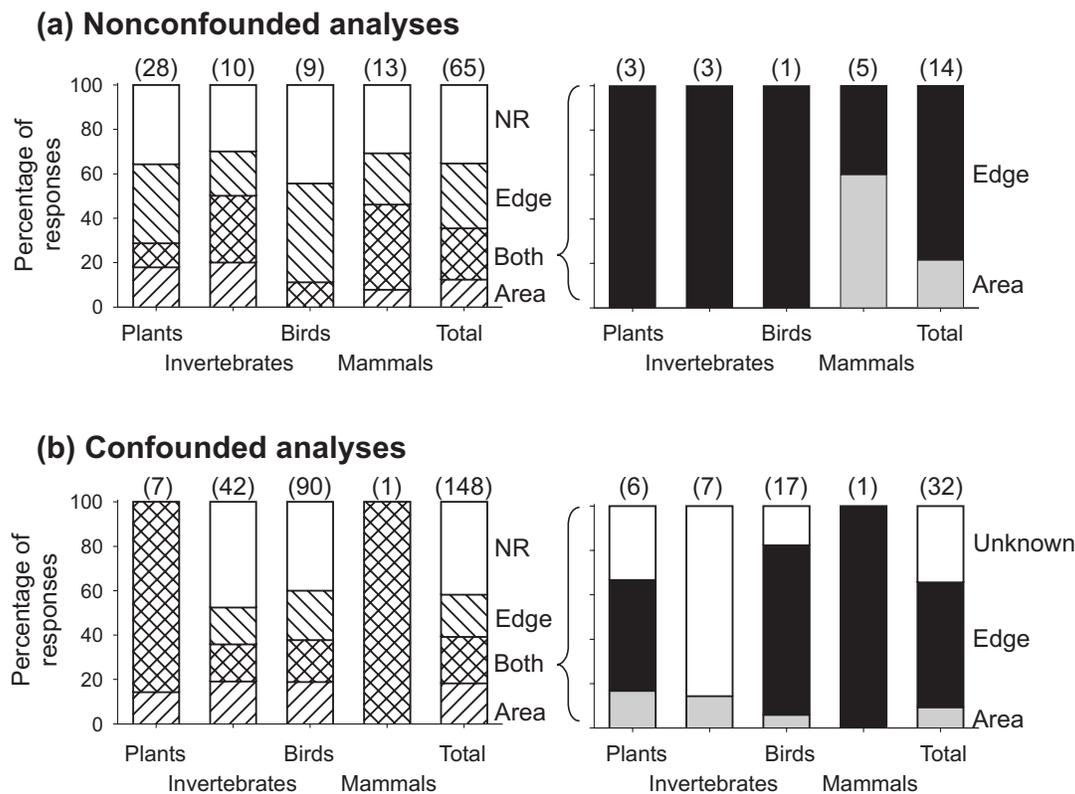
area and (or) edge effects in some studies (e.g., Martínez-Morales 2005) and area effects are likely to be harder to detect as a result of larger site-to-site variation (see below). Therefore, we focus on concordant and discordant responses.

We stratified the results based on taxonomic group, the type of response variable investigated, focal habitats, and mechanisms tested. We summarized response variables into three general categories of metrics: community (species richness, diversity, or species composition), distribution (occurrence, abundance, or density), and performance (e.g., clutch size, survival). We examined coarse effects of habitat types that had adequate sample sizes, including grassland and forest. Few studies provided explicit information on landscape context, so we did not attempt to address this issue. Finally, we noted when investigators explicitly addressed potential mechanisms for edge and patch size effects and whether such mechanisms were supported. The review data set is available upon request from the senior author.

Review results and discussion

Many studies testing for edge and area effects were confounded in their design and (or) analysis, with similar confounding for tests of area (42%) and edge (39%; Fig. 3). Only 16 of the 38 articles (42%) controlled for both area and edge in at least some tests for a given response variable (nonconfounded analyses hereinafter). Many studies that addressed edge and area effects had “interior” plots that increase in distance from edge in larger patches (Hickerson et al. 2005; Weakland and Wood 2005), which confounds patch size and edge in tests of both. Investigations that did attempt to control for such issues predominantly did so with statistical tests rather than study design (Fig. 3). The studies we reviewed controlled for potential confounding more

Fig. 4. Results from studies that tested for both edge and area effects on ecological patterns, summarized by taxonomic group for (a) nonconfounded analyses and (b) confounded analyses. Left panels show the percentage of response variables investigated that were influenced by area, edge, both edge and area (both), or had no reported effect (neutral response, NR), and numbers above bars represent the number of response variables investigated. Note that response variables for each taxa do not sum to the total because there were other taxa investigated that are not shown owing to limited sample size (e.g., herptiles). For those responses influenced by area and edge, the right panels show the percentage of response variables reported as being more influenced by edge or area (based on inferential statistics reported), and those that did not provide enough information to distinguish (unknown). For taxonomic groupings, we did not include studies that focussed on species interactions across different taxonomic groups. Only studies where the same response variable was tested for both factors were included.



often than those reported by Parker et al. (2005). This pattern is not surprising, because Parker et al. (2005) included many studies that only tested for either edge or area; such studies are more likely to be confounded than those testing for both effects. For further analyses, we compare these nonconfounded analyses to results from confounded analyses.

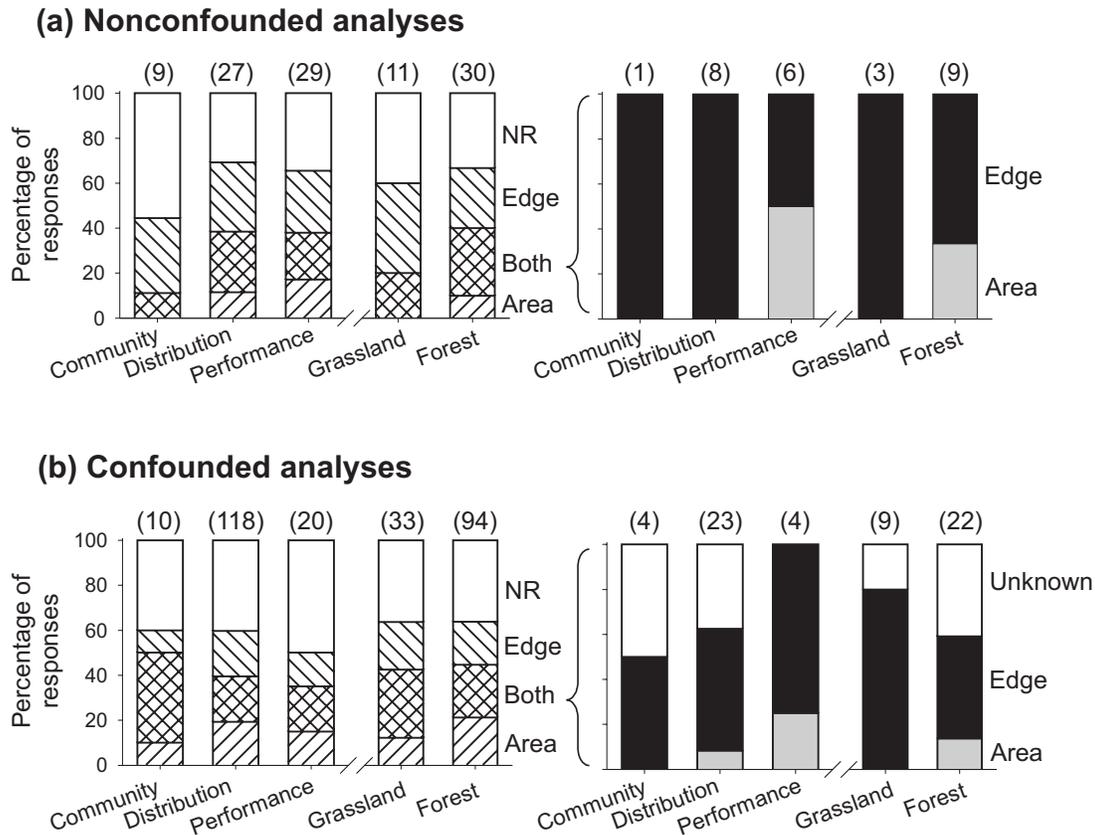
Nonconfounded analyses tended to find evidence for edge and area effects slightly more frequently (64.6%) than confounded analyses (58.1%; Fig. 4), with fewer nonsignificant responses reported. Sample size variation between confounded and nonconfounded analyses would actually predict the opposite, because overall sample sizes were greater for confounded analyses (nonconfounded: 61.3 ± 10.0 , confounded: 95.7 ± 5.4 ; $t = 3.27$, $P = 0.001$). Confounded analyses reported edge and area effects in approximately equal proportions (39.9% vs. 39.2%, respectively; Fig. 4), while nonconfounded analyses found evidence for edge effects (52%) more often than area effects (35%). This pattern was generally similar regardless of the metric investigated (Fig. 5). Similar patterns also occurred for different habitats (Fig. 5), with edge effects being particularly common in grasslands. When both effects were observed, edge effects were stronger than area effects for nonconfounded analyses (78.6% vs. 21.4% of response variables, respectively) and

confounded analyses (56.2% vs. 9.4% of response variables, respectively). The only exception was for investigations on mammals, with area effects being reported as stronger than edge effects for nonconfounded analyses (Fig. 4). Together, these results suggest that edge effects are either more common in nature or are easier to detect than area effects (or both). Edge effects may indeed be easier to detect because the most common study design, using within-patch measures of distances from edge, controls for site-level variation.

We caution that inferences about the relative occurrence and strength of edge versus area effects based on confounded studies differed from those based on nonconfounded studies. For example, nonconfounded investigations on birds found more evidence for edge effects, whereas confounded studies found similar evidence for area and edge effects (Fig. 4). Yet relatively few studies were not confounded, which limits generalizations for most taxa and highlights the need for rigorous study design and analysis in studies of habitat fragmentation.

There was a remarkable lack of discordance between observed area and edge effects, with only 1.6% of reported responses (1 of 64) for nonconfounded analyses and 2.4% (5 of 210; for 3 response variables, concordance–discordance could not be determined) for all studies combined showing

Fig. 5. Results from studies that explicitly tested for both edge and area effects on ecological patterns, summarized by metric used (distribution, community, performance) and habitat type (forest and grassland) for (a) nonconfounded analyses and (b) confounded analyses. Note that results for the metric used and habitat type separately summarize the same response variables. Format same as Fig. 4.



opposite patterns with respect to area and edge. The discordant responses were restricted to experiments on invertebrates in forested habitat (Davies and Margules 1998; Didham et al. 1998a). However, these results came from only two experiments, thus limiting our ability to assess the generality of the pattern. Concordance was observed for 57.8% of response variables in nonconfounded analyses (59.6% for confounded studies; Fig. 6). Given that discordance was rare (Fig. 6), that edge effects tended to be stronger when both effects were observed (Figs. 4, 5), and that nonconfounded analyses reported area effects less often and edge effects more often than confounded analyses (Fig. 4), we conclude that area effects reported by confounded studies may, in fact, often be the result of edge effects.

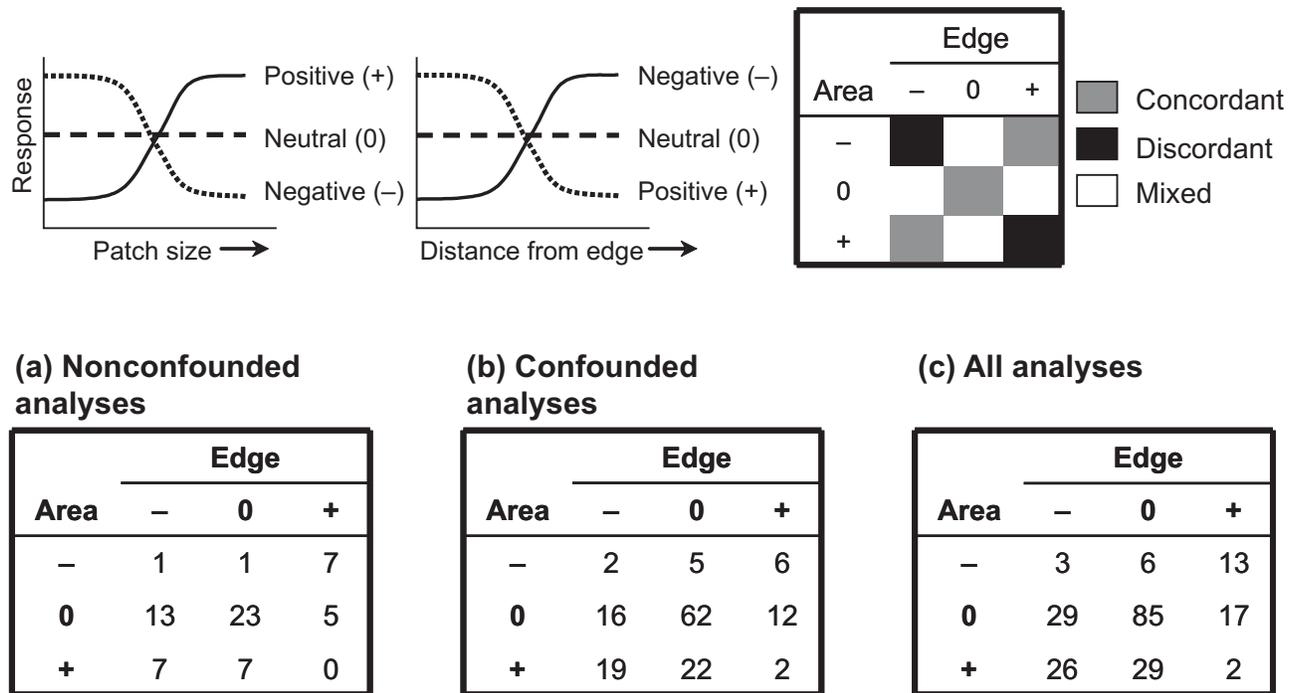
Relatively few studies explicitly tested for mechanisms generating edge or area effects (21.1%), with even fewer explicitly testing for mechanisms for both effects for at least one response variable (15.8% of studies reviewed). This was likely due, in part, to the difficulty of testing for mechanisms of both effects in a given investigation. Articles that did address mechanisms focussed on measures directly or indirectly related to resource mapping (Wilder and Meikle 2005) and (or) changes in species interactions (Storch 1991; Suarez et al. 1998; Lienert and Fischer 2003), both of which can occur from either edge or patch size effects (or both), thereby limiting inference about whether edge or patch size

governed observed responses. None of these articles addressed the direct processes influenced by area and edge to interpret their unique contributions. We note that investigations focussing entirely on edge or area have addressed mechanisms responsible for potential effects more often (Ambuel and Temple 1983; Askins et al. 1987; McGeoch and Gaston 2000; Cronin 2003a; Fletcher and Koford 2003; Ries and Fagan 2003). Because of the confounding nature of these effects, any attempt to understand the mechanisms of edge or patch size should do so by explicitly searching for the direct effects of each landscape element (Fig. 2).

Future research: avoiding the pitfalls of confounding factors

The results of our review, as well as other studies, suggest that edge effects can sometimes explain area effects (Sisk et al. 1997; Laurance et al. 1998; Schtickzelle and Baguette 2003; Fletcher 2005), yet the converse is less likely based on the fundamental mechanisms influenced by patch size. For example, in a rigorous experiment on fragmentation, Bowers et al. (1996) suggested that space use and reproductive behaviors of female meadow voles (*Microtus pennsylvanicus* (Ord, 1815)) near edges were responsible for the observed negative area effects (see also Wilder and Meikle 2005). Ambuel and Temple (1983) similarly invoked inter-

Fig. 6. Concordance of edge and area effects in fragmented landscapes for (a) nonconfounded analyses, (b) confounded analyses, and (c) all studies combined. Results are from studies that explicitly tested for both edge and area effects on ecological patterns. To be consistent with the literature, we report positive area effects as those that occur when the response variable increases with increasing patch size, whereas positive edge effects occur when a response variable increases near edges. Only studies where the same response variable was tested for both factors were included.



specific competition near edges as an explanation for observed area effects in migratory forest birds. As noted above, some edge effects can also explain other fragmentation effects, such as the use of conservation corridors (Haddad 1999; Levey et al. 2005). When patch size effects occur, however, edge effects are not explicitly predicted, either based on variation in resources influencing population size (MacArthur and Wilson 1967) or based on variation in emigration and immigration rates in patches that vary in size. Consequently, when investigators find support for both edge and area effects that are concordant in their directionality, and studies are confounded in their design and (or) analysis, such effects may be driven entirely by habitat edges alone (Laurance et al. 1998). When the strength of edge effects varies with patch size (Kiviniemi and Eriksson 2002), patch size effects could account for the additional variation. However, cumulative effects from multiple edges could also produce similar patterns (Fletcher 2005), thereby complicating the interpretation of the area–edge relationship.

The strongest study design for teasing apart the unique influence of area and edge occurs when investigators measure responses at similar distances from the nearest edge in fragments of different sizes, with replicates for each patch size category. Such a design controls for potential edge effects (from the nearest edge) in area tests, and potential area effects in edge tests, by addressing variation in edge effects across different patch sizes (see, e.g., Nour et al. 1993). Additionally, investigators can use statistical approaches to further limit confounding in this design (e.g., distances to multiple edges), whereas statistical approaches alone may

be fruitless in limiting potential confounding for some other study designs.

Another approach to isolate the effect of area independent of edge is to compare predictions derived from edge responses to observed responses that occur with variation in patch size. The effective area model (Sisk et al. 1997; Brand et al. 2006) provides one approach to do so. In this model, response variables are estimated for different patches via data from edge transects. Edge response patterns measured at survey plots at different distances from habitat edges can be extrapolated to patches of different sizes to predict the average response in a patch that would result entirely from edge effects. When controlling for other site-level effects, consistent discrepancies between predictions from the effective area model and observed data as a function of patch size may be attributed to patch size and not edge effects.

We emphasize that focussing on the direct influences of habitat area and edge on ecological processes provides a more rigorous framework with which to understand the impacts of habitat fragmentation. Ries et al. (2004) argued that resource mapping and species interactions are the drivers of most observed edge effects, yet these can also vary with patch size (Fig. 2). Even though indirect effects from patch size and edge may be inevitably intertwined, making it difficult to isolate the effects of each landscape element, direct effects are distinct. Therefore, focussing on response variables that illuminate these direct effects will provide novel insight into the unique roles of area and edge. Our conceptual frameworks (Fig. 2; Ries et al. 2004) suggest that studies focussing primarily on movement in relation to edge and

patch size can help to isolate the effects of these landscape elements. For instance, edge effects from ecological flows predict that organisms may change movement behaviors near habitat boundaries, whereas patch size should only influence the likelihood of encountering an edge. Likewise, patch size effects arising from “target” effects predict per capita immigration and emigration rates to vary with patch size but not with distance from edge. While there have been recent attempts to provide rigorous approaches to estimating movement in complex landscapes (Schtickzelle and Baguette 2003; Hamback and Englund 2005; Martin et al. 2006), none of the investigations we reviewed focussed on movement behaviors (e.g., encounter and turning rates) to disentangle the influence of both patch size and edge.

Conclusions

Habitat area and edge are key components of landscape structure, yet these components tend to covary within landscapes. Because habitat area and edge describe different aspects of landscape structure, the importance of each suggests different foci for conservation strategies, making it imperative to understand their unique roles in habitat fragmentation. Unfortunately, to date much of the literature testing for the influence of edge and area has been confounded. Information from nonconfounded studies suggests that edge effects may occur more frequently in nature than area effects. However, edge responses are likely easier to detect and our summaries made no attempt to measure overall effect sizes, such that area effects may, in some cases, be more important than these results suggest. In addition, we emphasize that variation in habitat area at landscape scales via habitat loss is widely known to be of considerable importance to population and community dynamics (e.g., Fahrig 1997; Flather and Bevers 2002). Future attempts to isolate edge and patch size effects need to pay careful attention to study design and focus on the direct, fundamental processes influenced by area and edge.

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