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Changes in community and population responses across a forest-field gradient

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The ground-layer vegetation of a forest-old field edge gradient was sampled to determine the effects of the edge on spatial patterns of plant species and community attributes. Species showed individualistic responses to the forest edge, with peak abundance at different spatial positions relative to the edge. Principal components analysis resulted in three axes which explained a total of 63.2% of the variation within the data set. The first two PCA axes were related to distance to the forest edge. The third separated plots into those that were dominated by *Solidago canadensis*, and those that were dominated by *Solidago juncea*. All population- and community-level attributes varied along the edge gradient. Species richness, Shannon-Wiener diversity, and total percent cover increased from the forest to the edge, with slight declines 60 m from the edge in the field. Among-plot heterogeneity was higher at the edge than in either the forest or the field. Exotic species had peak abundance within 20 m of the edge inside the forest and are restricted to the edge. Most population- and community-level attributes showed edge responses on both sides of the edge. This emphasizes the need to study edges as gradients that include both disturbed and undisturbed habitats.

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Habitat fragmentation is a major feature of many landscapes within the eastern deciduous forests (Pickett and Cadenasso 1995, Pimm and Askins 1995, Robinson et al. 1995). This fragmentation creates boundaries or edges where disturbed patches of vegetation are adjacent to patches of remnant habitat. These edges are common sources of spatial heterogeneity within the landscape. This spatial heterogeneity includes a variety of biotic and abiotic edge effects (Murcia 1995). Edges function as sources of propagules for both the disturbed and undisturbed habitats (McClanahan and Wolfe 1987, Johnson 1988, Greene and Johnson 1996). Edges also represent complex environmental gradients, with changes in light availability, temperature, humidity, wind speed, and soil moisture (Brothers and Spingarn 1992, Matlack 1993, Forman 1995, Cadenasso et al. 1997). Plant species often respond directly to these environmental changes with differential growth, establishment, and survival near edges (Wales 1972, Whitney and Runkle 1981, Sork 1983). Forest edges may also be invaded by exotic species (Brothers and Spingarn 1992, Hester and Hobbs 1992, Fraver 1994) which may then establish in forest interior habitats (Luken and Goessling 1995). Many animal species respond behaviorally to habitat edges (Bellinger et al. 1989, Sekgororoane and Dilworth 1995, Meiners unpubl.), which may directly affect the impact of that species on plant community structure (Murcia 1995, Didham et al. 1996). Edges have also been found to influence ecosystem-level processes through enhanced atmospheric deposition rates (Beier and Gundersen 1989, Lindberg and Owens 1993). Collectively, edges create a spatially heterogeneous landscape with which plants interact to shape community structure.

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A problem with many studies of edge effects is that the edges are studied in a one-directional manner. Most studies look at edges from the landscape boundary into the remnant vegetation patch (Brothers and Spingarn 1992, Chen et al. 1992, Fraver 1994, Matlack 1994). In reality, the zone of edge effect extends both into the undisturbed patch and into the disturbed patch. In old field-forest edges, the most dramatic changes in microclimate occur on the field side of the edge (Forman 1995, Cadenasso et al. 1997). Environmental variables that show edge effects on the forest side of the edge should also be expected to show similar patterns on the field side. For example, light declines with distance from the edge into forests (Matlack 1993), and should also be expected to increase with distance into an old field as distance from canopy shade increases (Cadenasso et al. 1997). As changes in light levels are often used to explain the distributions of species along edges in a forest (Brothers and Spingarn 1992, Luken and Goessling 1995), changes in light levels on the field side of the edge might also be expected to influence species distributions.

As with the traditional study of ecotones, studies of edge effects should incorporate both habitat types, as well as the zone of transition between the two. This study examines the edge as a gradient from forest to old field. We addressed the following questions: 1) does plant community composition change along the edge gradient? 2) Do community-level attributes change along the edge gradient? 3) How are individual plant species arrayed spatially along the edge gradient? Because of the prevalence of exotic species in the data set, we can also address the impacts of exotic species cover in these habitats.

Study site

This research was conducted at the Hutcheson Memorial Forest Center (HMFC) near East Millstone, NJ, USA (40°30′N, 74°34′W). The site contained an old field and the adjoining early successional forest. This site is typical of many northeastern agricultural areas with a mosaic of different successional ages. The site was originally two agricultural fields separated by a hedgerow of large oaks (*Quercus rubra*) which ran northeast to southwest. The northwestern side of the hedgerow was abandoned in the 1950's and at the time of this study was a young forest dominated by *Acer rubrum* and *Quercus palustris*. Approximately 2 m on the southeastern side of the hedgerow was also abandoned at this time. The remainder of the field on the southeastern side of the hedgerow was abandoned in 1986. The field had previously been used to grow corn and was dominated by herbaceous perennial species with a few scattered trees and shrubs. The site drains poorly, becoming waterlogged after heavy rains or snowfall. HMFC is the site of the Buell-Small succession study, a long-term monitoring of successional dynamics originated in 1958 (Pickett 1982). As a result, the temporal patterns of vegetation are well known for this location.

Sampling design

A series of permanent plots was used to determine spatial patterning within the ground-layer vegetation. A 100 × 100 m grid, which began 30 m inside the forest and extended 60 m into the old field, was established in May 1996. This created a site which included portions of old field beyond the shading effects of the edge and dense forest cover. Approximately 25 m beyond the innermost forest plots, the stand abuts the old growth forest of HMFC. For this reason, the grid was not extended further into the forest. Within this grid 100 1-m^2 plots were established and placed regularly at 10 m intervals (Fig. 1). Plots were shifted when the grid position would place the plot within another experimental project or in a human-made trail. Wherever possible, the distance from the forest edge was held constant, shifting plot position parallel to the edge. For this study, the forest edge (distance 0) was defined as a straight line that approximated the most recent forest-field border. The actual forest-field boundary was not linear, but slightly concave. Several of the large hedgerow trees had also died, resulting in a lack of canopy cover over plots in the middle of the edge (Fig. 1). Distance from the forest edge was defined as positive for the field side of the edge and negative on the forest side.

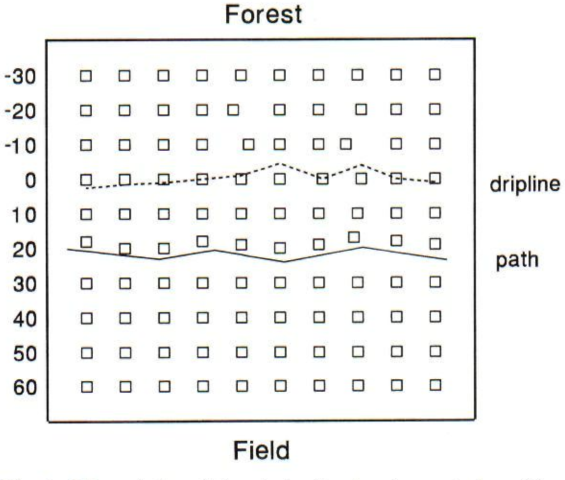

Fig. 1. Map of the of the study site showing actual positions of each plot (not drawn to scale). The plot extends from 30 m inside the forest to 60 m into the field. The dripline of the forest is drawn as a dashed line near distance 0. Plots were placed to avoid the mown path that crossed the grid (shown as a solid line).

Table 1. Significant correlations with factor scores and eigenvectors of species abundances for the first three principal components axes. Significance of Pearson correlation coefficients Bonferroni-adjusted for multiple comparisons ($\alpha_{0.05}$, $p = 0.0005$).

Species	PCA I		PCA II		PCA III	
	Corr	λ	Corr	λ	Corr	λ
Alliaria petiolata	NS	–	−0.36	−0.17	NS	–
Fragaria virginiana	−0.45	−0.25	0.68	0.61	NS	–
Hieracium caespitosum	−0.37	−0.11	0.50	0.24	NS	–
Lonicera japonica	NS	–	−0.57	−0.33	NS	–
Quercus palustris	NS	–	NS	–	0.63	0.33
Rosa multiflora	0.98	0.93	NS	–	NS	–
Solidago canadensis	NS	–	NS	–	0.93	0.87
Solidago juncea	−0.42	−0.22	0.58	0.49	−0.25	−0.24
Vitis vulpina	NS	–	NS	–	0.58	0.11

Within each plot, all vegetation under 2 m in height was sampled visually with the aid of a grid marked in 1% intervals to determine the percent cover of each species. Species present within a plot, but which did not reach 1% cover, were assigned a value of 0.5% for analysis. Data were collected from 29 June to 2 July 1996, 10 yr after abandonment of the field. Plots were revisited as necessary later in the season to identify unknown species as they flowered. Nomenclature follows Gleason and Cronquist (1991).

Analysis of population and community patterns

Principal components analysis was performed on the variance/covariance matrix of the vegetation to reduce the species composition data to a few interpretable independent variables (Proc FACTOR, Anon. 1989). The number of orthogonal axes retained in the analysis was determined by the method of Anderson (1963). Correlations between the original species data and the PCA axes were calculated and evaluated with Bonferroni-adjusted significance criteria for an overall α of 0.05 (Proc CORR, Anon. 1989).

The spatial patterns of the nine species significantly correlated with the first three PCA axes were then examined. For each distance from the forest edge, mean percent cover and standard errors were calculated. All nine species are common locally on abandoned agricultural land (Bard 1952, Pickett 1982, Myster and Pickett 1992). Three of the exotic species included – *Alliaria petiolata*, *Lonicera japonica*, and *Rosa multiflora*, are common invaders of disturbed land and are problematic for land managers (Cavers et al. 1979, Robertson et al. 1994).

For each plot, the species richness, Shannon-Wiener diversity (Shannon and Weaver 1949), total percent cover, and the total proportion of exotic species were calculated. Native vs exotic status follows Gleason and Cronquist (1991). Between-plot heterogeneity was calculated as the Euclidean distance between plots at one distance in the PCA ordination. To look for changes across the edge gradient, the data were analyzed by ANOVA with distance from the forest edge as the independent class variable (Proc GLM, Anon. 1989). These data were also analyzed separately for the forest (0– −30 m) and field (0–60 m) side of the edge to examine spatial patterns within each habitat type (traditional approach). For analysis, Shannon-Wiener diversity was transformed as e^x, and proportion exotic cover was arsine (square root) transformed. A non-parametric Kruskal-Wallis test (Proc NPAR1WAY, Anon. 1989) was used for heterogeneity data, which could not be transformed sufficiently to meet the normality assumptions of ANOVA. Means and standard errors were calculated for these variables for the 10 plots at each distance from the forest edge. Pearson correlation coefficients were calculated between PCA scores and community measures for each plot. Since heterogeneity is not a plot-based measure it was not included in this analysis. Correlations between exotic cover and other community attributes were calculated to determine the community-level effects of exotic invasive species.

Results

We observed 104 species of vascular plants within the sampling plots, 35 (34%) of which were exotic species. The first three PCA axes explained 63.2% of the variation within the data set, with individual axes explaining 38.2, 14.2, and 10.8%, respectively. Eigenvalues for axes 4 + were not significantly different than axis 3 and were dropped from the analysis (Anderson 1963). Nine plant species were significantly correlated with the PCA axes (Table 1). Axis I was positively correlated with the exotic shrub, *Rosa multiflora* and negatively correlated with *Fragaria virginiana*, *Solidago juncea*, and *Hieracium caespitosum*. Axis II was positively correlated with *Fragaria virginiana*, *Solidago juncea*, and *Hieracium caespitosum* and negatively correlated with two

Table 2. Correlation between PCA scores and distance of plots from the forest edge. n = 100 for all comparisons.

Axis	Pearson correlation	p
PCA I	−0.3989	0.0001
PCA II	0.6433	0.0001
PCA III	−0.0363	0.7197

exotic species, *Lonicera japonica* and *Alliaria petiolata*. Axis III was positively correlated with *Solidago canadensis*, *Quercus palustris*, and *Vitis vulpina* and negatively correlated with *Solidago juncea*.

The first two PCA axes were significantly correlated with distance from the forest edge (Table 2) with PCA I negatively associated and PCA II positively associated. For simplicity the axes can be interpreted as: PCA I = *Rosa multiflora* cover, PCA II = distance from the forest edge, and PCA III = *Solidago canadensis* cover. The third axis separates those field plots which are dominated by *Solidago canadensis*, and located closer to the edge, from those which are dominated by *Solidago juncea*, and located farther from the forest edge.

The spatial patterns of the nine species significant in the PCA analysis show individualistic responses to the forest edge (Fig. 2). Two of the exotic species had highest cover values inside the forest, *Alliaria petiolata* and *Lonicera japonica*. Three species, *Quercus palustris*, *Rosa multiflora*, and *Vitis vulpina*, reached peak cover values at the edge. The remaining species all had maximum percent cover in the old field. Abundance increased with distance into the field for all but *Solidago canadensis*, which reached peak cover at 20 m into the field.

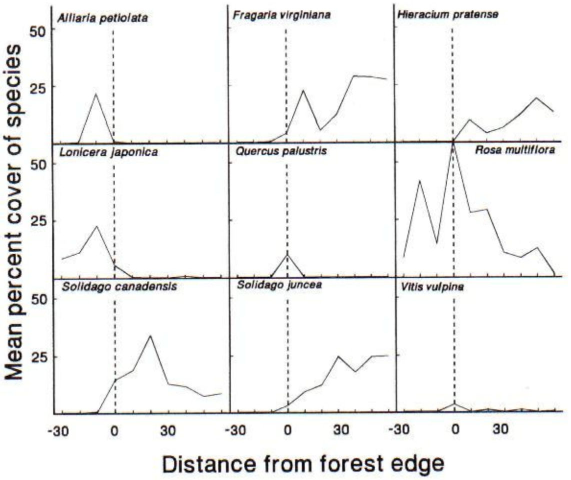

Fig. 2. Spatial distributions of the nine species that were significantly correlated with the PCA axes. Points at each distance represent the mean percent cover of the species from the 10 plots at that distance. Vertical dashed lines represent the position of the edge. Distances range from −30 (inside the forest) to 60 m (in the field).

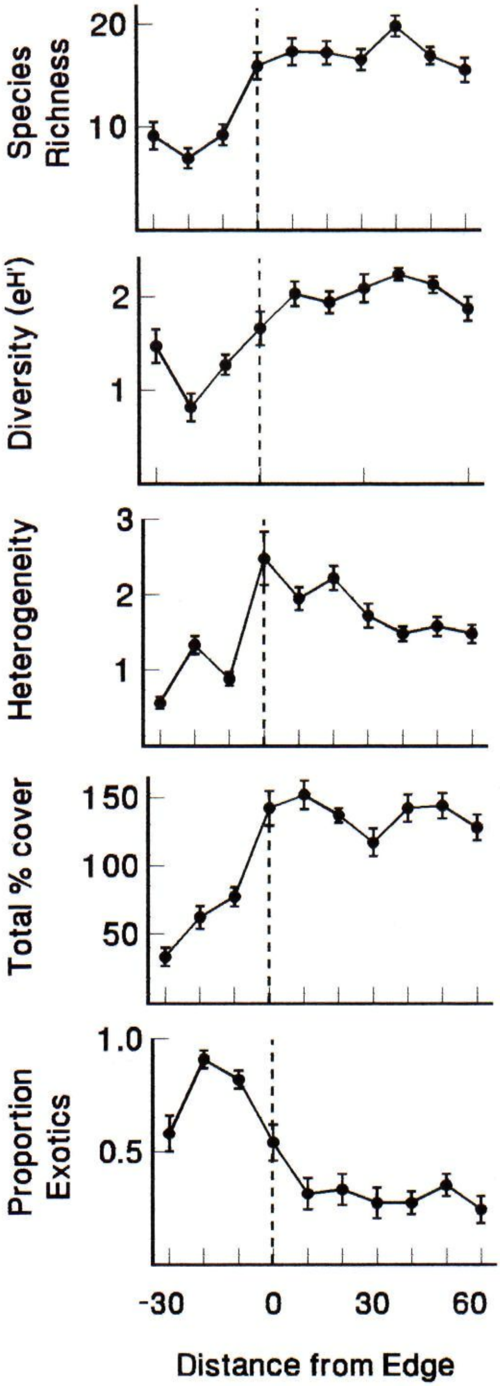

Fig. 3. The response of species richness, Shannon-Wiener diversity ($e^{H'}$), vegetation heterogeneity (Euclidean distance from PCA analysis), total percent cover, and proportion exotic cover to the forest-field edge. Points represent mean ± 1 SE for the 10 plots at that distance. Vertical dashed lines represent the position of the edge. Distances range from −30 (inside the forest) to 60 m (in the field).

All community measures varied significantly across the forest edge when the entire gradient was examined (Fig. 3). On the forest side of the edge (−30–0 m), all

Table 3. ANOVA results for the response of community attributes to distance from the forest edge. Data are presented for the entire gradient, forest side of the edge (0– −30 m), and field side of the edge (0–60 m). Heterogeneity data could not be transformed to meet ANOVA assumptions so a Kruskal-Wallis (χ^2) test is reported. NS = not significant, * = $p < 0.05$, ** = $p < 0.01$, and **** = $p < 0.001$.

Source	Entire gradient		Forest side		Field side	
	DF	F	DF	F	DF	F
Species richness	9,90	14.89****	3,36	11.11****	6,63	1.53^{NS}
Diversity	9,90	55.08****	3,36	5.41**	6,63	2.22^{NS}
Heterogeneity (χ^2)	9	104.3****	3	48.5****	6	15.73*
Total cover	9,90	20.36****	3,36	26.00****	6,63	1.43^{NS}
Percent exotics	9,90	15.26****	3,36	9.04****	6,63	2.30*

variables varied significantly with distance from the forest edge. Species richness, diversity, between-plot heterogeneity, and total cover are higher at the edge and decline from edge to forest interior. Percent exotic cover was highest 20 m inside the forest (91%) and declined towards the forest edge. On the old field side of the edge (0–60 m), only exotic cover and heterogeneity had a significant relationship with distance from the forest edge (Table 3). Both between-plot heterogeneity and proportion exotic cover declined from edge to open field. Diversity also declined with distance from the forest edge, but this relationship was not statistically significant ($p = 0.0529$).

Species richness and diversity were negatively correlated with PCA I and positively correlated with PCA II (Table 4). Total percent cover was positively correlated with PCA II. The proportion of exotic cover in each plot was positively correlated with PCA I and negatively correlated with PCA II and III. Percent exotic cover was negatively correlated with species richness (Pearson correlation coefficient $R = -0.64$; $p = 0.0001$) and diversity ($R = -0.71$; $p = 0.0001$).

Discussion

Species responses to the edge

The distributions of species changed spatially across the forest-old field edge. These spatial patterns may be in response to the microenvironmental gradient caused by the edge or may be caused by differential dispersal within the site. *Rosa multiflora*, *Vitis vulpina*, and *Lonicera japonica* all have bird-dispersed seeds and would be expected to have higher dispersal at the edge (Thompson and Willson 1978). *Quercus palustris* has seed that are cached by rodents and would have limited dispersal into the field. *Alliaria petiolata* was found predominately in the forest and is probably dispersed on the fur of mammals (Cavers et al. 1979). This species is common in moist forests and probably cannot physiologically tolerate the drier conditions within the field despite dispersal into those habitats.

The species common in the field are all wind-dispersed except for *Fragaria virginiana*, which is dispersed by tortoises and small mammals. Given the nature of these dispersal mechanisms, spatial patterns of these species cannot be explained by differential dispersal. All of the field species increased in abundance with distance from the forest edge, suggesting light limitation near the edge. However, the two *Solidago* species showed contrasting spatial patterns. *Solidago canadensis* is the more abundant species from 0 to 20 m into the field. Between 20 and 30 m from the forest edge, there is a switch in dominance, with *Solidago juncea* the more abundant species at ≥ 30 m into the field. *Solidago* species have been found to assort along moisture gradients in prairie old fields (Werner and Platt 1976) with *S. juncea* occurring in drier sites than *S. canadensis* (Potvin and Werner 1983). In this site, *S. canadensis* may be responding to soil moisture, which would be enhanced by shading near the edge.

Species responded to the edge gradient in an individualistic manner, without a generalizable 'edge response'. While hypotheses concerning the causes of spatial patterning have not been tested, it is clear that the edge is important in determining these spatial patterns. Furthermore, the gradient of responses to the forest-field edge indicates that the factors controlling species distributions may function at fairly small spatial scales. Several of the species also had an edge response on both sides of the forest-field boundary. For this reason, it is important to examine the entire edge gradient in determining a species' edge response.

Table 4. Pearson correlation coefficients between PCA scores and community-level measures. Sample size is 100 for each comparison. Statistical significance determined with Bonferonni-adjusted significance levels to control for multiple comparisons.

Measure	PCA I	PCA II	PCA III
Richness	−0.3339*	0.4853*	0.1234
Diversity	−0.5234*	0.2907*	0.0836
Total cover	0.0467	0.7661*	0.2787
Proportion exotic	0.6282*	−0.4545*	−0.3075*

Response of exotic species to the edge

Exotic species comprise 35% of all species within the site and average up to 91% relative cover inside the forest. As in other studies, the abundance of invasive species declines with distance from the edge into the forest (Brothers and Spingarn 1992, Hester and Hobbs 1992, Fraver 1994, Luken and Goessling 1995). Exotic species diversity and richness were also lower in the forest (Meiners unpubl.). The spatial pattern of exotics suggests that while edges are subject to invasion, edge populations do not serve as sources for establishment deeper into the forest (Matlack 1994, but see Luken and Goessling 1995). This spatial pattern may be only the result of insufficient time for complete colonization of the forest by the invasives. These data also suggest that only a subset of exotic species can successfully invade closed-canopy habitats. Little information is available on the field side of the edge with which to compare our results. The importance of Eurasian species in North American old field succession can be seen in the average relative cover of exotic species in the old field.

Exotic species are known to have many detrimental effects on plant communities by excluding native species (Cavers et al. 1979, Robertson et al. 1994). In this study, species with a rosette or creeping form (*Fragaria virginiana*, *Hieracium caespitosum*, and *Solidago juncea*) seem to be susceptible to exclusion by *Rosa multiflora*. This may result from competition for light with the taller exotic shrub. In a study of spatial relationships between old field species, Myster and Pickett (1992) found both *Lonicera japonica* and *Rosa multiflora* to have negative associations with many native species. In the current study, percent exotic cover was negatively correlated with both diversity and species richness. These correlations, while not focusing on individual species, emphasize the negative impacts of exotic species in plant communities.

Community-level responses to the edge

All of the community-level measures responded significantly to the edge gradient. Across the forest-field gradient, diversity increased to a maximum at 40 m into the field, and then begins to decline. This initial increase in diversity may be caused by the increase in light availability associated with the forest edge (Matlack 1993). The decline at greater distances may be caused by the combination of few shade-adapted species surviving in the absence of canopy shade and dispersal limitation for species established in the forest. Similar declines in old field species richness with distance from the edge were reported in Armesto et al. (1991). Species richness for invasive species has been found to peak at the edge and decline with distance into the forest (Brothers and Spingarn 1992, Fraver 1994, Meiners unpubl.).

In this study, between-plot heterogeneity was found to peak at the forest edge and to decline into both the field and forest. This relationship between heterogeneity and edges has been noted in other studies where variance in growth, seedling density, species richness, and plant cover was higher at the edge when compared to forest interior sites (Chen et al. 1992, Fraver 1994). This may reflect higher environmental variation at the edge (Chen et al. 1995) which would increase variation within the plant community. It may be that species better able to integrate across environmental heterogeneity (e.g. exotic species) will be better able to establish at edges. Because spatial heterogeneity has been shown to be an important factor influencing species' interactions (Fitter 1982, Tilman 1984, Hartgerink and Bazzaz 1984), we would expect changes in heterogeneity to lead to changes in plant community structure and composition (Peterson and Campbell 1993, Vivian-Smith 1997). The spatial patterns in heterogeneity associated with edges should be tested experimentally in other systems to determine their generality.

Total cover was found to increase from the forest interior to 10 m into the field. This pattern closely follows the pattern predicted for light availability (Brothers and Spingarn 1992, Matlack 1993, Chen et al. 1995, Cadenasso et al. 1997). The increase in light would allow more overlap between plant canopies while maintaining sufficient light for growth.

The changes in community-level attributes across the edge gradient further indicated the importance of studying edges as ecotones both sides of the edge. Examining only half of the gradient may lead to the erroneous conclusion that edges have no effects at the community level beyond changes in species composition. Because most studies focus on only one direction, the importance of edges in the landscape may be underestimated.

Conclusions

The prevalence of edges in modern landscapes emphasizes the need to understand the role of edges in plant population and community processes. Edges affect population- and community-level attributes in both the forest and the field, although most studies only focus on the forest side of the edge. Plant species responded individualistically to the edge gradient, with peak abundance at different distances from the edge. Species richness, diversity, total cover, between-plot heterogeneity, and exotic cover all changed significantly with position relative to the edge. The spatial patterns in these attributes were continuous across the gradient. For this reason, studies of edges as gradients from undisturbed to disturbed vegetation are needed to fully understand the role of edges in the landscape.

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