RESEARCH ARTICLE

Measuring edge contrast using biotic criteria helps define edge effects on the density of an invasive plant

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Abstract Habitat edges can alter population dynamics, influence community structure, determine the success of conservation efforts, and facilitate the spread of invasive species. Despite recognition that edges influence the nature and strength of ecological interactions, edges are generally characterized using abiotic measures that likely capture habitat quality for only the focal taxa, and ignore the potential for biotic interactions to explain edge effects. Here we describe the association between edges and the density of an invasive shrub, *Lonicera maackii*, and infer the functional role of edges by using multiple criteria to weight edge contrast. We define edge contrast using both an abiotic criterion in which contrast is weighted by differences in light availability, and a biotic criterion in which edge contrast is weighted by the association between edges and the abundance of the American Robin (*Turdus migratorius*), an important avian seed disperser. Biotically defining edge contrast significantly improved model fit in all cases, demonstrating that the large-scale distribution of an invasive shrub is best predicted using both abiotic and biotic edge characterization. More generally, our work suggests that weighting edge contrast using key biological interactions in addition to abiotic criteria may be a promising way to understand the multiple pathways by which edges influence the distribution and abundance of organisms.

Introduction

Habitat edges affect many ecological processes (Lidicker 1999; Ries and Sisk 2004; Ries et al. 2004; Fletcher 2005) and the degree to which edges comprise contemporary landscapes is increasing because of anthropogenic habitat destruction and fragmentation (Andrén 1994; Laurance et al. 2002; Koper et al. 2007). Edges affect population dynamics and community structure (Fahrig 2003; Ewers et al. 2007), mediate biological invasions (Gerlach and Rice 2003; Charbonneau and Fahrig 2004), and may compromise conservation efforts (Harper et al. 2005), making it imperative to quantify edges in an ecologically meaningful way. Despite the importance of edges and their continued creation via habitat destruction, edges are rarely defined with regard to the key ecological interactions they modify (Harper et al. 2005).

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Studies of landscape structure often utilize GIS analysis of aerial photographs or satellite-derived imagery. In addition to quantifying structural features of the landscape (e.g., total edge length, edge density), some programs allow researchers to input user-defined values that weight the contrast between specific habitat combinations. Often, contrast is weighted in terms of abiotic characteristics, or perceived differences in habitat permeability (Debuse et al. 2007; Guadagnin and Maltchik 2007). We suggest that utilizing both abiotic and biotic criteria to weight edge contrast will allow researchers to use landscape analysis software not only to describe patterns of edge structure, but also infer the functional significance of edges.

We illustrate our approach to assessing the functional role of edges by focusing on light and the abundance of an avian seed disperser as key abiotic and biotic filters that respond to edges and influence the distribution of an invasive plant. Light is a critical abiotic resource for plants (Tilman 1986) that varies considerably among micro- and macrohabitats (Chazdon and Fetcher 1984). Differences in light availability across habitat boundaries have important implications for the distribution of plant individuals and species (Didham and Lawton 1999; Valladares et al. 2000), suggesting that an edge contrast weighting scheme based on differences in light availability is ecologically relevant. Despite the myriad ways that edges modify species interactions (Fagan et al. 1999), edge contrast is rarely defined in terms of the strength of biotic interactions. For example, interactions between avian frugivores and landscape edges are known to have important effects on seed dispersal (Levey et al. 2005; Damschen et al. 2009), suggesting that edge-mediated changes in frugivore abundance may also be an important means by which edges shape plant distribution.

The Amur Honeysuckle, *Lonicera maackii* was introduced to the United States as an ornamental plant at the end of the nineteenth century, and is now established in most states east of the Rocky Mountains. The occurrence and abundance of *L. maackii* has been linked to abiotic conditions that may be altered by edges (e.g., light availability; Hutchinson and Vankant 1997), and studies have associated *L. maackii* density with edges at both local (Hutchinson and Vankant 1997) and landscape scales (Bartuszevige et al. 2006). Available evidence suggests that

birds are important dispersers of *L. maackii* seeds, with the American Robin (*Turdus migratorius*) implicated as a particularly important disperser because it is abundant, defecates viable seeds, and can move up to 1,500 m in the time it takes a seed to pass through its gut (Bartuszevige and Gorchov 2005; Bartuszevige et al. 2006). Particularly relevant to the current study is the expectation, based on radio tracking studies and known seed passage time, that *T. migratorius* deposit seeds at forest edges more frequently than expected given the availability of edges in the landscape (Bartuszevige and Gotrchov 2005).

Here we characterize edges based on contrast in light availability and how edges may affect a key ecological process: seed dispersal. We develop and test a method for edge characterization that describes associations between edges and the abundance of avian seed dispersers to understand how edges influence the local abundance of bird-dispersed plants (Fig. 1). Our data-driven approach to weighting edge contrast combines field observations from our study site with data obtained from large-scale regional inventories to explore relationships between local- and landscape-scale edge metrics and the density of an invasive shrub, *Lonicera maackii*.
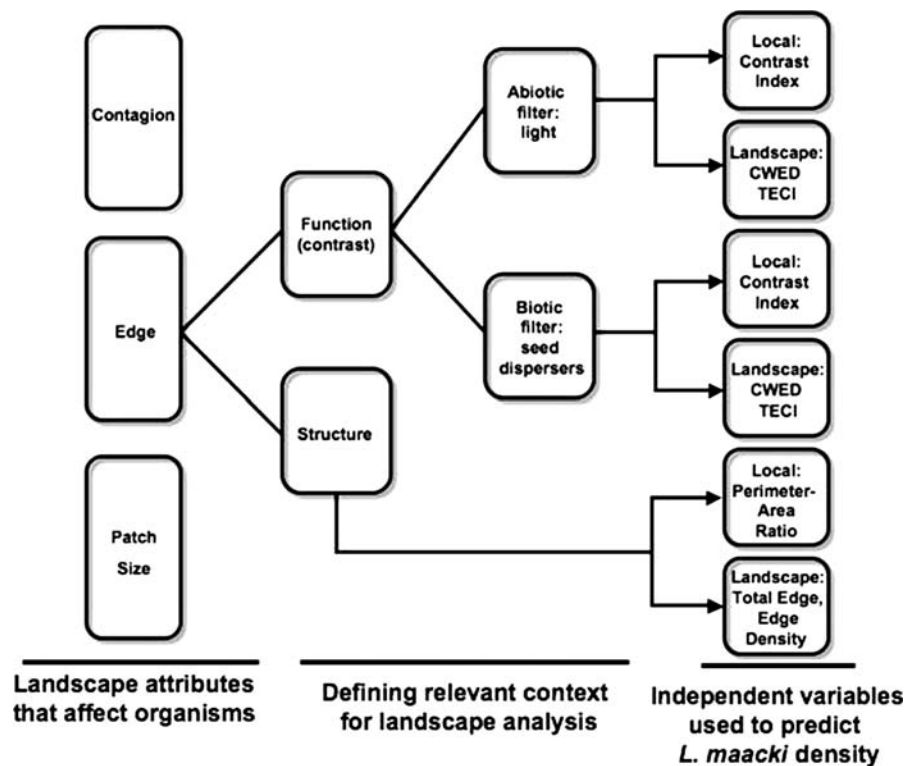
Methods

Study site and field sampling

We measured the density of *L. maackii* in forest patches in the August A. Busch Memorial Conservation Area (hereafter, Busch Conservation Area or BCA) in St. Charles county, MO (38°42′N, 90°44′W). The BCA is a 2,827 ha area comprised of a mosaic of habitat types, including forest and woodland, mowed lawns, restored prairie, agricultural plots, wetlands, and artificial lakes, and is traversed by hundreds of kilometers of paved and gravel roads.

In October and November 2008, we estimated the density of *L. maackii* in plots located in nine deciduous forest patches throughout the BCA. Patches were selected haphazardly to represent a gradient in area and invasion intensity, and were located throughout the BCA to minimize spatial autocorrelation. We sampled in deciduous forest because this is the most common forest type in the

Fig. 1 Conceptual model illustrating the approach to interpreting functional significance of landscape attributes illustrated in the current study. Abbreviations for landscape metrics: CWED, contrast-weighted edge density; TECI, total edge contrast index

Landscape attributes that affect organisms

Defining relevant context for landscape analysis

Independent variables used to predict *L. maacki* density

BCA (representing ∼47% of the total land area of the reserve, and 81% of total forest cover in the reserve based on spatial data classified by the Missouri Spatial Data Information Service, MSDIS http://msdis.missouri.edu). The number of plots sampled was scaled to the size of the patch such that one plot was installed for every 10 ha of forest. Random coordinates for plot locations were initially obtained from digital images; in a few cases the exact location of plots was moved slightly to avoid large discontinuities in the landscape (e.g., steep-sided ravines with stream beds >1 m). Density estimates were made every 10 m along three transects installed at 0, 15, and 30 m along one axis of each plot. At each of these 12 sampling points in every plot, we counted the number of *L. maackii* shrubs at least 1 m high within a 1 m radius of the observer.

Landscape cover

A map of habitat cover was created for the entire BCA, condensing the 15 habitats differentiated in the 2005 land use layer available from MSDIS into seven categories for further analysis: concrete, grassland, deciduous forest (>60% deciduous tree cover),

evergreen forest, deciduous woodland (<60% deciduous tree cover), wetland, and water. Because roads may be important conduits by which *L. maackii* disperses through a landscape (Castellano and Boyce 2007) and because we observed a relatively greater density of *L. maackii* near roadsides than in forest interiors at the BCA, we defined patch boundaries based on the meeting of distinct habitat types as well as dissection by major roads at the BCA. In October 2008 we obtained GPS points from throughout the road network at the BCA, focusing on paved and gravel roads used for public access throughout the reserve. We applied a buffer of 15 m to our road coverage and coded roads as concrete in our reserve-wide habitat map.

Edge characterization

We differentiate 'structural' edge classifications that describe length or density of edge boundaries from 'functional' edge classifications that weight edge boundaries by the expected strength of an edge effect. We use a common classification system for defining habitats (and therefore recognizing edges), and compare differences in the ability of edges to predict the

Table 1 Edge metrics calculated for forest patches at the BCA

Spatial scale	Metric	Classification
Local	Perimeter:area ratio	Structural
	Contrast index (light)	Functional
	Contrast index (avian)	Functional
Landscape	Total edge	Structural
	Edge density	Structural
	Contrast-weighted edge density (light)	Functional
	Contrast-weighted edge density (avian)	Functional
	Total edge contrast index (light)	Functional
	Total edge contrast index (avian)	Functional

Structural classifications include no information on edge identity, whereas functional classifications weight edges according to the identity of juxtaposed habitats

density of *L. maackii* when edges are defined structurally (e.g., all edges contribute equally to metrics of edginess, regardless of the habitats juxtaposed) versus when edges are defined functionally (e.g., edges are weighted differently based on the identity of juxtaposed habitats).

We utilized the program FRAGSTATS (McGarigal et al. 2002) to quantify patch area, edge length, and edge density. Patch area was calculated as the amount of deciduous forest (in ha) in a patch bounded by any combination of the other six cover types. We distinguish local edge metrics calculated around the perimeter of focal patches from landscape metrics that describe edge length and density in 1,500 m buffers around patches. Our choice of 1,500 m as the buffer radius follows the approach of Bartuszevige et al. (2006) for a similar analysis of local versus landscape determinants of *L. maackii* density. At the local scale, we utilized the perimeter to area ratio as a structural measure of edginess, and the edge contrast index as a functional measure of edginess (Table 1). Both perimeter to area ratio and the edge contrast index are based on edge length around patches; see McGarigal et al. (2002) for an explanation of edge metrics and details of their calculation. We note that the perimeter to area ratio reflects differences in patch shape that may affect *L. maackii* density in addition to describing the area-corrected edge availability we emphasize here. Because the 1,500 m buffers around patches varied in area depending on the size of focal patches, at the landscape scale we calculated metrics describing both total edge length (which do not account for differences in edge amount in landscapes of different size) as well as edge density (which are standardized by the total landscape area). We measured total edge and edge density as structural

metrics, and contrast-weighted edge density and total edge contrast index as functional edge metrics. Functional edge metrics require the user to input a matrix of contrast weights for all possible habitat juxtapositions. Contrast weights range from 0 to 1 such that high-contrast edges have greater weight than low-contrast edges.

We took two approaches to weighting edge boundaries. The first characterizes edge contrast in terms of discontinuities in the abiotic light environment. The second approach measured avian responses to habitat edges, recognizing that dispersers of *L. maackii* seeds can play an important role in the distribution of *L. maackii* and may experience edges differently than the plant itself.

Abiotic edge contrast

Previous work indicates that *L. maackii* density is highest in areas with high light availability (Hutchinson and Vankant 1997), so we weighted edge boundaries based on differences in the light environments between adjacent habitats. It is possible that *L. maackii* may respond to other abiotic gradients that are influenced by edges or covary with light availability (e.g., moisture) but because existing literature focuses on light as a key determinant of *L. maackii* distribution, we focus our approach on defining habitat-specific differences in light availability. We took six measurements of light availability at ground level in the seven habitats utilized in GIS analyses using an Apogee[TM] Quantum photon sensor. Measurements were taken within 3 h of each other on the same day in August 2009 to ensure uniformity of ambient light availability. An effort was made to take light measurements more then 50 m from habitat

edges (e.g., roughly corresponding to the spatial scale of change in vegetation structure and composition across edge boundaries, Harper et al. 2005) in six individual patches per habitat type, but in some cases the small size or limited number of patches required us to measure light availability multiple times in a single patch or <50 m from the nearest habitat boundary. Quantitative data on light availability were converted to an ordinal scale such that the habitat with lowest light availability (evergreen forest) was scored as 0, and the habitats with greatest light availability (water and concrete) were scored as 10, and other habitats were ranked intermediately (Supplementary material, Table 1). We calculated contrast weights as the absolute difference in light availability between each pair of habitats divided by 10 (to scale the weights from 0 to 1). Therefore, values close to 0 indicate edges that differ little in light availability, whereas values close to 1 indicate habitats that differ substantially in light availability (Supplementary material, Table 1). We hypothesized that highly contrasting edge boundaries would be preferred by *L. maackii* (Hutchinson and Vankant 1997; Bartuszevige et al. 2006).

Biotic edge contrast

To weight edge boundaries from the perspective of avian seed dispersers, we utilized a large-scale dataset of count data from the Breeding Bird Survey (BBS) combined with spatial data describing the landscape around survey routes to identify habitat juxtapositions most associated with bird abundance. Based on the observation that American Robin (*T. migratorius*) are important dispersers of *L. maackii* seeds (Bartuszevige and Gorchov 2005), data on *T. migratorius* abundance (average counts across 10 years, 1993–2002 inclusive) were obtained from 18 BBS routes located within a 100 km radius of BCA. We reasoned that the integrated abundance estimate was most biologically relevant because it captures long-term bird population dynamics. Our choice of a 100 km radius represents a balance between including an area large enough to include several BBS routes, but small enough to be relevant to the area where our estimates of *L. maackii* density were made. Preliminary analyses revealed that correlations between bird abundance and edge length were greater in 500 m buffers around BBS survey

routes than in 1,500 m buffers, so we present the results of analyses using the smaller buffers. Land cover data for Missouri were obtained from MSDIS, and data for Illinois were obtained from the Illinois Natural Resources Geospatial Data Clearinghouse (http://www.isgs.uiuc.edu/nsdihome/). Within each buffer, we calculated the total length of edge for all pairwise habitat combinations. We calculated correlations between bird abundance and edge length for all habitat combinations across the 18 survey routes (Supplementary material, Table 2a). We identified the edge combination most correlated with bird abundance regionally (evergreen forest-wetland, $r = 0.95$), subtracted correlations for all other edge combinations from 0.95 and rescaled all values to range from 0 to 1 (Supplementary material, Table 2b). To yield a more intuitive interpretation of the weighting metric, we subtracted the rescaled edge contrast weights from 1 so that edge combinations positively associated with abundance of seed dispersers had values close to 1 (Supplementary material, Table 2c). Thus, low values indicate edge combinations negatively correlated with *T. migratorius* abundance, and high values indicate edge combinations associated with many *T. migratorius* at the regional scale.

Statistical approach to detecting edge effects

Consistent with Bartuszevige et al. (2006), we used multiple linear regression to describe edge effects on the density of *L. maackii*. We used an all-subsets approach based on Type II sums of squares to evaluate combinations of variables at local scales, landscape scales, and both spatial scales simultaneously, then selected models based upon parsimony as measured by AIC (Burnham and Anderson 2002). Models within four AIC units were deemed equivalent. Final models obtained using this approach were identical to those obtained using other model-selection procedures (e.g., stepwise selection based on changes in model R^2). Contrast-weighted edge density (light) and total contrast index (light) were significantly correlated ($r = 0.72$, $P < 0.03$), as were contrast-weighted edge density (avian) and total contrast index (avian; $r = 0.77$, $P < 0.02$). To reduce collinearity, we selected one variable from each pair for entry into the models, based on the variable that exhibited the maximum correlation with *L. maackii*

density. Based on this criterion, total edge contrast index (light) and contrast-weighted edge density (avian) were used.

Results

When the spatial scales at which we explored the relationship between edges and *L. maackii* density were considered separately, the best-fit models included only functional edge metrics (Table 2), and both models had similar explanatory power. When we combined data on edges at both local and landscape scales, the two best-fit models included both structural and functional edge metrics (Table 2; plots of the two best-fit models were similar, so only one of the models is illustrated in Fig. 2). Importantly, defining edge contrast in terms of habitat associations with an important disperser of *L. maackii* seeds was an important component of all best-fit models of *L. maackii* density. Our biotic definition of edge contrast had opposing effects at the two spatial scales we considered: *L. maackii* density was negatively associated with the avian contrast index locally (negative coefficient values in Table 2), but positively associated with contrast-weighted edge density regionally.

Because of the limited number of independent variables, our use of all-subsets approaches and

model comparisons to select the most appropriate models, it is unlikely that collinearity affected the model-selection process (which can occur when using specific variable-selection routines, e.g., stepwise selection; Fox 1991). This is supported by examination of variance inflation factors (Quinn and Keough 2002): none were above 3.9, below the value of 10 indicative of collinearity (Quinn and Keough 2002).

Discussion

Our results suggest that modeling the effects of habitat edge on *L. maackii* density requires information on edge length and density at both local and landscape scales, and that weighting edge contrast utilizing both abiotic and biotic criteria provides more information than structural edge metrics alone. The approach we describe here sheds light on the multiple roles that edges play with respect to the density of *L. maackii*, and provides a practical model for exploring the functional significance of edges in the context of a widely-used spatial analysis tool.

Seed dispersers can play an important role in determining plant distribution (Levey et al. 2005; Damschen et al. 2009), and we found that an indirect measure of abundance of seed dispersers in the surrounding landscape was an important component

Table 2 Results of model selection describing associations between edge metrics and *L. maackii* density in nine forest patches at the BCA

Variables in final model	Standardized coefficients	P	Model parameters	
			AIC	R^2
Local scale				
Contrast index (Light)	0.69	0.010		
Contrast index (Avian)	−1.07	0.001	−19.36	0.84
Landscape scale				
Total edge-contrast index (Light)	0.61	0.010		
Contrast-weighted edge density (Avian)	0.46	0.040	−20.32	0.86
Combined models				
Contrast index (Avian)	−0.70	0.001		
Perimeter:area ratio	0.27	0.020		
Total edge	−0.55	0.008		
Total edge-contrast index (Light)	0.73	0.002	−36.95	0.99
Contrast index (Avian)	−0.56	0.005		
Total edge	−0.48	0.020		
Total edge-contrast index (Light)	0.70	0.003		
Contrast-weighted edge density (Avian)	0.30	0.020	−36.00	0.98

Fig. 2 Partial correlation plots for variables included in the first of two best-fit combined models describing edge effects on the density of *L. maackii*. The plotted dependent variables are changes in *L. maackii* residuals that account for variation due to other components in the model. Best-fit lines obtained by least squares are indicated. **a** Presents data for the contrast index (Avian), **b** presents data for the perimeter:area ratio, **c** presents data for total edge, and **d** presents data for total edge-contrast index (light)
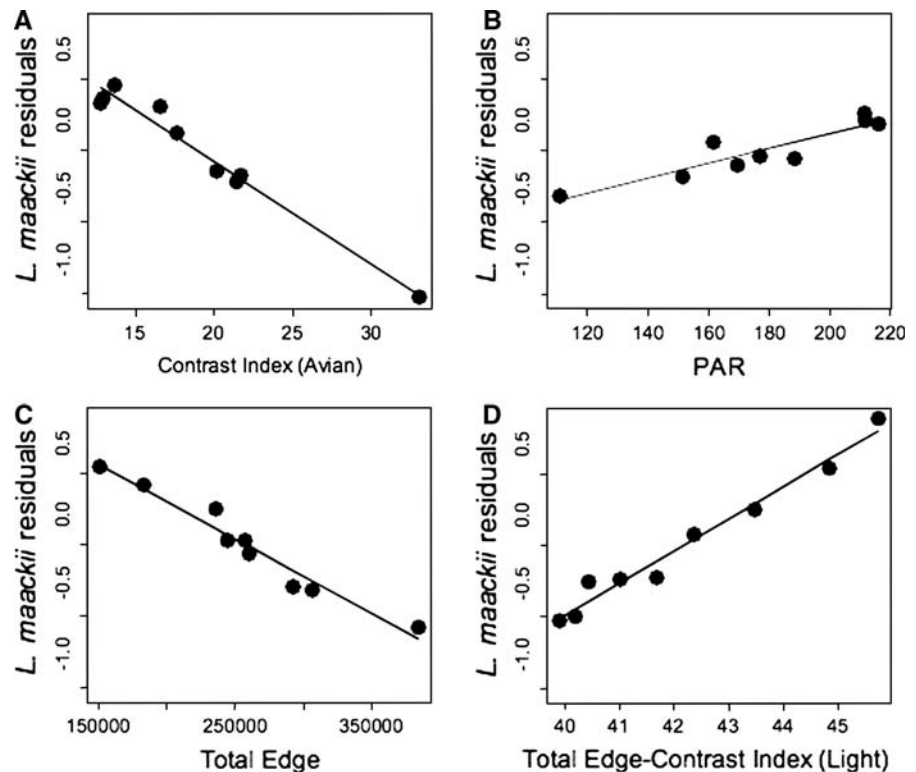
of models describing *L. maackii* density. The effect of seed dispersers is contingent on spatial scale; at local scales (e.g., around patches), *L. maackii* density was greatest in patches defined by edges associated with few seed dispersers, whereas at landscape scales, *L. maackii* density was greatest in patches embedded in landscapes with many edges associated with a high density of avian seed dispersers. This seemingly counter-intuitive observation probably results from our focus on *L. maackii* density in deciduous forest patches. Regionally, American Robin abundance was generally only weakly and negatively associated with amount of deciduous forest edge (Supplementary material, Table 2a), so it is not surprising that our local edge metric based on inferred bird abundance was negatively associated with *L. maackii* density. At a larger spatial scale, because avian seed dispersers move over a relatively large area (e.g., 1,500 m, Bartuszevige and Gorchov 2006), density of *L. maackii* may increase in landscapes with many seed dispersers even if birds are not particularly abundant in the forest patches we studied.

Although we lack observations on *T. migratorius* behavior at the study site, the literature provides

abundant evidence consistent with our hypothesis that landscape characteristics associated with a high density of seed dispersers may increase *L. maackii* density in forest patches. First, American Robins consume and defecate viable *L. maackii* seeds (Ingold and Craycraft 1983; Bartuszevige and Gorchov 2005). Robins are often relatively abundant frugivores in the eastern and midwestern United States (Sauer et al. 2008), and because *L. maackii* produce an average of 4.6 seeds per fruit (Bartuszevige and Gorchov 2005), seed deposition of *L. maackii* is likely to be substantial. Abundant evidence links robins to habitat edges (Hoppes 1987; Hawrot and Niemi 1996), at least in part because they prefer to forage in edge habitat (Oyugi and Brown 2003). American Robins move between foraging bouts more quickly than many sympatric frugivores (Hoppes 1987), and can move over a kilometer in the time it takes *L. maackii* seeds to pass through the gut (Bartuszevige and Gorchov 2005). In general, seed-fall increases in areas where avian frugivore abundance is high (Hoppes 1987), and detailed studies of American Robin behavior indicate disproportionately high seedfall of *L. maackii* along forest edges relative

to the availability of edge habitat in the environment (Bartuszevige and Gorchov 2005). Taken together, these observations suggest ample opportunity for *L. maackii* seeds to be spread throughout landscapes with many edges associated with high Robin abundance at the regional scale.

Although the data we present are consistent with the hypothesis that landscape structure around patches may be influencing the density of *L. maackii* via associations with an important avian frugivore, we acknowledge that our data are correlative and do not necessarily determine causation. The disconnect between correlation and causation is particularly common and problematic when utilizing indices of landscape structure, because of the difficulty of linking spatial pattern and process (Li and Wu 2004). However, large-scale landscape experiments are rare (although there are exceptions, e.g., Bierregaard et al. 1992; Tewksbury et al. 2002; Lindenmayer 2008), and many important questions in ecology and conservation rely on 'natural experiments' to make inferences about important relevant processes and they patterns they generate. For example, much of the large literature on habitat fragmentation (synthesized in Fahrig 2003; Watling and Donnelly 2006; Prugh et al. 2008) relies on natural experiments to achieve insight. Coupling natural experiments with large scale organism inventories and monitoring data integrates spatial and temporal variation in ecological dynamics that suggest broad patterns and coarse filters the define organism distributions (Boulinier et al. 2001). Here we utilize large-scale regional monitoring data and the natural experiment provided by a biological invasion coupled with autoecological observations of Robin behavior obtained from throughout the species' geographic range to interpret landscape effects on the distribution of an invasive plant. Our approach suggests an important link between landscape structure (amount of habitat edge) and the abiotic (light) and biotic (abundance of avian seed dispersers) filters that interact to influence the density of an invasive shrub; future studies that explicitly test these links are needed to confirm the mechanistic basis of the patterns we have described.

The differences in species abundances often associated with habitat edges (Fagan et al. 1999; Ries and Sisk 2004; Ries et al. 2004) suggest that the strength of many biotic interactions is likely to vary across edges, and empirical data suggest this may be the case

(Ostfeld et al. 1997; Ness 2004). In the present study, we weighted edge boundaries based on the abundance of important seed dispersers; our work clearly illustrates how this approach can provide insight into understanding the distribution of an invasive bird-dispersed shrub, *L. maackii*. We suggest that other variables describing key species interactions, such as parasite loads, pollinator availability, and the presence of fungal mutualists could be readily used to weight edge contrast. For example, predation (e.g., nest predation for birds, seed predation for plants) is a model biological interaction that is known to influence prey distribution and abundance across habitat boundaries (Chalfoun et al. 2002; Thompson et al. 2008), and can be readily translated into contrast weights (e.g., by rescaling observed predation rates to a scale of 0–1).

The procedure we illustrate here provides a data-driven approach to quantifying the relative importance of ecological interactions and the abiotic environment as filters that shape organism responses to habitat edges. A key feature of our approach is that it can be readily implemented using widespread software such as FRAGSTATS that allows users to define weights that contextualize structural landscape attributes. Our case study highlights the importance of biotic and abiotic edge effects in determining the density of an invasive shrub and illustrates a method for weighting edge boundaries to better understand how landscape structure influences the distribution and abundance of species.

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