



Responses of a small mammal community to heterogeneity along forest-old-field edges

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Abstract

Despite the importance of edges effects in ecological systems, the causes and consequences of animal responses to habitat edges are largely unknown. We used three years of live-trapping and measures of the plant community around trap stations to explore the responses of white-footed mice (*Peromyscus leucopus*), meadow voles (*Microtus pennsylvanicus*), and short-tailed shrews (*Blarina brevicauda*) to forest-field edges in upstate New York. We found that capture probabilities of voles were highest in grass- and forb-dominated micro-habitats and in old-field zones distant from the forest edge. In contrast, capture probabilities of white-footed mice were highest in shrub-dominated microhabitats and in zones near the forest edge. Short-tailed shrews did not show strong micro- or macrohabitat associations. The responses by voles, the competitive dominant in our system, to variation along forest-field edges were more consistent across years than were those of the competitively inferior, white-footed mouse. Mice were less likely to use the old-field interiors when vole density was high than when it was low, suggesting competitive displacement of mice by voles. Finally, we found good agreement between the spatial activity patterns of mice and voles in old-fields and their impacts on patterns of survival of tree seeds and seedlings in concurrent studies. These results suggest that a dynamic interaction exists between the plant and animal communities along forest edges.

Introduction

Changes in land use in eastern North America over the last several centuries have produced a highly fragmented landscape in which forest-old-field edges are a dominant feature (Glitzenstein et al. 1990). These edges can influence a variety of ecological processes such as dispersal and the community composition of both animals and plants (Hansen and di Castri 1992; Pickett and Cadenasso 1995; Risser 1995). Organisms can respond either positively or negatively to forest edges depending on a wide range of factors operating at a variety of spatial scales (Bowers et al. 1996; Cappuccino and Martin 1997; Mills 1995; Murcia

1995; Yahner 1988). Such factors include the physical structure of edges (Murcia 1995), the intensity of competition and predation along edges (Bowers and Dooley 1991; Lima and Dill 1990; Yahner 1988), as well as the type of matrix surrounding patch fragments (Donovan et al. 1997; Wiens et al. 1985). Identifying which factors are important for a particular species as well as how these factors interact across the range of scales that typify natural landscapes are critical issues in determining the nature and magnitude of edge effects (Levin 1992; Lidicker 1995, 1998; Murcia 1995). Small mammals have been used as 'experimental model systems' (EMS) to study the effects of edges on demography and behavior (Ims and Stenseth 1989;

Wiens et al. 1993). The approach in EMS studies is to create artificial landscapes, typically by mowing around patches of grassy habitat, to evaluate the impact of landscape features such as patch size, shape, and connectivity on mammal populations (Bowers et al. 1996; Diffendorfer et al. 1995; Harper et al. 1993; Lidicker 1995; Wolff et al. 1997). However, because experimentally created edges may differ considerably in structure from natural ones, the applicability of results within the micro-landscapes of EMS to natural landscapes is still largely unexplored.

We monitored small-mammal populations along forest-field edges in eastern New York to explore how environmental heterogeneity along these ecotones influences the distribution and abundance these organisms. The dominant small-mammal species in northeastern old-fields span a broad range of habitat specialization and include meadow voles (*Microtus pennsylvanicus*), which are found primarily in grass-dominated microhabitats (Getz 1985; Grant and Morris 1971), white-footed mice (*Peromyscus leucopus*), which use a broad variety of habitats but prefer structurally complex areas (Kaufman et al. 1983; M'Closkey and Feldwick 1975), and short-tailed shrews (*Blarina brevicauda*), which appear to be extreme habitat generalists (Adler 1985; Dueser and Shugart 1978). Previous studies (Manson et al. 1998; Ostfeld et al. 1997) have shown that: (1) two of these species, meadow voles and white-footed mice, can have dramatic impacts on the survival of tree seedlings and seeds, respectively, in old-fields; (2) competitive interactions between these herbivores can mediate their effects on seed and seedling survival; and (3) variation in the vegetation dominating particular old-fields may be important in influencing the relative abundance of these species, and thus their overall impacts on tree invasion dynamics in old-fields.

The current study extends these results, using three years of trapping data to explore the relationships between habitat specialization in small mammals and their responses to micro- and macrohabitat variation in vegetation cover along forest-field edges. We consider how these responses might influence the impacts of these herbivores on patterns of edge expansion and edge structure. Specifically, we address the following questions:

(1) How well do the microhabitat and macrohabitat variation in vegetation cover along forest-field edges predict the activity of small mammals? We define microhabitat variation as that occurring at a scale measured at trapping stations, and macrohabitat vari-

ation as that occurring along a gradient from forest edges into old-field interiors.

(2) Do voles or their competitive inferiors, white-footed mice, change their response to either small-scale or large-scale habitat heterogeneity with changing vole density?

(3) How consistent are the responses of small mammals to this variation across different years?

(4) What is the relationship between the response of mice and voles to variation in vegetation along forest-field edges and the implied impacts of these organisms on tree invasion dynamics along these gradients?

Methods

Trapping protocol

As part of an ongoing research agenda designed to elucidate the role of seed and seedling predation by small mammals in tree invasion dynamics in old-fields, small-mammal trapping and density manipulations of meadow voles were conducted at six study sites located at or near the Institute of Ecosystem Studies (IES) in southeastern New York (41°50' N, 73°45' W). Previous publications describe general experimental protocols and the study sites in greater detail (Manson et al. 1998; Ostfeld et al. 1997, 1999). Data reported here are from the first three years (1994–1996) of trapping during these studies representing 11,100 trap-nights. Each study site contained two (40 m by 40 m) partial enclosures that shared a common middle fence and were located along the forest-field edge (Figure 1). One enclosure of each pair was randomly assigned to a high, and the other a low, vole density treatment. Since voles tend to perceive forest edges as dispersal barriers (Tamarin et al. 1984), they remained largely within enclosures during density manipulations despite the lack of a fence along the forest-field edge (Figure 1; Ostfeld et al. 1997). In contrast, mice and shrews appeared to move freely in and out of enclosures from adjacent forests.

Within each enclosure vole density was manipulated, and the community of small mammals in the field portions was monitored, using trapping grids that consisted of a 5 by 5 array of traps with 7.5 m spacing between them (Figure 1). A standard mark-recapture protocol was used bi-weekly from May to November each year. Medium-sized Sherman traps (5.1 cm by 6.4 cm by 15.2 cm) and Longworth traps were alternated at trap stations. The vole density treatment

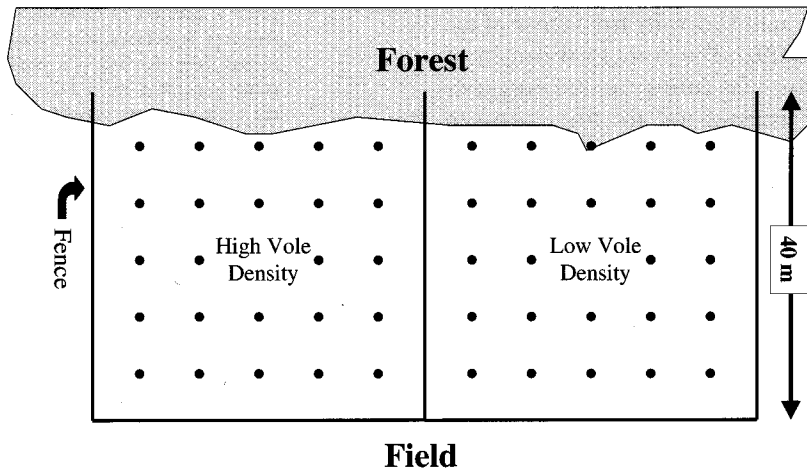


Figure 1. Diagram of one of the six study sites showing the arrangement of paired enclosures relative to the forest edge. Enclosures extended five meters into forest and 35 m into the field. Dots represent trap stations, which were located 7.5 m apart in rows 5, 12.5, 20, 27.5 and 35 m out into the field.

consisted of adding or removing juvenile and subadult voles to or from designated high- and low-vole density enclosures, respectively, although animals were never transferred to adjacent enclosures. Trapping was conducted for two consecutive days during each trapping period with traps checked in the morning and reset in the late afternoon. We estimated the abundance of voles and mice at our study sites using minimum number known alive (MNA) due to the high capture probabilities of these species. Because of lower capture probabilities for *Blarina*, we used the number of captures instead of MNA.

Vegetation quantification

Previous studies suggest that small mammals are highly sensitive to plant growth forms and other associated variables such as structural complexity (M'Closkey and Fieldwick 1975; Adler 1985), as this may alter the risk of predation for these organisms (Lima and Dill 1990). Therefore, the percent cover of grasses, forbs, vines, and woody shrubs and seedlings was measured in our old-field study sites in July 1995. As inter-annual changes in vegetation structure in old-fields are relatively minor compared to the dynamics of animal populations living within them, we assumed that a single census during year two would be sufficient to provide the microhabitat data needed for comparisons with three years of trap data. Percent cover was quantified using a 1 m² quadrat placed 0.5 m from each of the 300 trap stations using a constant compass bearing. In addition, the percent

of bare ground and leaf litter cover were recorded as these variables may also influence small mammal utilization of different microhabitats. The effects of macrohabitat-level variation in vegetation structure on small mammal activity were measured by calculating changes in the frequency of capture as a function of distance from the forest edge.

Statistical analysis

We used three years of trapping data to examine how micro- and macrohabitat-level variation in vegetation cover along forest-field edges influenced animal activity at each trap station. Relatively low small mammal abundance throughout the study resulted in the percentage of traps occupied on any given night rarely exceeding 50%. Therefore, we chose to examine how well our vegetation cover variables explained the activity of small mammals at trap stations using binary response variables. We used trap station-specific captures (yes/no) during each trap week for each of the three most abundant small mammals at our study sites as the dependent variables in a series of stepwise logistic regressions (PROC LOGISTIC of SAS Institute 1990). These regressions examined the effects of distance from the forest edge (macrohabitat variation) and vegetation cover (microhabitat variation) on the probability of capture of meadow voles, white-footed mice, and short-tailed shrews. Additional variables describing enclosure-specific density (MNA) of mice and voles for each trap week were added to these models as covariates, thus allowing us to partition the

effects of conspecific animal density from those of the habitat variables quantified. The overall low density of animals observed at our sites during the study suggests that there was little competition for traps between these species and thus, that trap competition played no appreciable role in influencing capture probabilities.

We used logistic regression analysis to fit a parallel-lines regression model based on the cumulative distribution probabilities of the two response categories (p and $1 - p$) and to construct a model of the following form:

$$\begin{aligned}\text{logit}(p) &= \log(p/(1 - p)) \\ &= \alpha + \beta_1 x_1 + \beta_2 x_2 \dots \beta_k x_k,\end{aligned}$$

where α and β are the intercept parameters and vectors of slope parameters, respectively, and there are 1, 2, 3... k explanatory variables. We tested the joint and individual significance of the explanatory variables included in the model using a likelihood ratio Chi-square test statistic. We also computed maximum likelihood estimates of the regression parameters from the combined models using the Iteratively Reweighted Least Squares (IRLS) algorithm. By inverting the expected value of the Hessian matrix for the final iteration, we produced an estimated covariance matrix of the maximum likelihood estimates which was then used in subsequent univariate analyses (Wald Chi-square) examining the strength of individual explanatory variables. Finally, the LOGISTIC procedure was used to generate estimates of the predictive ability of the models generated by comparing all possible pairs of observations in the data set with different responses and comparing the number of concordant versus discordant pairs in an index of rank correlation. Logistic regressions were performed, (1) for all years combined, (2) separately for each year, and (3) under each vole density treatment. The stepwise logistic regression procedure added and/or removed variables from models based on their ability to meet the specified $P = 0.05$ significance level.

A categorical modeling, contingency table, approach (PROC CATMOD; SAS 1990) was used to test for the effects of vole density and for potential interactions between explanatory variables. Again, trap-station specific captures (yes/no) of the three focal species were used as the dependent variables in linear models fit to functions of response frequencies using maximum likelihood estimation of parameters for the analysis of generalized logits. The maximum likelihood estimates were then examined statistically using likelihood ratio Chi-squares (G^2).

Table 1. Results of correlation analysis examining the relationship between the factor scores from the first two principle components generated by a PCA and the original percent cover variables. Relationships are described by Pearson Correlation Coefficients followed by respective P-values.

Variable	Factor 1	Factor 2
Grass	-0.04805	-0.00036
	0.4069	0.9950
Forb	-0.13377	-0.54033
	0.0205	0.0001
Vine	-0.85334	0.44035
	0.0001	0.0001
Wood	0.35150	-0.51641
	0.0001	0.0001
Bare ground	0.78279	0.54829
	0.0001	0.0001
Leaf litter	0.45985	0.37727
	0.0001	0.0001

We used principal components analysis (PCA) to generate a smaller number of orthogonally independent axes explaining the variation in microhabitat cover around trap stations. The factor scores from the first two principal components were then compared to the original cover variables in a correlation analysis in order to interpret the biological significance of each principal component axis. Factor scores from the first two principal components were used in all stepwise logistic regression procedures.

Results

Vegetation data

The first two principal component axes explained a total of 68% of the variation in vegetation cover around trap stations with the first (PC1) and second axes (PC2) accounting for 44% and 24% of this variation, respectively. The factor loadings from the PCA revealed strong negative associations between PC1 and forb and vine cover, while woody cover, bare ground, and leaf litter were all positively associated with this axis (Table 1). These results suggest that PC1 represents a gradient in shrub cover and corresponding bare ground and leaf litter. In contrast, the correlation analysis indicated that PC2 represents a gradient in structural complexity (Table 1). Upright vegeta-

tion, such as forbs and shrub cover, were negatively correlated, while vines, leaf litter, and bare ground were all positively correlated with this axis. Additional regression analyses indicated that neither PC1 ($F_{4,295} = 0.48$, $P = 0.752$) nor PC2 ($F_{4,295} = 1.07$, $P = 0.373$) varied consistently with distance from the forest edge, suggesting that plant community composition and structure were not strongly influenced by proximity to the forest edge at our study sites. Therefore, both the PCA axis scores and distance from the forest edge were entered into subsequent stepwise logistic regression analyses as independent variables.

Overall responses by small mammals

For all three years of trap data combined, our logistic regression model incorporating grid-specific vole density, distance from the forest edge, PC1, and PC2 was highly significant in explaining trap station-specific captures of *Microtus* (model $X^2 = 2048.2$, d.f. = 4, $P = 0.0001$). A model concordance of 82.1% indicated that there was good agreement between model predictions and the data. As expected, the grid-specific vole density variable (MNA) explained the most variation in captures of voles around individual trap stations (Table 2). Thus, an overall higher abundance of voles at a site translates into a higher probability of capture for this species in logistic regression models. After removing the variation explained by the vole density covariate, distance from the forest edge, PC2, and PC1 scores were sequentially the next most important factors to enter into the model (Table 2). The model predicted that the probability of vole capture at a trap station increases rapidly with distance from the forest edge but decreases rapidly with increasing shrub cover and to a lesser extent increasing structural complexity (Figure 2). Furthermore, categorical modeling indicated that distance from the forest edge and shrub cover interacted to determine the probability of vole captures ($X^2 = 12.32$, d.f. = 1, $P = 0.0004$), with vole responses to distance from the forest edge being much stronger in grass-dominated than shrub-dominated sites (Figure 3A). A similar but weaker interaction was observed between the structural complexity of vegetation (PC2 scores) and distance from the forest edge ($X^2 = 6.36$, d.f. = 1, $P = 0.0117$), with lower structural complexity enhancing the probability of vole captures further away from the forest edge.

Grid-specific mouse density (MNA) was the best predictor of mouse captures at the level of the trap

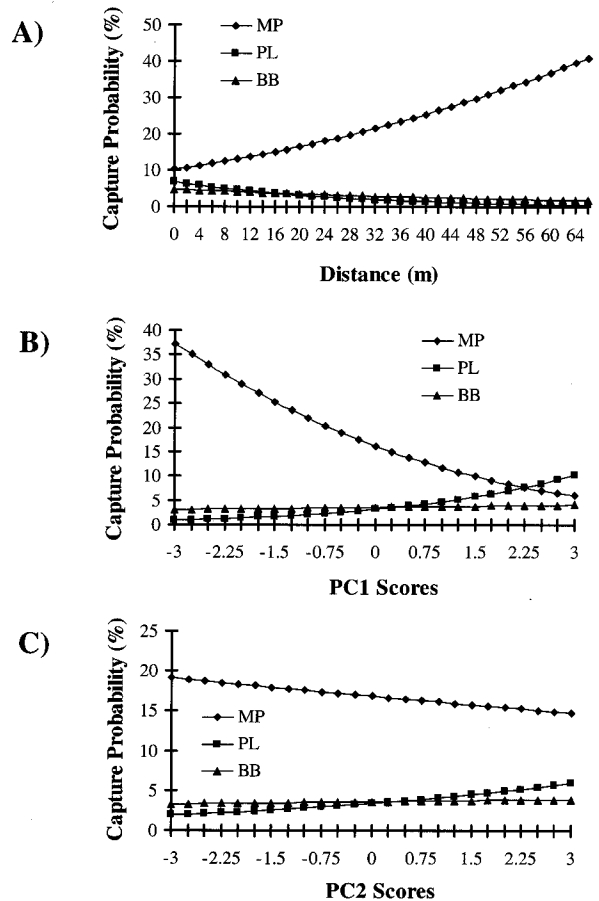


Figure 2. Logistic model predictions of the capture probability of meadow voles (MP), white-footed mice (PL) and short-tailed shrews (BB) as a function of (A) distance from the forest edge (slopes of exponential univariate regression lines were 0.0273, -0.0398 and -0.0155 for voles, mice and shrews, respectively), (B) a gradient in shrub cover reflected in PC1 scores (slopes of -0.3709 , 0.4165 and 0.0485 , respectively) and (C) a gradient in structural complexity reflected in PC2 scores (slopes of -0.0515 , 0.193 and 0.0278 , respectively). Data represent all three years of trap data combined. See the text for an interpretation of PC scores.

station (model $X^2 = 633.4$, d.f. = 1, $P = 0.0001$; Table 2). The probability of capture of white-footed mice at specific trap stations was also significantly affected by distance from the forest edge, the structural complexity of the vegetation, and shrub cover. However, the magnitude of these effects was smaller than for voles (Table 2, Figure 2). The logistic regression model predicted that mouse captures should decrease with distance from the forest edge (Figure 2A). Mouse capture probability was positively correlated with both increasing shrub cover (Figure 2B) and increasing structural complexity (Figure 2C). Distance from the forest edge interacted with both the gradient in shrub

Table 2. Results of stepwise logistic regressions performed separately on captures (yes/no) of each species of small mammal during each trap week for all three years combined. MNAMP and MNAPL are grid-specific estimates of vole and mouse density, respectively, calculated for each trap week; PC1 and PC2 are factor scores corresponding to the first two principle components of the percent cover data (Table 1); DIST = distance from forest edge. Slope parameter estimates are also provided for each variable entered into stepwise logistic regressions. Numbers in parentheses represent the total number of trap stations at which each species was captured, summing over all trap weeks during the study.

Species	Variable	Slope	Chi-square	P-value
<i>M. pennsylvanicus</i> (1871)	MNAMP	0.1937	1405.8	0.0001
	DIST	0.0341	153.0	0.0001
	PC2	-0.1487	22.4	0.0001
	PC1	-0.0746	5.1	0.0234
<i>P. leucopus</i> (383)	MNAPL	0.4451	589.1	0.0001
	DIST	-0.0454	65.6	0.0001
	PC2	0.1357	6.7	0.0099
	PC1	0.1319	5.9	0.0151
<i>B. brevicauda</i> (399)	MNAPL	0.1710	84.2	0.0001
	DIST	-0.0156	10.4	0.0013

cover (PC1; $X^2 = 7.56$, d.f. = 1, $P = 0.0060$; Figure 3B) and grid-specific vole density (PC2; $X^2 = 12.30$, d.f. = 1, $P = 0.0005$). In the absence of shrub cover, the probability of capturing mice declined exponentially with increasing distance from the forest edge; however, when shrub cover was high this distance effect was less consistent (Figure 3B).

In contrast to mice and voles, the micro- and macrohabitat variables quantified performed poorly in predicting captures of short-tailed shrews, with a model concordance of only 59.5%. The only factors significantly affecting the probability of *Blarina* captures at the trap station level were grid-specific mouse density and distance from the forest edge (Table 2). Shrew activity was accentuated by increases in overall mouse density within trapping grids. The response of shrews to distance from the forest edge was similar to, although weaker than, that of mice; shrew activity gradually decreased with distance from the edge (Figure 2A).

Consistency across years

The macrohabitat measure of habitat heterogeneity, distance from the forest edge, was consistently the best predictor of vole captures during each year of the study (Table 3). In contrast, the importance of microhabitat variables appeared to shift between years. Shrub cover was the next most important in predicting vole

captures during the first year, structural complexity most important in the second year, and no microhabitat attributes were important in predicting vole captures in the third year of the study (Table 3). Model concordance varied from 72% to 76% and 92% in years one to three, respectively. At no time did the relationship between the probability of vole captures and the variables graphed in Figure 2 change in a qualitative manner. However, a significant year-by-PC1 interaction indicated that the negative responses of voles to increasing shrub cover was much stronger in year two compared to other years ($X^2 = 16.31$, d.f. = 2, $P = 0.0003$).

Factors best predicting *Peromyscus* activity at the trap station level were extremely variable across years, switching from PC2, to distance from the forest edge, and finally PC1 in years one to three, respectively (Table 3). However, concordance between the predictions of annual logistic regression models and the data collected were generally high, with values of 83%, 79%, and 97% for years one to three, respectively. As with voles, there was a significant change across years in the effect of shrub cover on the probability of capturing mice ($X^2 = 12.11$, d.f. = 2, $P = 0.0023$), with mouse activity decreasing more sharply with declining shrub cover in year two compared to other years. In a separate series of logistic regression analyses, the probability of mouse capture at a trap station was consistently negatively correlated with grid-specific vole

Table 3. Results of stepwise logistic regressions performed separately on capture (yes/no) of each species of small mammal for each trap week during each of three separate years. MP, PL and BB correspond to *M. pennsylvanicus*, *P. leucopus* and *B. brevicauda*, respectively; MNAMP and MNAPL are grid-specific estimates of vole and mouse density respectively, calculated for each trap week; PC1 and PC2 are factor scores corresponding to the first two principle components of the percent cover data (Table 1); DIST = distance from forest edge. Slope parameter estimates are provided for all variables used in stepwise logistic regressions. Numbers in parentheses represent the total number of trap stations at which each species was captured, summed for all trap weeks in a given year.

SPP	Year one				Year two				Year three			
	Variable	Slope	X ²	P-value	Variable	Slope	X ²	P-value	Variable	Slope	X ²	P-value
MP	MNAMP	0.1630	213.2	0.0001	MNAMP	0.1509	458.3	0.0001	MNAMP	0.7605	137.4	0.0001
	DIST	0.0264	28.6	0.0001	DIST	0.0356	110.2	0.0001	DIST	0.0583	14.9	0.0001
	PC2	-0.1274	5.5	0.0195	PC2	-0.1401	13.0	0.0003	(57)			
	(521)				PC1	-0.1465	12.1	0.0005				
				(1293)								
PL	MNAPL	2.3381	22.15	0.0001	MNAPL	0.3241	239.2	0.0001	MNAPL	1.4913	53.7	0.0001
	PC2	0.9135	5.4	0.0203	DIST	-0.0453	62.0	0.0001	PC1	0.5829	3.9	0.0494
	(7)				PC1	0.1429	6.1	0.0138	(18)			
					PC2	0.1089	4.2	0.0394				
				(358)								
BB	-	-	-	-	MNAPL	0.1383	33.7	0.0001	MNAMP	0.0745	10.84	0.0010
	(79)				DIST	-0.0155	6.1	0.0133	MNAPL	0.1509	13.1	0.0003
				(242)				(81)				

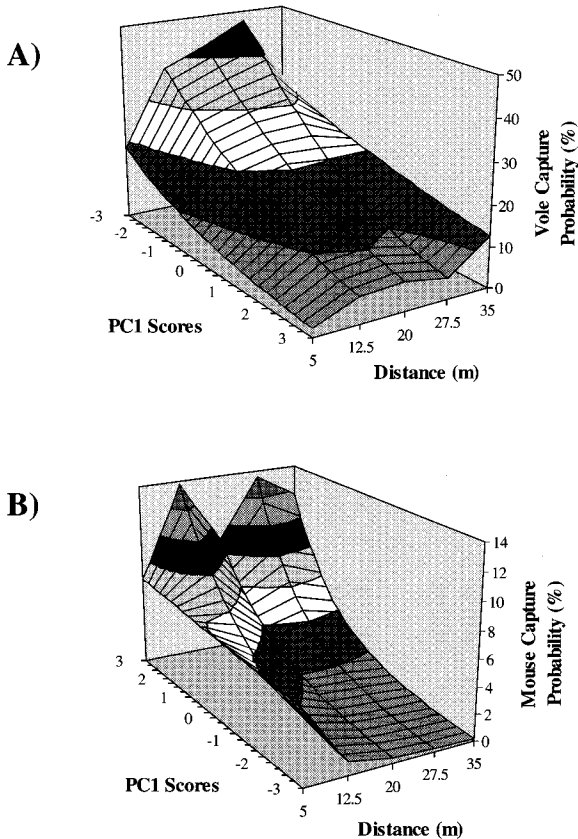


Figure 3. Effects of interactions between distance from the forest edge and a gradient in shrub cover on the probability of capturing (A) voles and (B) mice. Regression lines were calculated separately for each distance from the forest edge using PC1 as the independent variable. The axis for PC1 is reversed for the two species to facilitate observation of trends.

density although this effect was significant only during year two (model slope = -0.0739 , $X^2 = 51.33$, d.f. = 1, $P = 0.0001$).

None of the factors in the logistic regression model for shrew captures during the first year of trapping was significant (Table 3). In general, microhabitat variables did not influence the probability of shrew captures at the trap station level. Grid-specific mouse density and distance from the forest were the only variables predicting shrew captures during year two, while both vole and mouse density were important during year three (Table 3). During year three the probability of capturing shrews was positively related to the grid-specific density of both mice and voles despite the negative association between these two species noted earlier. Concordance values of annual models predicting shrew activity at trap stations were generally low,

ranging from 60% to 43% in years two and three, respectively.

Effects of vole density

The probability of vole captures was significantly different in the high versus the low vole density grids ($X^2 = 18.44$, d.f. = 1, $P = 0.0001$). However, the vole density manipulations had little effect on the relative importance of other factors influencing the probability of capturing voles at a particular trap station (Table 4; concordance of 81% and 84% for models run using grids with high and low vole density treatments, respectively). Distance from the forest edge was consistently the most important factor predicting vole captures, followed by the gradient in shrub cover and the structural complexity of vegetation around trap stations in the high and low vole density treatments, respectively.

The probability of mouse captures also differed significantly between high and low vole density treatments ($X^2 = 11.40$, d.f. = 1, $P = 0.0007$), being higher when vole densities were low. As with voles, distance from the forest edge was consistently the most important factor predicting mouse activity regardless of vole density treatment. However, the relative importance of microhabitat factors shifted across the vole density treatments (Table 4). No microhabitat features were important in explaining mouse captures under high vole conditions but the structural complexity of old-field vegetation appeared important under low vole conditions (Table 4). In addition, there was a significant interaction between PC1 and the vole density treatment ($X^2 = 4.49$, d.f. = 1, $P = 0.0341$). Mice were much more sensitive to the gradient in shrub cover when vole density was high than when it was low (Figure 4). The overall concordance of the models generated to predict mouse captures under different vole density treatments was high, ranging from 87% to 83% in low and high vole density treatments, respectively.

Finally, grid-specific mouse density was consistently a good predictor of shrew activity across both vole density treatments (Table 4), with shrew activity positively related to mouse abundance. The relative importance of micro- and macrohabitat features shifted with the vole density manipulation. Distance was the most important determinant of shrew activity, under the high vole density treatment. In the low vole density treatment, however, the grid-specific density of both mice and voles followed by PC1 entered into

Table 4. Stepwise logistic regression performed separately on capture (yes/no) of each species of small mammal during each trap week for each vole density treatment. Year three was excluded as vole abundance during this year was too low for effective vole density manipulations. Species symbols are as in Table 3. MNAMP and MNAPL are grid-specific estimates of vole and mouse density respectively, calculated for each trap week; PC1 and PC2 are factor scores corresponding to the first two principle components generated by the PCA of the percent cover data; DIST = distance from forest edge. Slope parameter estimates are also provided for each variable entered into stepwise logistic regressions. Numbers in parentheses represent the total number of trap stations in each vole density treatment at which each species was captured, summing over all trap weeks.

Species	High vole density				Low vole density			
	Variable	Slope	X^2	P-value	Variable	Slope	X^2	P-value
MP	MNAMP	0.1392	286.5	0.0001	MNAMP	0.1883	436.8	0.0001
	DIST	0.0310	70.9	0.0001	DIST	0.0348	64.3	0.0001
	PC1	-0.1335	8.6	0.0034	PC2	-0.2569	25.7	0.0001
	(1113)				(758)			
PL	MNAPL	0.4438	253.9	0.0001	MNAPL	0.3880	220.6	0.0001
	DIST	-0.0469	24.4	0.0001	DIST	-0.0470	42.7	0.0001
	PC2				PC2	0.2044	9.25	0.0004
	(145)				(238)			
BB	MNAPL	0.1260	15.0	0.0001	MNAPL	0.1737	37.0	0.0001
	DIST	-0.0317	12.6	0.0004	MNAMP	-0.0729	12.7	0.0004
	PC1				PC1	-0.1898	5.5	0.0187
	(184)				(215)			

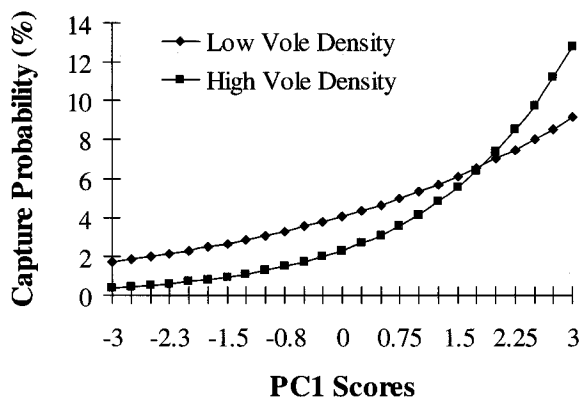


Figure 4. Changes in the probability of capturing mice at a particular trap station as a function of a gradient in shrub cover (PC1) across different vole density treatments. Data are from the first two years of trapping, during which vole abundance was high enough for density manipulation. The more negative the values of PC1, the greater the cover of shrubs around trap stations.

the model for predicting *Blarina* activity (Table 4). In general, the concordance of model predictions of shrew activity with the data was low, ranging from 60% to 65% under the high and low vole density treatments, respectively.

Discussion

Effects of small- and large-scale heterogeneity

Microtus, *Peromyscus*, and *Blarina* differed considerably in the way they responded to environmental heterogeneity along forest-field edges. Both shrub cover and high structural complexity had negative effects on the probability of capturing meadow voles, which agrees with previous studies, suggesting that this species prefers grass-dominated areas (Getz 1985; Grant and Morris 1971). These habitats are used by *Microtus* because they provide both food and cover for these herbivores (Batzli 1985; Getz 1985). Similarly, the negative response of *Microtus* to forest edges corroborates previous findings that suggest that voles avoid forest habitat-types (Grant 1971; Tamarin et al. 1984). However, the fact that distance from the forest edge better predicted vole captures than did variation in vegetation cover at the microhabitat level was unexpected. Previous studies suggest that *Microtus* responds to patchiness at a hierarchy of scales (Ostfeld 1992). In contrast, our results indicate that microhabitat variation may be less important than larger-scale gradients between patch types in determining the distribution of this species. If potential vole predators are

more active along forest edges (Lima and Dill 1990) then avoidance of these areas might be expected as well.

The probability of capturing white-footed mice was enhanced by increased structural complexity and shrub cover, as well as by proximity to the forest edge. Mice are known to prefer areas of high structural complexity, such as shrubs, as these areas presumably provide greater protection from predators (Bowers and Dooley 1993; Manson and Stiles 1998). Although some studies suggest that mice prefer forest edges and interiors (M'Closkey and Feldwick 1975; Nupp and Swihart 1996), Heske (1995) found no significant response of *P. leucopus* or other small and medium-sized mammals to a forest-agricultural field ecotone in southern Illinois. Buckner and Shure (1985) found that densities of white-footed mice increased with distance from forest edges into recent clearcuts. The different responses of *P. leucopus* to these various forest edges suggest that the particular combination of landscape elements may be important in determining the responses of organisms to habitat edges. Distance from the forest edge was typically a better predictor of mouse presence than microhabitat variables in our study. Therefore, studies that focus exclusively on small-scale variation (Dueser and Shugart 1978; M'Closkey and Feldwick 1975) may miss critical habitat features influencing the distribution and abundance of this species.

Overall, the microhabitat variables measured in this study were poor predictors of *Blarina* activity, a result that supports previous contentions that this species is an extreme habitat generalist (Adler 1985; Dueser and Shugart 1978). However, shrews did respond positively to both mouse and vole density, as well as to proximity to the forest edge. Although primarily insectivorous, shrews can prey on young meadow voles inhabiting old-fields (Boonstra et al. 1982; Eadie 1952; Fulk 1972). Shrews may also feed opportunistically on mice if they encounter them. Thus, the positive effect of mouse density on shrew captures may be a response of predator to prey. This interpretation may also explain the modest increase in shrew activity near forest edges, where mice were also most active.

Species interactions and annual variation

The responses of organisms to both micro- and macro-habitat variation along edges may change through time. However, few studies of small mammals

have examined such temporal variation or its causes (Dueser and Shugart 1978; Heske 1995; M'Closkey and Feldwick 1975). One exception is a study by Adler (1985) who examined microhabitat preferences of *M. pennsylvanicus*, *P. leucopus*, and *B. brevicauda* over four years. He found substantial variation in the preferences *Microtus* and *Peromyscus* exhibited over both a seasonal and multi-annual basis, and speculated that these differences were due to density fluctuations and corresponding shifts in the intensity of competition within and between these species. Other studies have also suggested that competition with *Microtus* influences microhabitat use by *P. leucopus* (Grant 1971; M'Closkey and Feldwick 1975; Ostfeld et al. 1997; Pearson 1959), and results from the current study support this conclusion. Mouse capture probability was negatively associated with grid-specific vole density in all three years of the study. Furthermore, the factors that best predicted the distribution of vole activity, the competitive dominant in our old-fields, were consistent through time while factors important in describing mouse and shrew distributions appeared to fluctuate greatly across years. Finally, mice were more sensitive to distance from the forest edge during the year (1995) in which overall vole abundance was greatest (Ostfeld et al. 1997). These findings suggest that competitive interactions, known to be important in determining within-habitat preferences of organisms (Adler 1985; Hallett et al. 1983; Morris 1983), are operational along habitat interfaces as well. These types of interactions may be critically important in determining edge permeability, or the ease with which organisms can move across landscape boundaries in fragmented landscapes (Buechner 1987; Duelli et al. 1990; Stamps et al. 1987).

Small mammals and ecological model systems

While some researchers using artificial landscapes (EMS's) have focused on the responses of individual species (Andreasson et al. 1996; Wiens et al. 1993; Wolff et al. 1997), others have taken a more community-based approach (Bowers and Dooley 1993; Diffendorfer et al. 1995). We found that *Microtus* was repelled by, *Peromyscus* attracted to, and *Blarina* relatively unaffected by proximity to forest-field edges. Small mammals are clearly capable of exhibiting a wide range of responses to natural habitat boundaries (see also Lidicker 1998; Lidicker and Koenig 1996; Mills 1996; Seamon and Adler 1996). Combined with the evidence from this study that the

responses by *Peromyscus* and *Blarina* to forest-field edges were contingent upon vole and mouse density, respectively, our results suggest that EMS's using a community-based approach may provide greater insights into the factors influencing animal responses to habitat edges.

A central issue confronting the EMS approach, which uses artificial landscapes, is whether these types of landscapes can account for interactions between factors operating at larger spatial scales (Bowers and Matter 1997). Our results indicate that the capture probabilities of mice, voles, and shrews are better predicted by macrohabitat features than by variation in the microhabitat around individual trap stations. In addition, distance from the forest edge and the gradient in shrub cover interacted strongly to determine the probability of capturing mice and voles in this study. These findings suggest that EMS's should be designed to test for interactions between variables at various spatial scales with special emphasis on larger-scale features.

An additional concern with the EMS approach is whether the edges between mown and unmown patches simulate the edges between habitat patches in natural landscapes. Substantial variation in the responses of animals to the edges of patches within experimentally created landscapes makes comparisons among studies difficult to interpret. For example, voles have been observed to respond in a positive (Berg 1995; Bowers et al. 1996; Robinson et al. 1992), negative (Bowers and Dooley 1993; Mills 1996; Lidicker 1998), or neutral manner (Harper et al. 1993) to edges in artificially fragmented environments. Species-specific differences in behavior and the community context in which these studies are conducted (evidence from this study), as well as the metric used to quantify edge effects may account for some of this variability. Comparing the responses of organisms in EMS's and natural systems will be important in predicting the effects of edges on the population and community dynamics of organisms.

Plant-animal interactions and edge effects

This study suggests that the activity of small mammal consumers, and thus their impacts on old-field succession, are mediated by gradients along forest-field edges. Mice were more active under shrubs and near forest edge, sites that experience the most intense seed predation (Ostfeld et al. 1997). Similarly, vole activity was found to increase with increasing distance

from the forest edge and with decreasing shrub cover. Seedling predation studies revealed highest seedling predation rates by voles further out into the field and in areas dominated by grass (Ostfeld et al. 1997). Growing evidence from this research program and others (Bryant et al. 1991; Ostfeld et al. 1997; Pastor et al. 1993; Turner et al. 1994) suggests that a dynamic interaction exists between mammalian consumers and plant communities. Understanding the factors influencing patterns of herbivory by small mammals on tree invasion in old-fields may allow researchers to better predict patterns of succession in these habitats (Manson et al. 1998; Ostfeld et al. 1998). Increased understanding of the factors influencing changes in forest edges may, in turn, allow better predictions of the long-term effects of these edges on animals living in fragmented landscapes.

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