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Edge effects on species composition and exotic species abundance in the North Carolina Piedmont

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Abstract

Edges between forest and non-forest habitats often have significant effects on forest microclimate and resource availability, with corresponding effects on species composition and abundance. Exotic species are often increased in abundance near forest edges. This increase in abundance could be either because of the increase in resource availability near edges, or because of increased dispersal into forest edges. We measured species composition and a set of geospatial variables on transects at 66 edges in the North Carolina Piedmont in an attempt to distinguish between these two factors. Mantel tests show that species composition is significantly different in forest edges than in the forest interior, but that this effect only penetrates about 5 m into the forest. Indicator species analysis finds several species that are indicative of edge communities, including trumpet vine (*Campsis radicans*), two drought-tolerant oak species (*Quercus stellata* and *Q. falcata*), a serviceberry (*Amelanchier arboreum*), and a common exotic species, tree-of-heaven (*Ailanthus altissima*). Poisson regression techniques showed that in both the seedling and tree strata of the forest, exotic species increased in abundance on flat sites with a high potential seed source. Mapping predicted exotic species abundance onto the landscape. We find that large-scale variation in exotic species abundance is due mostly to variation in potential seed sources, while small-scale variation relates more to edaphic factors. Our results stress that both dispersal and environmental filters are important for determining exotic species abundance, but potentially the filters operate at different spatial scales.

Introduction

Across the world, forests are being fragmented into smaller and smaller forest patches (Harrison and Bruna 1999), with significant effects on species composition and abundance (e.g., Bowers and Dooley 1999). The effects of forest fragmentation may be divided conceptually into three categories (Sharpe et al. 1981; Saunders et al. 1991; Murcia 1995; Caley et al. 2001). First, there is the reduction in total forest area caused by any process of forest destruction; such effects have often quantified using simple species-area relationships (e.g., Harris 1984; Simberloff 1988). Second, there is an increase in the distance between forest patches; such effects have often been considered in a metapopulation framework (e.g., Aizen and Feinsinger 1994; Norton et al. 1995; Hanski 1998; Hanski and Ovaskainen 2000; Fahrig 2002, 2003). Third, the physical characteristics of the remnant patches are altered, usually because of the increased edge/area ratio of the patches (Chen et al. 1999); such effects have often been explored with field investigations of altered abiotic and biotic conditions near edges (e.g., Euskirchen et al. 2001; Weathers et al. 2001; Watkins et al. 2003). Edge effects are arguably the most important of these three trends (Murcia 1995), given that they have affected the abundance of almost all taxa tested previously (e.g., Laurence et al. 2002). Moreover, edges are quite widespread, with about 44% of trees estimated to be less than 90 m from an edge in the continental US (Riitters et al. 2002). In this paper, we present a landscape-level analysis of edge effects on woody species composition in general and on exotic species abundance in particular, partitioning the relative importance of edge effects on dispersal and environmental variation.

Edge effects on abiotic and biotic processes in forest ecosystems are varied and significant (e.g., Laurence et al. 2002). Forest edges usually have increased solar insolation, increased daily maximum temperatures, and in some conditions greater daily temperature ranges than the forest interior (Chen et al. 1999). Shade-intolerant taxa are usually favored near edges (Ranney et al. 1981), and their growth rates are often significantly elevated above what they would be in the forest interior (McDonald and Urban 2004). Seed dispersal processes in the edge zone are altered from those in the forest interior (Cadenasso and Pickett 2001), with exotic species often able to capitalize on the altered conditions near edges (Gelbard and Belnap 2003; Pauchard and Alaback 2004). Effects of edges on abiotic and biotic processes can interact in novel, synergistic ways (Fagan et al. 1999; Hobbs 2001; Laurance and Cochrane 2001), changing species composition (cf., Weiher and Keddy 1995) and population dynamics significantly (Fagan et al. 1999; Laurance 2002).

Two different perspectives on edge effects can be discerned in the literature. Authors researching edge effects have tended to focus on the change in the abiotic and biotic conditions, contrasting the disturbance of the edge relative to the forest interior (e.g., Hobbs and Huenneke 1992). Those studying exotic species spread have focused on the role of forest edges and especially roads as corridors for species invasion (e.g., Gelbard and Belnap 2003). Contrasting these two perspectives is not meant to imply they are independent, for the role of edges as conduits and the role of edges as disturbances can interact in subtle, synergistic ways (e.g., Fagan et al. 2002; With 2002). Moreover, a more complex classification of perspectives of edge effects can subdivide these further. For example, Fagan et al. (1999) recognize three separate issues (i.e., changes in mortality, 'spatial subsidies', and creation of novel interactions) that we discuss here under the general heading of 'abiotic and biotic changes'. The two perspectives discussed in this paper are not meant to imply that other conceptual classification schemes are not equally valid, but instead are meant to be heuristic.

Here we empirically separate the importance of edges as a disturbance, something altering the abiotic and biotic conditions within the habitat patch, from the importance of the proximity of any site to nearby potential populations of exotics. At any given site, we can conceive of the probability of finding a specific taxon as the product of the separate probabilities of dispersal to the site and the successful establishment (and survival) after arrival. We refer to the former factor as the dispersal filter on abundance, and the later factor as the environmental filter on abundance. The absence of exotics near an edge could be because of either, or both, of these filters.

We conduct an analysis of species composition near forest edges in the North Carolina Piedmont to take into account both of these filters. We answer the following specific questions: (1) Are edges having an effect on species composition? (2) What species appear to respond? (3) How do dispersal and abiotic filters govern exotic abundance? We predict that shade-intolerant taxa, and particularly exotics, will increase in abundance near forest edges. Furthermore, we predict that both a dispersal filter and an environmental filter will affect exotic species abundance.

Methods

Study area

The forest/non-forest edges used in this study are located in the Duke Forest (35.0° N, 78.9° W), NC, USA, an area that has been extensively studied for more than 70 years (Billings 1938; Oosting 1942; Keever 1950; Peet and Christensen 1980; McDonald et al. 2002). Duke Forest has several non-contiguous sections throughout Durham and Orange counties, 3200 ha in total, all of which are used in this study. Summers are hot, with a mean daily maximum of 31.5 °C in July, and relatively moist, with slightly more of the mean annual precipitation of 1052 mm falling in summer than in the winter, although severe droughts do occur. Winter temperatures reach a mean daily minimum of −1.2 °C in January, with one to two snowfall events per year (North Carolina Climate Office 2003). Soil parent material ranges from Triassic Basin sediments to metamorphic Carolina slate to diabase intrusions (Bain 1966).

The dominant vegetation on relatively undisturbed sites that have never been fully cleared by humans is a temperate cold-deciduous forest dominated by oaks (*Quercus* spp.) and hickories (*Carya* spp.), along with many other hardwood species (Ashe 1897; Braun 1950; Christensen and Peet 1984; McDonald et al. 2002). Sites that were clear-cut or converted to agricultural land and then abandoned are dominated by loblolly pine (*Pinus taeda*). Hardwood species are slowly establishing in these stands, and the spatial pattern of succession has created a mosaic of patches in different successional states (Oosting 1942; Trimble 1974). Today within the two-counties that contain the sites used in this study, 29% of the landscape is covered by sparse vegetation (e.g., agricultural fields) and 12% is developed (McDonald and Urban, in press), while the remainder is a mix of hardwood and pine patches. The landscape is highly fragmented, with the median tree around 30 m from an edge (McDonald and Urban, in press), and with road densities (km of road per km^2) that vary from more than seven in cities to less than one in rural areas (c.f., Forman and Deblinger 2000).

There are several woody exotics in North Carolina Piedmont forests that are the focus of the latter part of this study. The three main exotic tree species are shade intolerant: tree-of-heaven (*Ailanthus altissima*), mimosa (*Albizia julibrissin*), and Princess tree (*Paulownia tomentosa*). The two main exotic shrub species are somewhat more shade tolerant, particularly once-established: multiflora rose (*Rosa multiflora*) and Chinese privet (*Ligustrum sinense*). Two exotic vine species are common in many forests: wisteria (*Wisteria sinensis*) and Japanese honeysuckle (*Lonicera japonica*).

Biotic data

During the summers of 2001 and 2002, 66 forest/non-forest edges of varying edge orientation, edge age, and forest composition were randomly selected using aerial photos and satellite imagery. Edges occurred in forests of a variety of successional states and edaphic conditions. To control for variation in forest management histories, selected edges had not had recent (within 10 years) logging or other management activity within the remaining forest. The forest/non-forest edge was defined to occur at the farthest horizontal extension of canopy trees over the non-forest area (i.e., the canopy dripline). We selected a random point along the edge and then ran a 30-m transect into the forest from the forest/non-forest edge into the forest interior, placing the transect perpendicular to the edge. Many studies (e.g., Davies-Colley et al. 2000; Rheault et al. 2003) have found edge effects at distances greater than 30 m, so it would have been ideal if the transects could have been extended farther. However, in our highly fragmented study area, it was difficult to find areas of a consistent management history that have core areas more than 30 m from an edge. Therefore, the limited depth of our transects represents a compromise, and edge effects that penetrate farther into the forest, such as effects on birds (c.f., MacNally and Bennett 1997), will be present over the whole length of our transects.

Each transect was divided up into 5 m quadrats within which vegetation was sampled. Within 5 m of the transect, all woody plants greater than 1 cm in diameter at breast height (DBH) were tallied by species and their distance from the edge recorded (these data hereafter referred to as the ‘tree’ stratum). Increment cores were taken on all trees larger than 10 cm DBH. Trends in growth rate in relation to distance to edge are discussed in a companion paper (McDonald and Urban 2004). Within 1 m of the transect (i.e., centered within the larger transect described above) all woody plants were tallied by species in four height classes (0–10 cm, 10–30 cm, 30–100 cm, and greater than 100 cm but less than 1 cm DBH), and their distance from the edge recorded. Due to low sample size, and because there was no apparent difference in pattern between these four height classes, the smaller size class data were pooled, and are hereafter referred to as the 'seedling' stratum.

Environmental data

A broad set of environmental variables was measured to characterize factors that might affect plant establishment and growth. First, we measured canopy closure using a hemispherical densitometer, held at breast-height, at the forest/non-forest edge and every 5 m along each transect. At each measurement point, we took readings in each of the four cardinal directions, and the average canopy closure calculated. In each transect the direction the edge faced was measured using a compass, and is hereafter referred to as 'edge orientation'.

As one of the objectives of this paper was to provide a landscape-scale estimate of abundance of exotic species along edges, we obtained geospatial soil data for the region (SURGO data, USDA), rather than using in situ values that were also collected (McDonald and Urban 2004). Four variables were extracted from the SURGO database for each transect: pH, percent clay in the A horizon, percent clay in the B horizon, and the plasticity of clay in the B horizon. SURGO variables are only moderately correlated ($R < 0.5$), but the moderate multicolinearity may make P-values for these variables difficult to interpret.

The type of management (sensu Ranney et al. 1981) maintaining the edge from woody encroachment was summarized by describing the edge state in one of three states. The edge was classified as 'expanding', if there was visual evidence that the forest was expanding into the non-forested area, such as lots of young seedlings and saplings. The edge was classified as 'stationary', if the edge appeared to be spatially stationary over time. Finally, the edge was classified as 'contracting', if there was visual evidence that the non-forested area was expanding into the forested area over time, such as a relatively open understory that appeared to have been thinned out by mowing. We also determined stand age from Duke Forest management records and from the cores of dominant canopy trees. The age of the edge was determined to within 5–10 years using Duke Forest management records, aerial photographs, and satellite images.

Using digital elevation models from the Shuttle Radar Topography Mission database (USGS), a topographic convergence index (TCI, Beven and Kirkby 1979) was calculated for each site as a proxy for soil moisture. TCI is a function of upslope contributing area divided by slope: high values of TCI correspond to wet bottomlands, while low values of TCI correspond to dry ridgetops. Slope aspect was transformed following Beers et al. (1966), to reflect differences in solar radiation and evapotranspiration on different slope facets. This transformation aligns the index in a NE/SW axis, reflecting minimum relative heat loads on NE-facing slopes: values of −1 occur on NW facing slopes, and values of 1 on SW facing slopes. Edge orientation was similarly transformed, to reflect differences in solar radiation on edge facing different directions: values of −1 occur on NW facing edges, and values of 1 on SW facing edges.

Dispersal index

To capture differences in land-cover and potential seed source for exotic species, a classified Thematic Mapper image from May 2001 with 30-m spatial resolution was used to calculate a potential seed source index (SSI). The classification scheme had seven classes (deep water, shallow water, sparse vegetation, evergreen forest, mixed forest, deciduous forest, and developed). Training pixels were located from high-resolution aerial photographs, and classification was done using a maximum likelihood classification in Erdas Imagine (see McDonald and Urban, in press).

The SSI is defined for each of our transects as:

$$\mathrm{SSI}(d) = \sum_{i}^{n} e^{-\beta d_i}$$

where d is the distance between the plot and a potential source pixel in the map, defined as pixels that were classified as sparse vegetation (e.g., agricultural fields) or developed (e.g., parking lots), or that were adjacent to a road. These two land-cover types were selected as source areas for seeds, as preliminary field observations found most exotics associated with these two cover types. It should be stressed that this is an assumption of the index, which will be supported if SSI is correlated with exotic abundance. SSI provides a measure of the possible seed source of exotics from the landscape to a particular transect, with β controlling the size of the neighborhood in which seed dispersal is likely. The parameter β controls the rate at which seed dispersal drops off from each source pixel. A range of values of β were selected by assuming that 99% of each source pixels exotic seeds fall within 60, 120, 240, 480, and 960 m of each source pixel (hereafter referred to as SSI60, SSI120, SSI240, SSI480, and SS960, respectively), distances that seemed likely to bracket the dispersal distance of the exotic species of the region (but see Clark et al. 1999; Cain et al. 2000).

Is there an effect of forest edges on species composition?

To answer this question, we used a series of Mantel tests (Mantel 1967; Endler 1982; Legendre and Legendre 1998). Mantel tests involve calculating a correlation between two distance matrices, and are useful when dealing with multivariate community ecology data. For all Mantel tests in this paper, the standardized Mantel coefficient, r_M, was calculated on rank distances, which is equivalent to calculating a Spearman correlation coefficient between two distance matrices (Dietz 1983). Significance of the observed r_M was tested by permutation using the method of Smouse et al. (1986) using custom functions in S-Plus (Insightful Inc., Seattle).

Two synthetic species dissimilarity matrices were calculated using the Relative Sørenson distance metric (Legendre and Legendre 1998) on the tree and sapling density data. These matrices describe how different the species composition is between any two pairs of quadrats. Similarly, a synthetic environmental dissimilarity matrix was calculated by calculating Euclidean distance between sites on the *z*-scores of the environmental variables. This matrix describes how different the environmental conditions are between any two pairs of quadrat. Two distance matrices were calculated to account for spatial autocorrelation due to spatial proximity, one within the transect and one between transects. These matrices describe how far apart the quadrats are, which is important given the likelihood that quadrats close to one another will be similar in species composition.

The species composition matrix was compared to the matrix based on the dissimilarity in distance to edge, after partialing out the dissimilarity in environmental conditions between transects and the spatial autocorrelation within and between transects. The question answered with this Mantel test is: Are quadrats that are at similar distances from an edge compositionally similar, after controlling for similarity in the environment and for spatial autocorrelation?

How far does the edge effect penetrate into the forest?

We created a set of six design matrices (i.e., binary matrices), corresponding to six different distances from an edge (0–5 m, 5–10 m, 10–15 m, 15–20 m, 20–25 m, and 25–30 m). In each design matrix pairs of quadrats that are both a certain distance from an edge are coded 1, and all other pairs are coded 0. With each design matrix, we calculated the r_M between the design matrix and the species composition matrix, after partialing out the dissimilarity in environmental conditions between transects and the spatial autocorrelation within and between transects. Significance was assessed with permutation tests as above, but since there were multiple statistical tests, significance was tested using the sequential Bonferroni procedure (Legendre and Legendre 1998). This approach is similar statistically to the multivariate Mantel correlogram described in Legendre and Legendre (1998). These tests answer the question: Are quadrats at a certain distance from an edge compositionally similar, after controlling for similarity in the environment and for spatial autocorrelation?

Which species are affected in abundance by forest edges?

Based on the results of the multivariate Mantel correlogram described above, each quadrat was assigned into two groups: near an edge (0–5 m) and away from an edge (5–30 m). An Indicator Species Analysis was performed on abundance data in both the tree and seedling strata, following the method of Dufrêne and Legendre (1997) as implemented in the program PC-Ord (see McCune and Grace 2002). This analysis generates an indicator value for each species, which is a synthetic measure of both its specificity and fidelity to forest edges. Significance of each indicator value was assessed through 10,000 permutation tests. Since there are 72 species, there is a danger of a type I error due to multiple statistical tests. To account for this, we followed the procedure that at least one of the 72 species in each stratum must be significant at the $0.05/72 = 0.0007$ level for the results from that stratum to be worth interpreting. If this criterion was met, all species with P-values less than 0.05 were considered significant.

What environmental and landscape factors govern exotic species abundance?

We calculated total exotic abundance in both the seedling and sapling strata. The total exotic abundance of each strata was then treated as the dependent variable in a Poisson regression using the generalized linear model function *glm* in S-Plus. A Poisson distribution is an appropriate selection for the distribution of the error term in the model since the total exotic abundance is in the form of discrete counts. Explanatory variables were selected by stepwise forward regression, drawing from a possible pool of all the environmental and dispersal variables described previously. The assumptions of the Poisson regression were checked graphically for both regressions and were well supported.

Results

Is there an effect of forest edges on species composition?

Forest edges have a clear effect on forest composition in both the seedling (Table 1a) and tree (Table 1b) strata. Note that values for r_M are usually substantially lower than conventional Spearman correlations, and should be interpreted accordingly (Legendre and Legendre 1998), with significance being assessed using the P-value from permutation tests. There is a significant simple r_M between the species composition matrix and the distance-to-edge matrix for both strata. The significance of this relationship persists even after accounting for spatial autocorrelation in the data. Further, for both strata there is a significant r_M between the species composition matrix and the distance-to-edge matrix, even after accounting for spatial autocorrelation and for the transect-level environmental variables. The tree stratum seems to respond more to the

Table 1. Mantel Correlations for seedling (a) and tree Stratum (b). The symbol * refers to all other variables, and thus the correlation between Species|* and a variable of interest is the Mantel correlation between the variable of interest and Species after partialing out spatial autocorrelation (i.e., the geographic distance between transects) and all other variables.

	Distance to edge	Environmental variables
(a) Seedling stratum		
Spatial autocorrelation	−0.0068 (NS)	0.0897 ($P = 0.004$)
Species	0.0210 ($P = 0.048$)	0.1611 ($P < 0.001$)
Species|spatial autocorrelation	0.0229 ($P = 0.040$)	0.1463 ($P < 0.001$)
Species|*	0.0240 ($P = 0.033$)	0.1465 ($P < 0.001$)
(b) Tree stratum		
Spatial autocorrelation	−0.0068 (NS)	0.0897 ($P = 0.007$)
Species	0.0320 ($P = 0.006$)	0.0723 ($P = 0.005$)
Species|spatial autocorrelation	0.0332 ($P < 0.001$)	0.0615 ($P = 0.012$)
Species|*	0.0336 ($P = 0.004$)	0.0617 ($P = 0.005$)

forest edge than the seedling stratum, as the r_M values are generally higher and the *P*-values are generally lower. Conversely, the seedling stratum seems to change more in species composition due to the environmental variables than the tree stratum.

How far does the edge effect penetrate into the forest?

The effect of forest edges appears to only affect the species composition of forests within the first 5 m of an edge (Figure 1). The partial r_M between the species composition matrix and the model matrix for the first distance class, after controlling for spatial autocorrelation and environmental conditions, is significant, whereas it is insignificant for all other distance classes. The general shape of the curve at further distance classes contains little information, since the partial r_M for those distance classes are not significant, and should not be over-interpreted.

Which species are affected in abundance by forest edges?

Generally, a few shade-intolerant taxa were indicative of forest edge communities in both the tree (Table 2a) and seedling strata (Table 2b). Trumpet vine (*Campsis radicans*) has a significant affinity for edges in both strata, as do two drought-tolerant oak species (*Quercus stellata* and *Q. falcata*), a serviceberry (*Amelanchier arboreum*), and a common exotic species, tree-of-heaven. Loblolly pine (*Pinus* taeda) and chestnut oak (*Q. prinus*) are indicative of forest edges in the seedling stratum, but apparently few individuals of these two species survive into the tree stratum, as they have non-significant indicator scores and low densities (data not shown). Blackberries (*Rubus* spp.) are similarly indicative of edges in the seedling stratum but have a non-significant indicator score in the tree stratum, probably because blackberries are generally of small stature. Winged sumac (*Rhus copallina*) is indicative of edges in the tree stratum but not in the

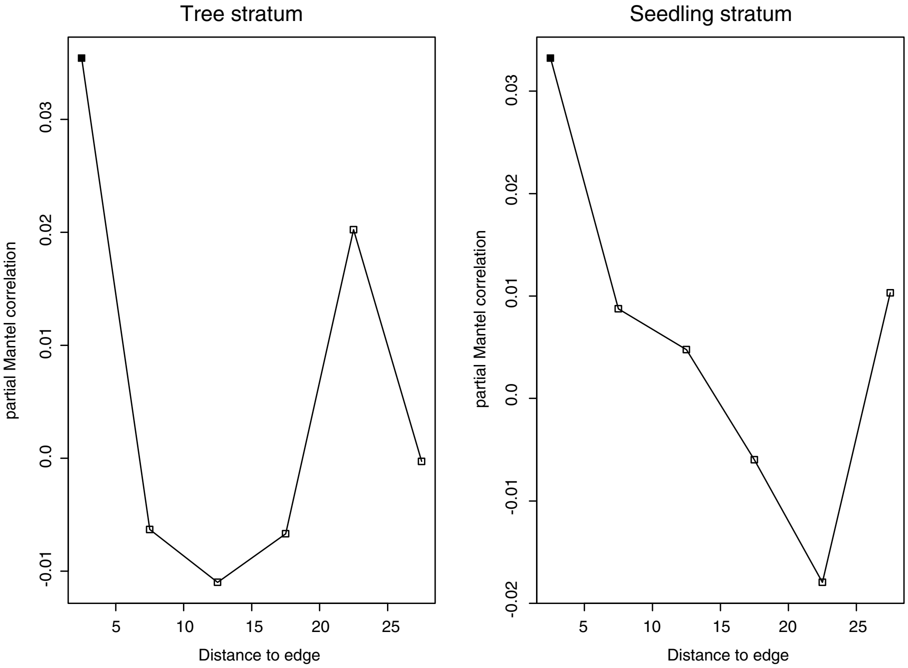

Figure 1. The effect of forest edges on forest composition in the tree and seedling strata. Filled squares indicate distances at which the partial Mantel correlation is significant, while unfilled squares are not significant.

Table 2. Indicator species for seedling (a) and tree (b) stratum.

Species	Group	Indicator value	*P*
(a) Seedling stratum			
Pinus taeda	Edge	45.3	0.012
Rubus spp.	Edge	25.7	< 0.001
Campsis radicans	Edge	23.5	< 0.001
Quercus falcata	Edge	18.7	0.040
Quercus stellata	Edge	7.3	0.045
Ailanthus altissima	Edge	6.4	0.002
Amelanchier arboreum	Edge	3.2	0.024
Quercus prinus	Edge	3.2	0.032
(b) Tree stratum			
Acer rubrum	Interior	46.5	0.040
Quercus falcata	Edge	16.5	0.029
Campsis radicans	Edge	14.8	< 0.001
Quercus stellata	Edge	7.8	0.017
Ailianthus altissima	Edge	6.3	0.004
Amelanchier arboreum	Edge	3.2	0.027
Rhus copallina	Edge	3.2	0.030

seedling stratum. Conversely, red maple (*Acer rubrum*) is indicative of forest interiors in the tree stratum but not in the seedling stratum, although it is present in the seedling stratum.

What environmental and landscape factors govern exotic species abundance?

Exotic species abundance increased near edges in the seedling stratum (Table 3a), with only the quadrats from 0–5 m from an edge having significantly higher densities than the quadrats in the other distance classes. Transects in older stands have less exotics, as do transects with steeper slopes, higher values of transformed edge aspect (i.e., more southerly exposures), and more clay in the A horizon. There are more exotics on sites with low TCI (i.e., drier sites) and high soil plasticity. A significant seed source effect for exotics occurs at large spatial scales, with seed dispersal

Table 3. Poisson regression response table for seedling (a) and tree (b) stratum. Distance to Edge is treated as a categorical variable, and hence does not have a single coefficient.

Variable	Df	Deviance	Residual Df	Residual deviance	*P*	Coefficient
(a) Seedling stratum						
Intercept	371	586.81				2.912
Distance to edge	5	36.85	366	549.96	0.000	
Stand age	1	27.09	365	522.86	0.000	−0.013
Slope	1	20.79	364	502.08	0.000	−1.644
TCI	1	32.27	363	469.80	0.000	−0.672
Plasticity	1	14.18	362	455.62	0.000	0.044
Source960	1	10.85	361	444.78	0.001	0.023
Edge orientation	1	13.35	360	431.42	0.000	−0.734
Clay in A horizon	1	13.87	359	417.56	0.000	−0.109
(b) Tree stratum						
Intercept	371	619.32				−3.456
Clay in A horizon	1	76.13	370	543.20	0.000	0.075
Source120	1	40.60	369	502.60	0.000	0.710
Edge orientation	1	28.53	368	474.08	0.000	0.719
Stand age	1	4.41	367	469.67	0.036	0.005
Slope	1	3.22	366	466.44	0.073	−0.382
TCI	1	2.50	365	463.94	0.114	−0.126

from potential seed sources up to the maximum 960 m tested. The results from the seedling stratum, while highly significant, should be interpreted with some caution as there is one datum with high leverage. Exclusion of this datum does not change the size or sign of the coefficients, but does increase the *P*-value of a few of the coefficients to marginal significance ($P < 0.10$).

Exotic species abundance in the tree stratum display no clear trend with relation to distance-to-edge (Table 3b), with all quadrats at different distances from the edge having statistically identical exotic abundances. This surprising result may be simply due to the lower levels of exotic species abundance in this stratum and hence the lower statistical power of the forward stepwise regression. As with the seedling stratum, transects with steep slopes or high TCI (i.e., wetter sites) have fewer exotics, although these trends are not significant at the $P < 0.05$ level. In contrast with the seedling stratum, transects with less clay in the A horizon and higher values of transformed edge aspect have fewer exotic trees. This contrast may be a statistical artifact, or may reflect ecological differences between the two strata. Moreover, transects in older stands have more exotic trees, perhaps simply because it takes some time for exotic stems to mature into the tree stratum. Finally, there is a significant seed source effect for exotics that occurs at intermediate spatial scales, with seed dispersal from potential seed sources up to 120 m showing the strongest association.

The predictions of these two models are displayed graphically in Figure 2. The values shown are the predicted mean exotic abundance right at a forest edge on a hypothetical SE-facing edge, and are displayed such that red colors indicate high mean exotic abundance and blue colors indicate low mean exotic abundance. The color scale is overlayed on a black and white hillshade of the topography, such that NE facing slope facets appear relatively dark and SW facing slope facets appear relatively light. Since the abundance of exotics at any particular edge depends on the small-scale distance to edge (for the seedling stratum) and the local orientation of any edge, the results in Figure 2 are best viewed as a relative index of potential exotic abundance. The predictions of both strata are similar, in that they both appear to be largely determined by the seed source variable at the landscape scale, while effects of topographically-derived variables appear to be more important at small scales.

Discussion

Forest/non-forest edges in the North Carolina Piedmont have a significant effect on woody species composition, but this effect is limited to within 5 m of an edge. This result is consistent with some papers that have found edge effects on composition to be limited to a narrow zone near the edge. For example, Watkins et al. (2003) found that species diversity was only increased within 5 m of a forest road. On the other hand, some studies have found much deeper penetration of forest edges into the forest interior, such as Euskirchen et al. (2001) who found edge effects on composition up to 30 m in from a clearcut. Clearly, more work needs to be done to quantify the factors that cause variation in the depth of influence of edge effects. As Moen and Jonsson (2003) caution, ‘the response of species to edges is strongly species-specific and context-dependent.’

As we had hypothesized, many of the woody species that increase in abundance are shade-intolerant (and often exotic), usually early-successional species such as loblolly pine and tree-of-heaven. However, some of the other species that are indicative of edge communities are somewhat surprising. For example, several oak species seem to have responded positively to the increased light conditions near edges, further questioning the notion that oaks are a relatively late-successional species in the North Carolina Piedmont (cf. Lorimer et al. 1994; McDonald et al. 2002). Overall, while all taxa that increased in abundance near edges could be characterized as somewhat shade-intolerant, they were from different points along the traditional old-field successional sequence of Oosting (1942), suggesting that plant community response to edges is more complex than the simple successional analogy of Ranney et al. (1981), and supporting other studies that have found complex, synergistic

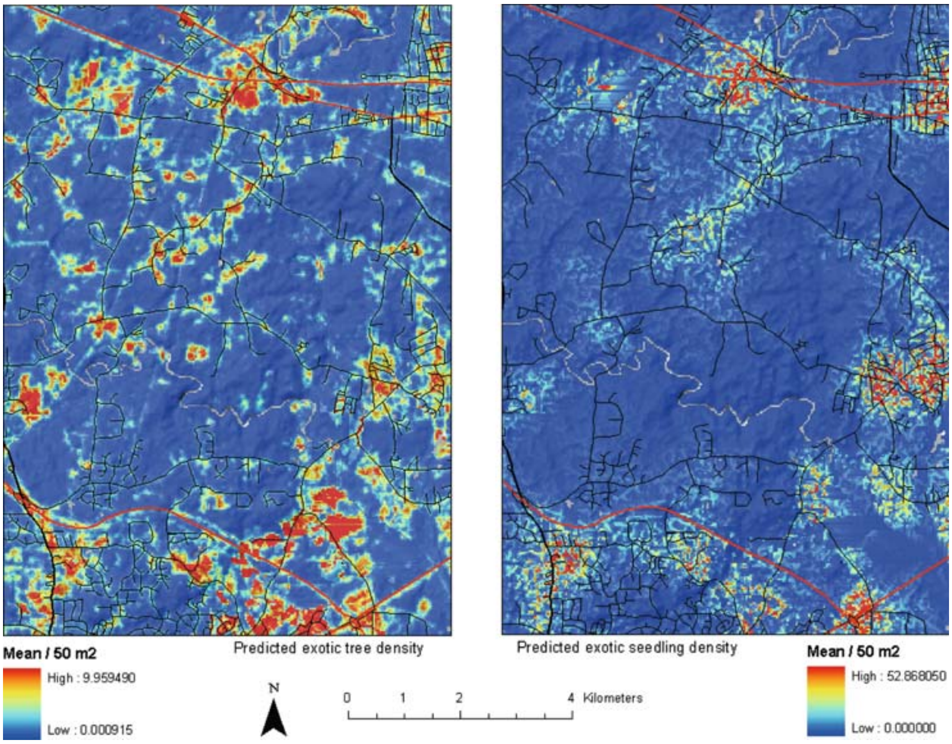

Figure 2. Predicted exotic tree density for the tree and seedling strata for an area around the Durham Division of the Duke Forest. See text for details.

response of plant communities to edges (e.g., Fagan et al. 1999; Hobbs 2001; Laurance and Cochrane 2001).

Exotic species abundance is affected by the distance to an edge in the seedling strata, but shows no response in the tree strata. This could be because of the generally lower number of exotics in the tree strata, which would limit the ability to detect a pattern. In both strata, seed source effects via a dispersal filter are important. The significance and strength of these trends are less in the tree strata, as might be expected because the environmental filter on establishment has had longer to be active on stems in this strata. Finally, many of the same environmental variables are significant in both strata, especially edge orientation, TCI, and soil plasticity. It is interesting that exotic species were abundant on sites with greater soil plasticity and lower values of TCI (i.e., drier sites). This may be due to the ability of several of the regions exotic species, such as multiflora rose, to survive on upland sites.

Our results stress that both the dispersal and environmental filters are important for determining exotic species abundance (cf. Murcia 1995). Moreover, we find that large-scale differences in exotic species abundances are controlled mostly by the dispersal filter (cf. Brown and Peet 2003) and smaller-scale difference in exotic species abundance are controlled mostly by environmental factors that change over small spatial scales (Figure 2, see methods for details of interpretation). Thus, the factors that are important to an environmental manager who is determining invisibility will be scale dependent. However, the short length of our transects (30 m), as well as the short distance of edge influence (5 m in this study), may limit our ability to fully separate the dispersal and environmental filters, as dispersal processes that occur at scales smaller than a transect will be lumped in with our estimate of the general edge effect. Nevertheless, our results suggest that the dispersal filter may deserve more attention, particularly at the landscape scale.

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