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Temporal consistency in the spatial pattern of seed predation across a forest – old field edge

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Abstract

Seed predation is an important factor in determining the rate of tree establishment in abandoned agricultural land. Edges, through altered habitat use by small mammals, may influence the spatial pattern of forest regeneration in these successional sites. To determine the spatial pattern of seed predation across a forest-old field edge, we used a grid that began 30 m inside the forest and extended 60 m into the old field. Seed stations were placed at regular 10-m intervals and were monitored for removal of *Acer rubrum* seed for 50 d. This design was repeated over four years (1995–1998). Small mammal trapping was conducted in the final year of the study to determine the spatial pattern of seed predators within the site. Removal rates varied among the four years of the study with years of high and low removal rates. However, the spatial pattern of seed removal rate was similar in all years. Final survival ranged from 0.7–15.5% of seeds, with lower final survival in years with faster rates of seed removal (1996 and 1998). Seed removal rates and rates of discovery were greatest at the forest edge and decreased with distance into the old field. The number of seeds surviving to the end of the experiment also varied across the edge gradient, with highest survival at greater distances into the old field in low predation years. Seed removal rate covaried with spatial pattern of *Peromyscus leucopus* captures within the site. Seed removal and discovery was also higher under the exotic shrub *Rosa multiflora*, which may have provided cover for foraging seed predators. These indirect effects of edges on plant communities can potentially alter the rate and spatial pattern of tree invasion into disturbed lands and illustrate the importance of understanding plant-animal interactions in the context of habitat fragmentation.

Introduction

Habitat fragmentation is an inevitable consequence of development. While the direct effects of fragmentation are primarily due to habitat loss, more subtle effects arise from the creation of edges in the landscape (Forman 1995 Murcia 1995). To understand vegetation dynamics in anthropogenically fragmented landscapes, it is necessary to discern the mechanisms by which edges affect plant community development.

Factors that affect the invasion and establishment of woody plants are especially important in abandoned agricultural land, influencing long-term community structure (Myster and Pickett 1993). In a hierarchical view of succession (Pickett et al. 1987), seed dispersal into a site determines the potential composition of the invading community, but post-dispersal interactions, such as seed predation, determine which species from the seed rain will then become established (DeSteven 1991 Gill and Marks 1991 Manson et al. 1998). As edges alter habitat use by seed predators (Cummings and Vessey 1994 Notman et al. 1996 Ostfeld et al. 1997 Manson and Stiles 1998 McCormick and Meiners 2000), edges may indirectly affect tree invasion dynamics by altering the spatial pattern of seed predation (Murcia 1995 Ostfeld et al. 1999).

Much work has been done to identify the forces that influence seed predation. Studies have identified primary seed predators in old fields (Gill and Marks 1991 Whelan et al. 1991 Bowers and Dooley 1993) and investigated many of the variables that can affect the behavior of these seed predators. These variables include seed density (Webb and Willson 1985 Willson and Whelan 1990 Manson et al. 1998), distance from parent tree (Webb and Willson 1985 Schupp 1988a Bustamante and Simonetti 2000), microhabitat (Whelan et al. 1991 Bowers and Dooley 1993 Manson and Stiles 1998), macrohabitat (forest vs. field or treefall gap; Webb and Willson (1985) and Schupp (1988a), Willson and Whelan (1990), Whelan et al. (1991)), seed species (Willson and Whelan 1990 Meiners and Stiles 1997 Ostfeld et al. 1997 Manson and Stiles 1998), season of dispersal (Willson and Whelan 1990 McCormick and Meiners 2000) and interspecific interactions among predators (Ostfeld et al. 1997 Manson et al. 1998).

However, relatively little work has been done on the spatially explicit effect of edges on seed predation (but see Ostfeld et al. (1997)). Those studies that do address the effects of edges on seed predation in fragmented landscapes have been relatively short term (1–2 yr.) and generally have examined edges at only a few spatial positions (e.g. edge vs. non-edge; but see Ostfeld et al. (1997)). Because of the high spatial and temporal variation characteristic of seed predation studies (Mittlebach and Gross 1984 Webb and Willson 1985 Willson and Whelan 1990 Gill and Marks 1991 Whelan et al. 1991 Ostfeld et al. 1997 Russell and Schupp 1998), we utilized a gradient approach over multiple years to examine the dynamics of seed predation across a forest – old field edge. To our knowledge, no other study has investigated the effect of distance from the edge over more of the potential seed dispersal range in a habitat.

This study was designed to determine the spatial and temporal influences of a forest -old field ecotone on seed predation intensity. We experimentally assessed seed predation rates across the edge gradient in each of four years to address the following questions: 1) How does the presence of a forest edge influence the spatial pattern of seed predation; and 2) Does the spatial pattern of seed predation vary with time? To verify the role of mammals as seed predators in this system, we conducted small-mammal trapping in the final year of the study. The purpose of this research was to improve our understanding of the indirect influences of habitat fragmentation on tree regeneration.

Methods

Study area and species description

The study site was at the Hutcheson Memorial Forest Center (HMFC), located approximately 10 km east of New Brunswick, New Jersey, USA (40°30′ N, 74°34′ W). The site consisted of an old field (last tilled and farmed in 1986) and the adjacent second growth forest. The forest edge used in this study faced southeast. Herbaceous cover in the field was dominated by several species of *Solidago*, *Aster* spp. and *Fragaria virginiana* Duchesne and contained scattered trees and shrubs including a few large *Juniperus virginiana* L trees. (Meiners and Pickett 1999). *Rosa multiflora* Thunb. is the dominant shrub across the site. The forest was approximately 50 yr old and dominated by *Fraxinus americana* L., *Acer rubrum* L. and *Quercus palustris* Muenchh. with a few much larger and older *Q. rubra* L. near the edge. A mixed oak old growth forest was located beyond the second growth forest. Understory vegetation was very sparse. The vegetation at the forest edge was dominated by exotic species, largely *Rosa multiflora* and *Lonicera japonica* Thunb., and the overhanging forest canopy. Nomenclature follows Gleason and Cronquist (1991).

Based on capture data at HMFC, the numerically dominant predators of small woody plant seeds are white-footed mice, *Peromyscus leucopus* Rafinesque (Pearson 1959 Myster and Pickett 1993 Manson and Stiles 1998), which are abundant in both old fields and forests of northeastern North America (Pearson 1959 Cummings and Vessey 1994 Manson and Stiles 1998). *P. leucopus* prefer to forage in areas of high structural complexity, particularly under woody cover (McMillan and Kaufman 1995 Manson and Stiles 1998), which provides protection from avian and mammalian predators. Selective use of habitat by *P. leucopus* is thought to be the dominant factor that determines the spatial pattern of seed predation at HMFC (Manson and Stiles 1998).

Other potential seed predators observed at HMFC include gray squirrels (*Sciurus carolinensis*), southern flying squirrel (*Glaucomys volans*), and eastern chipmunk (*Tamias striatus*). These species are largely restricted to edge and forest habitat and were never observed foraging in the field. Meadow voles (*Micro-*

tus pennsylvanicus) are present in the fields of HMFC and may also consume seeds (Lindroth and Batzli 1984) or indirectly affect seed predation via competition with *P. leucopus* (Ostfeld et al. (1997, 1999) Manson et al. 1998). Avian seed predators include white-throated sparrows (*Zonotrichia albicollis*), song sparrows (*Melospiza melodia*) and house finches (*Carpodacus mexicanus*). Seed-eating birds in the site appear to forage largely on herbaceous species (S. J. Meiners, pers. obs.; Webb and Willson (1985) and Whelan et al. (1991)).

We used *Acer rubrum* as a test species for seed predation intensity. *Acer rubrum* is a common, wind-dispersed (fresh seed mass 8–10 mg) tree species in old field succession (Buell et al. 1971 Pickett 1982) and a dominant species within second growth forest at HMFC. For this reason, predators at HMFC have previous experience with seeds of this species. While *A. rubrum* is a spring-dispersing species, we used it as a prey item in the fall. Seeds of this species can be found on the ground and under leaf litter in the fall and are readily taken by predators at that time (Myster and Pickett 1993). The phenological difference allowed us to clearly identify experimental seeds and to follow the fate of those seeds without contamination from naturally dispersing seeds. The use of a spring dispersing species as an indicator of predator activity in the fall is equivalent to using a novel food item in seed or nest predation studies (Wong et al. 1998). However, our prey item has the benefit of being familiar to resident predators.

Previous work done at this site (Manson and Stiles 1998) found no differences in the spatial pattern of seed predation among seed species at HMFC and concluded that microhabitat preferences of *P. leucopus* determined local predation intensity rather than preferential foraging on individual seed species. For this reason, predation on *Acer rubrum* seed should act as an unbiased indicator of predator foraging activity in this habitat. We used predation on *A. rubrum* only as an indicator for seed predator activity in general, not as indicative of the population biology of this tree species.

Experimental design

In a one-hectare portion of the site, a 90 × 90 m grid was set up across the forest-old field edge. The grid began 30 m inside the forest and extended 60 m into the old field. Within this grid, one hundred 1 m^2 plots were arranged in a regular pattern at 10 m intervals. The boundary of the experimental forest with old growth forest at HMFC occurred at approximately 60 m from the study edge, limiting the depth of the grid into the forest. The edge was defined as a straight line that approximated the position of the most recent plow line. This spatial range should encompass the majority of the seed shadow for wind-dispersed seeds produced within the forested portion of the site (Greene and Johnson 1996 Hughes and Fahey 1988 Hughes and Bechtel 1997) and as such, should illustrate the spatial effects of seed predators on the vast majority of tree seeds.

Within each plot, a 90 mm petri dish filled with 15 *Acer rubrum* samaras was placed, for a total of 1500 seeds. Seed densities much higher than those presented in this study did not affect fall removal rates of *A. rubrum* at HMFC (Myster and Pickett 1993), so initial seed density within the dishes should not affect results. A hole was drilled in the center of each dish to allow for drainage. This design allowed access by the entire seed predator guild. Seeds were collected in the previous spring and stored under refrigeration until the experiment. Seeds stored in this way remain viable, even after storage for longer than a year (S. J. Meiners, pers. obs.). Seeds were sorted before deployment to remove undeveloped or damaged seeds. The experiment was initiated in late October of each year, 1995 – 1998. Dishes were monitored on days 5, 10, 15, 20, 30, 40, and 50 to determine seed removal.

While most studies only document seed removal, we also recorded the number of empty samaras and partially eaten seeds in the dish and surrounding area to verify predator activity. To minimize seed loss from wind, rain and animal activity, a 30 cm radius around each dish was searched for missing seeds, and any located seed replaced. Undamaged seeds were generally found directly next to the dish, while empty samaras moved much greater distances. For this reason, number of empty samaras and partially eaten seeds is a conservative measure of seeds eaten at the dishes. All analyses presented here use seed removal data. Seeds not found as remains or located within 30 cm of the dish were assumed to have been removed by seed predators, which often cache seeds during the fall. A small number of seeds may have been lost due to abiotic factors, but this did not appear to be problematic. At the end of the experiment in each year, cut tests were done on all remaining seeds to determine viability. This ensured that predator rejection was not based on seed quality (Notman et al. 1996 Kollman et al. 1998). The percent cover of all species present in each 1 m^2 plot was recorded in 1996 with the aid of a sampling frame. This data is reported in detail elsewhere (Meiners and Pickett 1999). For this analysis, we use only percent cover of the dominant shrub, *Rosa multiflora*.

Cox regression analyses (PROC PHREG; SAS Institute Inc. (1989)) were used to compare seed removal rates among years. Pairwise comparisons between years were made with Bonferroni-adjusted significance criteria for multiple comparisons. Spatial variation in seed removal across the edge gradient was analyzed with Cox regression using the exact protocol to handle tied data (PROC PHREG; SAS Institute Inc. (1989)). Survival model parameter estimates and standard errors from the Cox regression were calculated for each distance class. These coefficients were calculated relative to seeds at the edge (distance = 0). The number of seeds surviving to the end of the experiment (day 50) was analyzed with log-linear analysis (Proc CATMOD; SAS Institute Inc. (1989)), which allows analyses similar to ANOVA to be performed on binary (*e.g.* survival: yes/no) data.

To compare the spatial pattern of seed removal among years, the average number of days seeds survived in each dish (mean survival time) was calculated for each year. We used the last census that a seed was located within a dish to calculate this survival time in days. Similarity between the spatial patterns of seed removal among years and between mean survival time and final survival were analyzed with non-parametric Spearman rank-order correlations of plot data (PROC CORR; SAS Institute Inc. (1989)).

Seed predation data were also separated into seed encounter and exploitation rates (Hulme 1994 Hulme and Borelli 1999), which represent two distinct phases in predator activity. Encounter rates were defined as the time until the first seed was removed from a dish, while exploitation rates were determined by the rate at which seeds were removed from dishes following encounter. Cox regressions of seed encounter and exploitation were conducted for data pooled across all four years of the experiment to determine the overall edge response. Survival model parameter estimates and standard errors from the Cox regression were calculated for each distance class. In the final year of the experiment, small mammal populations were censused to test for a relationship between small mammal activity and seed removal. Previous work in this site (Manson and Stiles 1998), found that *Peromyscus leucopus* was the dominant seed predator. For this reason, trapping efforts focused on the spatial pattern of this species. In late November and early December 1998, two small (5.1 × 6.4 × 15.2 cm) Sherman traps were set at each grid marker and baited with crimped oats and sunflower seeds. Pressed cotton bedding material was included on cold nights to prevent hypothermia. Traps were set at dusk and checked within 4 hours and at dawn. Animals were tagged with monel-type eartags for individual identification. All animals captured in the evening trap check were held for unrelated behavioral experiments and released in the morning at the point of capture. Animals captured in the morning were immediately released. An initial trapping session of 3 consecutive nights was followed by 2 consecutive nights of trapping 10 days later for a total of 1000 trap nights. Shrub cover is known to affect *P. leucopus* activity and seed predation rates, therefore the cover of the dominant shrub in the site, *Rosa multiflora*, was included in the analysis of this experiment. The influences of *R. multiflora* cover and small mammal captures on seed removal rate in 1998 were analyzed with Cox regressions. The relationship between *P. leucopus* capture and *R. multiflora* cover was analyzed with a Spearman rank-order correlation (PROC CORR; SAS Institute Inc. (1989)).

Table 1. Summary of seed predation over the four years of study. All numbers are percents across the entire site. Seeds are considered eaten if empty samaras or damaged seeds are found in or around the seed dish. Animal activity is recorded as at least one seed being found eaten at a dish. Seed viability assessed by a cut test at the termination of the experiment.

	1995	1996	1997	1998
Final % remaining (day 50)	13.4	3.0	15.5	0.7
% eaten (of seed removed)	39.7	52.2	59.6	74.7
Animal activity (% of dishes)	83	90	86	99
% viable (day 50)	99.5	100	99.1	90

Results

Based on empty samaras and damaged seeds recovered, the proportion of seeds that were verified as eaten ranged from 39–74% of all removed seeds (Table 1). We observed these signs of predation in 83–99% of dishes during the four years studied. The vast majority of the surviving seeds remained viable at the end of the study in all years.

Table 2. Effect of distance from the forest edge on the seed removal rate and number of seeds surviving to the end of the experiment for the four years of the study. Results are from Cox regression for removal rate (Wald χ^2, 9 df) and log-linear analysis maximum likelihood estimates for final survival (df in parentheses).

	Removal rate		Final survival	
Year	Wald χ^2	P	χ^2	P
1995	273.3	< 0.0001	$74.82_{(8)}$	< 0.0001
1996	364.8	< 0.0001	$39.08_{(5)}$	< 0.0001
1997	498.3	< 0.0001	$66.66_{(7)}$	< 0.0001
1998	303.9	< 0.0001	$8.14_{(3)}$	0.0433

Seed removal rate varied across the edge gradient in all four years of the study (Table 2) and was generally highest at the forest edge (Figure 1). Removal rate generally decreased with distance into both the forest and field and this pattern was consistent in all four years. Seed survival to the end of the experiment was generally highest at greater distances into the old field but varied somewhat inter-annually (Figure 2). Edge effects on final survival were significant in all four years of the study (Table 2).

The spatial pattern of seed removal was consistent among years of the study, with mean survival time at each position positively correlated over all four years (Table 3). Similarly, final survival was also positively correlated over the four years of the study, but only 1 of 6 correlations were significant at an overall $P < 0.05$ after Bonferroni correction. Mean survival time was also positively correlated with final number of seeds surviving in all years of the study ($r_S = 0.26$–0.81; $P < 0.01$; all years).

Risk of seed encounter and exploitation differed across the edge gradient (Figure 3). Risk ratios for encounter were relatively constant 20 to 60 m into the field and lower than seeds located closer to the edge and inside the forest. This variation in encounter rates across the edge was significant (Wald $\chi^2 = 33.99$; df = 9; $P < 0.0001$). Seed exploitation rates also varied significantly across the edge (Wald $\chi^2 = 840.66$; df = 9; $P < 0.0001$). Risk of exploitation in the forest was less than 50% that of seeds at the edge. Risk decreased from the edge out into the old field.

Seed removal rates across the entire site differed among the four years of the study (Figure 4). Final survival ranged from 0.7–15.5% of seeds with lower survival in years with faster rates of seed removal (1996 & 1998). Seed survival curves separated into two groups, with 1997 and 1995 not significantly different from each other, and 1996 and 1998 not differing significantly (Table 4). Survival curves differed significantly between these two groups.

Twenty-five *Peromyscus leucopus* were captured 123 times in 1000 trap No other potential seed predators were captured despite trapping protocols suitable for capture of *Tamias striatus, Microtus pennsylanicus* and *Glaucomys volans*. *Peromyscus leucopus* trapping success was highest at the edge (45 captures) generally decreasing with distance from the edge into the field and forest (Figure 1). The total number of animals captured per seed station varied significantly across the edge gradient (Kruskal-Wallis $\chi^2 = 30.76$; df = 9; $P = 0.0003$). Seed survival in 1998 was negatively associated with both the number of *P. leucopus* captures (Wald $\chi^2 = 43.03$; df = 1; $P < 0.0001$; Risk ratio per capture = 1.124) and the cover of *Rosa multiflora* (Wald $\chi^2 = 138.7$; df = 1; $P < 0.0001$; Risk ratio per % cover = 1.014). Risk of seed encounter was increased by *R. multiflora* cover (Wald $\chi^2 = 4.56$; $P = 0.0327$) but was unrelated to mouse captures (Wald $\chi^2 = 0.21$; df = 1; $P > 0.05$). Seed exploitation was increased by both *R. multiflora* cover (Wald $\chi^2 = 57.21$; df = 1; $P < 0.0001$), and mouse captures (Wald $\chi^2 = 83.93$; df = 1; $P < 0.0001$). Mouse captures were positively associated with *R. multiflora* cover ($r_S = 0.32$; $P = 0.0011$).

Discussion

Spatial variation – the edge response

Functional responses of seed predators to edges have been studied in several forest types. However, most of these studies have used only a few spatial positions to test for edge effects, making interpretation of results difficult. In tropical forests there is evidence that seed predation is higher at edges for some species (Notman et al. 1996). However, other species show no edge effects (Notman et al. 1996 Holl and Lulow 1997 Wong et al. 1998 Duncan and Duncan 2000) and some species have higher seed predation in forest interior habitat than at edges (Restrepo and Vargas 1999). In old fields of eastern North America, seed predation by small mammals appears to be higher close to forest edges for some tree species (Myster and Pickett 1993 Ostfeld et al. 1997 Manson et al. 1998) while predation in forest fragments may be lower at the edge (Sork 1983). Some tree species

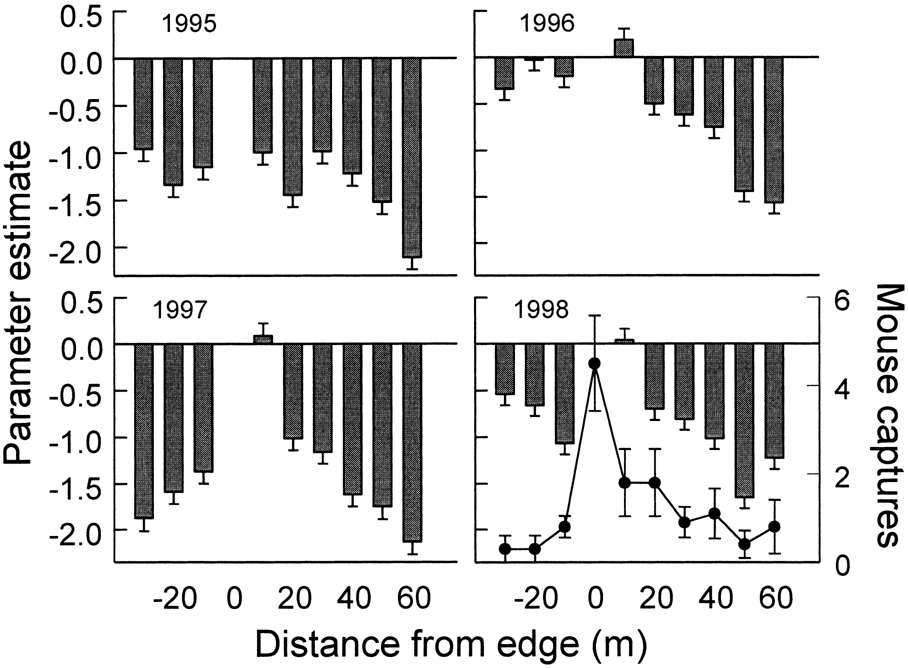

Figure 1. Spatial variation in seed removal with distance from the forest edge over the four years of the experiment. Values presented are parameter estimates from Cox regression for seed removal at each distance class (compared to distance = 0). Positive parameter estimates indicate increases in seed removal rate relative to seeds at the edge; negative parameter estimates represent decreases in seed removal rate. The mean number of captures of *Peromyscus leucopus* per plot is also shown for 1998. Distances relative to the forest edge are indicated as negative for positions in the forest and positive for positions in the field (the edge is distance 0). Bars represent mean ± 1 SE for the plots at each distance interval.

show no edge responses in seed predation (Myster and Pickett 1993).

Because studies employ different techniques, edge definitions, and perspectives (i.e. forest fragment vs. disturbed side of the edge), generalizations are difficult. Edge responses are perhaps best understood as a large-scale gradient response rather than through few discrete spatial positions. For example, Myster and Pickett (1993) studied *Acer rubrum* seed predation at HMFC and found no differences between seeds placed at the edge and 15 m from the edge. Based on the present study, seeds placed 15 m into the old field would have high seed predation rates, comparable to those of the edge. Studies utilizing only a few spatial positions or a limited spatial range may miss edge effects in communities with strong edge influences.

The results from the present research are qualitatively consistent with Ostfeld et al. (1997), who measured seed predation at −5, 0, 5, 10 and 20 m from the forest/field edge. Both studies showed higher seed survival in the forest interior and far ($\geqslant$ 20 m) into the field. In contrast to the present study, which generally found the highest seed removal at the edge, Ostfeld et al. (1997) found higher seed predation 5 and 10 m into the field than at the edge. This discrepancy may be due to microhabitat differences such as those caused by *R. multiflora*, which is concentrated at the edge in our study site (Meiners and Pickett 1999). The edge effect observed by Ostfeld et al. disappeared when mouse density markedly increased in the second year of their study. This is also consistent with the pattern of final seed survival found in the present study, which appeared and disappeared in alternate years (Figure 2). However, the spatial pattern of removal rate was consistent among years in the present study. Ostfeld et al. (1997) focused on only a small fraction of the potential dispersal distance for wind-dispersed seeds at edges (Greene and Johnson 1996 Hughes and Fahey 1988 Hughes and Bechtel 1997). By monitoring seed removal at greater distances into the old field, we show that seed survival probabilities continue to increase up to 60 m from the edge. We find that the strongest influences of edges on seed predation occur at greater distances than have been previously studied.

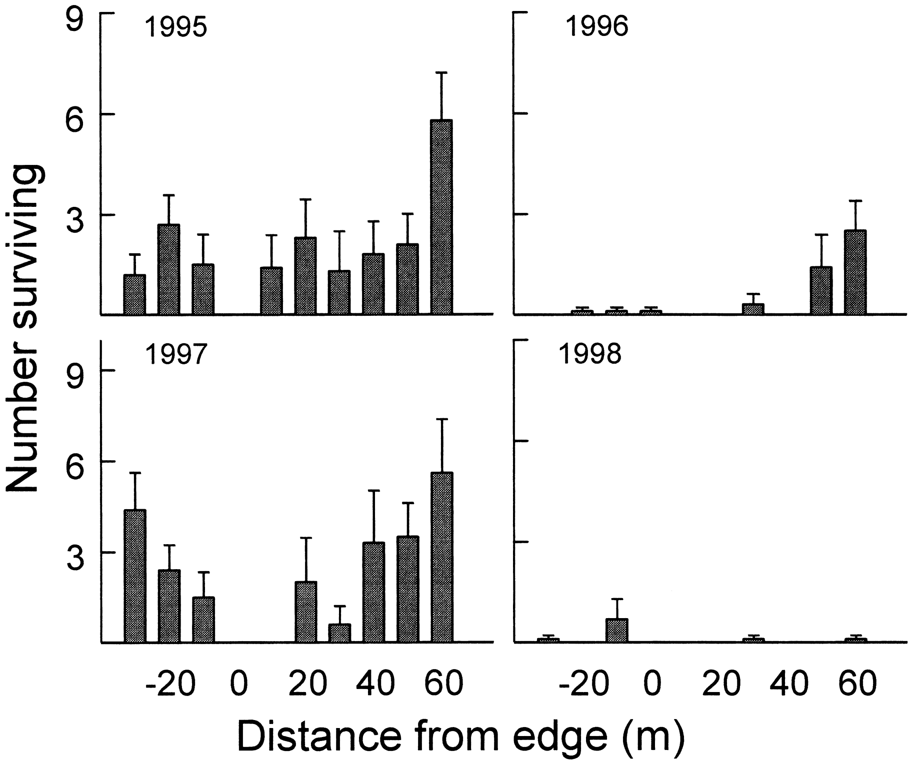

Figure 2. Spatial variation in final survival with distance from the forest edge over the four years of the experiment. Distances from the edge are as in Fig 1. Bars represent mean ± 1 SE for the plots at each distance interval.

Table 3. Temporal consistency of mean survival time and final number of seeds surviving among the four years of the study. Values presented are Spearman rank-sum correlation coefficients. Bonferroni-adjusted $P_{0.05}$ is $P < 0.0034$.

	Mean survival time		Final survival	
Years	r_S	*P*	r_S	*P*
95–96	0.36	0.0002	0.18	0.0771
95–97	0.51	0.0001	0.38	0.0001
95–98	0.33	0.0009	0.16	0.1087
96–97	0.38	0.0001	0.25	0.0109
96–98	0.39	0.0001	0.05	0.5969
97–98	0.57	0.0001	0.19	0.0611

Inter-annual variation in predation

Seed survival varied an order of magnitude (0.7–15.5%) over the four years of the study. This inter-annual variation in seed survival is characteristic of seed predation studies conducted in multiple years (Schupp 1988a Willson and Whelan 1990 Maron and Simms 1997). Habitat differences in predation rates may also show variation among years (Willson and Whelan 1990 Whelan et al. 1991 Ostfeld et al. 1999). The present study found overall similarity in the spatial pattern of seed removal rate over the four years tested. Like Kollman et al. (1998), we found that yearly differences in seed predation rate are small when compared with consistent differences in preferred foraging habitat. The temporally and spatially consistent pattern of seed predation represents a continuous limitation on tree establishment within this site.

Fluctuation in the population size of *P. leucopus* may have been responsible for differences among years in seed removal rate, with years of higher *Peromyscus leucopus* population density having higher rates of seed predation. Populations of *P. leucopus* have been found to fluctuate in response to mast seeding by *Quercus* spp. (Wolff 1996). *Quercus* at HMFC had mast years in 1995 and 1997 (S. J. Meiners, Personal observation). The effects of masting can be seen in the increased rate of predation in 1996 and 1998, when small mammal populations would have been higher (Crawley 1992 Crawley and Long 1995 Wolff 1996). *Peromyscus leucopus* population density was very low in another portion of HMFC in 1997 (K. LoGiudice, Unpublished data), supporting population

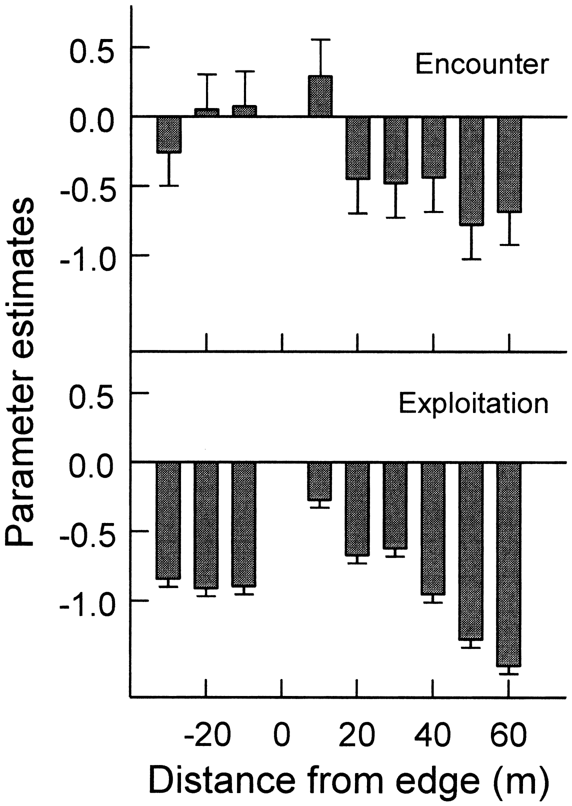

Figure 3. Spatial variation in seed encounter and exploitation with distance from the forest edge. Data pooled over the four years of the experiment. Values presented are parameter estimates from Cox regression for each distance class (relative to distance = 0). Positive parameter estimates indicate increases in risk relative to seeds at the edge; negative parameter estimates represent decreases risk. Distances from the edge and parameter estimates are as in Fig 1. Bars represent mean ± 1 SE for the plots at each distance interval.

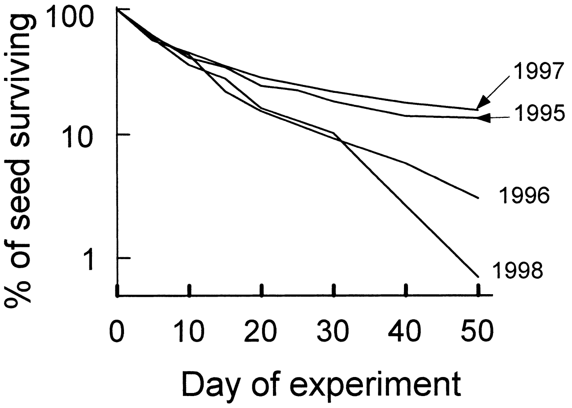

Figure 4. Inter-annual variation in seed removal across the entire site. Survival curves for each year plotted on a log scale.

fluctuations as the source of inter-annual variation in predation rates. Alternatively, interactions with fluctuating populations of *Microtus pennsylvanicus* may have displaced *P. leucopus* into forest interiors (Ostfeld et al. 1997).

Table 4. Pairwise comparisons of survival curves for the four years of the study. Bonferroni-adjusted $P_{0.05}$ is $P < 0.0034$.

Years	Wald χ^2	df	P
95–96	50.73	1	< 0.0001
95–97	3.18	1	0.0744
95–98	71.68	1	< 0.0001
96–97	78.65	1	< 0.0001
96–98	1.84	1	0.1744
97–98	104.11	1	< 0.0001

Despite inter-annual variation in predation intensity, the spatial pattern of removal rate was consistent among years. This result was unexpected, as higher population densities often push subordinate animals into non-preferred habitats (Linzey 1989). For *P. leucopus* this would mean displacement into the more open, herbaceous-dominated portions of the field where seed survival was highest. The inter-annual variation in other studies may be the result of focusing on small-scale spatial structure within plant communities, which reflects habitat utilization by individual animals (Whelan et al. 1991 Hulme 1994). By focusing on responses to landscape features such as edges, we may have been better able to detect spatial patterns than studies focusing on small-scale vegetation characteristics, which may only be important once landscape-level factors are accounted for (Bowers and Dooley 1993 Manson et al. 1999).

Seed predation and tree regeneration

The spatial pattern of seed predation can have strong implications for tree regeneration within a site. Seed dispersal from edges usually results in a negative exponential distribution pattern, with the greatest density of seeds occurring closest to the forest edge (Greene and Johnson 1996 Hughes and Fahey 1988 Hughes and Bechtel 1997). The edge was also the location of the greatest seed predation pressure in our study. Increased seed removal at edges would act to slow the establishment of trees where the majority of seeds were dispersed (Bustamante and Simonetti 2000). Janzen (1970) proposed a similar mechanism for distance- or density-responsive predation to regulate the spatial pattern of tree regeneration in the tropics. *Peromyscus leucopus* have been found to forage on seeds in a distance-responsive manner within old fields (Manson et al. 1998), leading to higher rates of predation near seed sources. In this study, the forest would serve as the source for the majority of seeds within the site, potentially generating the spatial patterning in predation rates observed. While the number of seeds dispersed at the edge may be sufficient to outweigh seed loss to predation (Hubbell 1980), seed predation can be sufficient to uncouple seed dispersal patterns from establishment patterns (Houle 1992 Herrera et al. 1994). At greater distances into the old field, where wind-dispersed seeds arrive in low density (Greene and Johnson 1996 Hughes and Fahey 1988 Hughes and Bechtel 1997), seed survival appears to be much more likely.

Temporal consistency in the spatial pattern of seed predation has the potential to influence the spatial structure and composition of regenerating forests. While fluctuations in the population density of seed predators may allow temporal windows for tree invasion to occur (Ostfeld et al. 1999), the results of this study show that the spatial pattern of seed removal is not expected to vary among years. Because seed predators often preferentially forage on some species and avoid others (Hulme 1993 Meiners and Stiles 1997 Ostfeld et al. 1997 Hulme and Borelli 1999), predation rates are expected to vary among species. A consistent foraging pattern and seed preference may generate differential tree establishment across an edge gradient with preferred species only able to establish at microsites where predation pressure is low. Such zonation in tree regeneration across edges has been noted in several studies (Wales 1972 Whitney and Runkle 1981 Chen et al. 1992), but has been explained by the physiological requirements of species. Herbivores clearly have the potential to cause differential establishment across edge gradients (Louda 1989 Cadenasso and Pickett 2000) and should be explored further.

Removal rate vs. final survival

The majority of seed predation studies employ very short-term experiments to assess relative predation risk among species, habitats, or other experimental treatments (Hulme 1993). Relatively few use long-term seed exposure to assess predation risk (but see Schupp (1988a) and Ostfeld et al. (1997)). The ultimate goal of these studies, from a phytocentric point of view, is to determine the likelihood of a seed surviving to germination and becoming part of the local plant community (Hulme (1993, 1996)). For this reason, final survivorship of seeds is the parameter of interest.

By monitoring seed removal more frequently than other studies, we were able to distinguish between the rate of seed removal and total seed removal (Figure 1 vs. Figure 2). This is not an irrelevant distinction, as seed predation studies typically do not present seeds in a natural setting, where seeds often quickly become incorporated into the litter (but see Schupp (1988b)). Burial in soil or under litter greatly reduces seed predation by small mammals (Myster and Pickett 1993 Hulme (1993, 1994) Maron and Simms 1997 Hulme and Borelli 1999), thus a slower removal rate would increase the probability that a seed would reach the relative safety of the litter or soil layer. Seeds contained within dishes, which are prevented from becoming buried over time, may have artificially high removal rates over the long term, resulting in lower final survival. Since the actual number of seeds being monitored in these studies tends to be dramatically lower than those available in nature, actual seed survival may be a less meaningful metric than removal rate.

In our study, seed removal rate was correlated with final survival, suggesting that short-term studies may reveal season-long patterns of survival. However, the spatial patterns of final survival varied greatly among years, while the pattern of seed removal did not. Future ecological studies must specifically address these methodological limitations before we can adequately incorporate the results of seed predation experiments into our understanding of community regeneration.

Conclusions

The more subtle, indirect effects of habitat fragmentation on plant community structure via plant-animal interactions are very poorly understood (Murcia 1995). The spatial context of a site not only determines the seed input for that site, but also the predation pressure those seeds will be subjected to. The increasing presence of edges in managed and natural landscapes makes edge influence on plant-animal interactions an even more important determinant of community dynamics. Spatially explicit studies of seed predation and other plant-animal interactions are needed to understand and manage the modern fragmented landscape.

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