NEIGHBORHOOD ANALYSES OF SMALL-MAMMAL DYNAMICS: IMPACTS ON SEED PREDATION AND SEEDLING ESTABLISHMENT

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Abstract. The spatial distribution of canopy trees in the temperate deciduous forests of the northeastern United States creates "neighborhoods" that vary in species composition as well as understory features. These neighborhoods may affect the distribution and abundance of generalist small-mammal seed predators by creating spatial variation in the availability of food resources, protective cover, and interactions with competitors. Small-mammal distribution and abundance may then influence tree population dynamics through variation in seed predation and seedling establishment. To determine if small-mammal activity patterns, seed survival, and seedling recruitment varied with neighborhood structure, we designed a study conducted at two habitat levels: canopy-tree neighborhoods, which reflected variation in seed production, and understory neighborhoods, which reflected differences in protective cover and interactions among animals. We live-trapped small mammals during the summer and fall of 1995 and 1996, experimentally measured seed survival in the falls of 1995 and 1996, and quantified total tree seedling recruitment in the spring of 1997. We developed a new method for nonlinear Poisson regression to relate canopy and understory neighborhood composition to small-mammal distribution and activity, seed survival, and seedling establishment. Small-mammal activity patterns changed between 1995 and 1996 in response to seed production. Canopy tree neighborhoods were a good predictor of overall small-mammal activity, and neighborhoods with high small-mammal activity had low seed survival. The canopy-tree neighborhoods with sufficient seed rain and high seed survival displayed increased seedling recruitment. Understory structure was a poor predictor of seed survival and seedling recruitment but appeared to be the primary axis along which habitat partitioning among mammal species took place when population densities were low. This study demonstrates that small-mammal seed predators influence tree recruitment patterns through their actions as seed predators in temperate deciduous forests, and that local effects of small mammals on seedling recruitment can be predicted from the species composition of tree neighborhoods.

Key words: canopy-tree neighborhoods; Clethrionomys gapperi; *maximum likelihood estimation; microhabitat neighborhoods; nonlinear Poisson regression;* Peromyscus *spp.; principal components analysis; seedling recruitment; seed survival; small-mammal dynamics;* Tamias striatus; *temperate forests.*

INTRODUCTION

The distribution and abundance of small mammals in temperate forests are influenced by a suite of factors including predator avoidance (Barnum et al. 1992, Morris 1996, 2002), competition with other species (Falkenberg and Clarke 1998, Perri and Randall 1999), and resource levels, especially the availability of food and water (Getz 1962, 1968, Miller and Getz 1977, McShea and Gilles 1992, Ostfeld et al. 1996, Wolff 1996, McCracken et al. 1999). Most studies of small-mammal distribution in temperate forests have examined coarse habitat characteristics such as density and distribution of adult trees (regardless of species), as well as microhabitat measures such as distribution of woody debris and percent cover of structural features

such as shrubs (Dueser and Shugart 1978, Kitchings and Levy 1981, Morris 1984, Buckner and Shure 1985, Seagle 1985). Studies demonstrating effects of particular tree species on small-mammal activity tend to concentrate on the regional effects of mast-producing species with large seeds (McShea and Gilles 1992, Ostfeld et al. 1996, Wolff 1996, McCracken et al. 1999). However, whether the spatial distribution of small mammals is predictable from the small-scale distribution of specific tree or understory species is unknown.

The effects of small mammals on tree population dynamics in temperate forests have received little attention. Effective seed dispersal distances of many tree species are limited (Ribbens et al. 1994, Clark et al. 1998), and recruitment limitation may play a role in the maintenance of tree species diversity (Pacala et al. 1996). Small mammals potentially can reduce recruitment limitation through secondary dispersal (Sork 1983, Kollmann and Schill 1996, Hoshizaki et al.

1999), but the more obvious effects of small mammals are as seed predators (Whelan et al. 1991, Ostfeld et al. 1997, Hulme and Hunt 1999, LoGiudice and Ostfeld 2002, Schnurr et al. 2002). Seedling establishment in these forests is highly episodic due, in part, to mast seeding and predator satiation (Sork 1983, Schnurr et al. 2002).

Recent models of forest dynamics focus on the importance of fine-scale spatial interactions among tree species (e.g., Urban et al. 1991, Pacala et al. 1993, 1996). Many processes in forest ecosystems can be viewed as "neighborhood" phenomena, in which the critical interactions occur over the spatial scales of adjacent dominant canopy trees (i.e., tens of meters). These include seed dispersal and seedling establishment (Ribbens et al. 1994, Clark et al. 1998, LePage et al. 2000), shading and competition for light (Canham 1989, Canham et al. 1994, Finzi and Canham 2000), and tree species effects on soil properties and nutrient availability (e.g., Finzi et al. 1998*a*, *b*).

Tree seed size and, hence, suitability as a food resource for rodent seed predators, varies dramatically among temperate tree species. Most species of northeastern trees disperse seeds in the autumn (Fowells 1965), and tree seeds represent an important food resource for rodents during this period. Home ranges of the major rodent species in North American temperate forests (i.e., *Peromyscus* species, *Clethrionomys gapperi*, and *Tamias striatus*) can range from 0.03 to 0.5 ha, which would include the crowns of 1–10 canopy trees (Merritt 1981, Snyder 1982, Lackey et al. 1985). Thus, neighborhood-scale variation in canopy tree composition may well act as a critical determinant of habitat quality for small mammals at both individual and population levels in these forests.

Understory community structure can be an important factor in small-mammal habitat selection (Dueser and Shugart 1978, Kitchings and Levy 1981, Vickery 1981, Yahner 1982, Parren and Capen 1985, Seagle 1985). Understory habitats can vary in (1) predation risk due to cover by shrubs or herbs (Kaufman et al. 1985, Longland and Price 1991); (2) availability of food resources such as fruit and fungi that can be important when tree seeds are scarce (Vickery 1979, Hansson 1985, 1999); and (3) structure such as exposed rock and coarse woody debris that can serve as runways (Barnum et al. 1992, Waters and Zabel 1998, Loeb 1999). Thus, both canopy tree and understory microhabitat neighborhoods can influence small-mammal activity and distribution, and may affect patterns of seed predation and, ultimately, seedling recruitment.

We designed a study to examine feedbacks between neighborhood-scale spatial variation in plant community composition and structure, and the spatial distribution, abundance and activity of the small-mammal seed predators in a temperate deciduous forest of the northeastern United States. Using newly developed methods for nonlinear Poisson regression, we examined

PLATE 1. Red oaks (*Quercus rubra*) in a mature, second-growth stand of the transition oak–northern hardwood forests of Great Mountain Forest in northwestern Connecticut. The understory in the foreground is dominated by hayscented fern (*Dennstaedtia punctilobula*). Photo by C. D. Canham.

the influence of variation in the composition of the canopy tree neighborhoods on small-mammal abundance and activity. We also conducted a similar analysis of the effects of neighborhood-scale variation in the structure and composition of the forest understory. We then investigated the effects of the seed predators on seed survival and seedling establishment, as a function of canopy and understory neighborhood types. We conducted our study for two years, which allowed us to incorporate the effects of temporal changes in seed production, seed survival, and small-mammal activity. Specifically, we asked: (1) do the major small-mammal genera partition habitat with respect to either canopy or understory neighborhoods; (2) do small mammals influence patterns of seed survival; and, (3) does seedling recruitment reflect the patterns of small-mammal habitat occupancy or seed survival?

METHODS

Study area

This study was conducted at the 2500-ha Great Mountain Forest (GMF), located in Litchfield County, Connecticut, USA (41°57′ N, 73°15′ W; see Plate 1). The major tree species included red oak (*Quercus rubra* L.), beech (*Fagus grandifolia* Ehrh.), black cherry

(*Prunus serotina* Ehrh.), sugar maple (*Acer saccharum* Marsh.), red maple (*Acer rubrum* L.), white pine (*Pinus strobus* L.), white ash (*Fraxinus americana* L.), and eastern hemlock (*Tsuga canadensis* (L.) Carr.). The major small-mammal seed predators in this area were *Peromyscus maniculatus* (deer mice), *P. leucopus* (white-footed mice), *Clethrionomys gapperi* (southern red-backed voles), and *Tamias striatus* (eastern chipmunks).

In the summer of 1995, nine 1-ha sites were chosen throughout GMF on the basis of adult tree composition: three were in locations dominated by red oak, two were in locations dominated by sugar maple, two were in locations dominated by eastern hemlock, and two were in mixed red maple and black cherry stands. All sites were located in continuous habitats ≥100 m from any roads or edges, the minimum distance between the sites was 200 m, and most sites were ≥1 km apart. These sites included the most common mixtures of canopy tree species and understory structure at GMF.

Small-mammal live trapping

A 9 × 9 small-mammal live-trapping grid with 12.5-m spacing between stations was established covering each 1-ha site. Live trapping was conducted for three consecutive days, four times from June to November in 1995, and three times from June to November in 1996. We used large folding Sherman live traps (8 × 9 × 23 cm; Sherman Traps, Tallahassee, Florida, USA) baited with crimped oats and, in November, supplied with cotton bedding. Traps were opened at ~1700 hours and were checked and closed beginning at 0700 hours daily. Captured small mammals were identified to species, given a numbered ear tag (Monel fingerling tags, #1 size; National Band and Tag Company, Newport, Kentucky, USA), weighed, checked for reproductive condition, and released at the point of capture. Total numbers of captures of each genus for each trapping location were used in these analyses to reflect activity densities.

Canopy tree and understory neighborhoods

We mapped all adult trees (stems > 10 cm dbh) within each 1-ha site. Because the average crown radius of the major tree species at GMF ranges from 4.5 to 6.5 m (Canham et al. 1994) and most seed dispersal occurs within 10 m of an adult (Ribbens et al. 1994), we defined the neighborhood surrounding each live-trapping location to be the area within a 10 m radius of the trap. For trap stations located on the outer edge, the neighborhood only included those trees within the mapped hectare. The total basal area of each tree species within the 10 m radius neighborhood for each trap location at every site ($N = 729$) was used in a principal components analysis (PCA) to describe the variation in canopy tree neighborhoods in the study area.

We characterized understory neighborhoods within each 12.5 × 12.5-m quadrat defined by trapping lo-

cations. We estimated the percent cover of fern, herbaceous vegetation, woody vegetation, woody debris (such as fallen logs), and exposed rock, each to the nearest 10%. The values for quadrats surrounding each trap station (four for most locations; fewer quadrats were used for edge trap locations) were averaged and analyzed using PCA.

Seed removal and seedling recruitment

Seed removal trials were conducted in randomly located 1 × 1-m quadrats during the fall of 1995 (nine quadrats per site) and 1996 (15 quadrats per site). Within each quadrat, we chose 25 random points separated by ≥10 cm. These 25 points were then randomly assigned one of five different tree seeds: red oak, black cherry, sugar maple, red maple, or white pine. The five locations for each tree seed were marked with a 15-cm wooden coffee stirrer (the top 0.5 cm was colored to identify seed species), and a single seed was placed directly on the ground at the base of the stirrer. Latex gloves were worn while handling the coffee stirrers and seeds to avoid scent contamination. Seeds were checked daily for three days, after which the total number of seeds surviving was recorded. Separate trials demonstrated that seed removal rates saturated very quickly (usually within three days). As time progressed, direct visual evidence of predation (such as seed coat fragments) disappeared. Most seed removal in these forests is from small mammals; bird and insect removal is insignificant (Ostfeld et al. 1994).

To correlate seed survival with seedling recruitment, the total numbers of newly germinated seedlings were counted in the spring of 1997 from the 1996 seed removal quadrats. Few seedlings occurred near the seed markers, indicating that most newly recruited seedlings were from natural seed rain and not from our experimental seeds. We estimated seed rain within each of the 1996 seed removal quadrats by estimating the average number of seeds produced by all trees in the surrounding neighborhood, using the data from Schnurr et al. (2002).

Data analyses

To identify relationships among small-mammal captures, seed survival, seed rain, and seedling recruitment, we used the values for the first PCA axis for both the canopy tree and understory neighborhoods as independent variables in all analyses (canopy tree neighborhood explained 18.8% of the variation, and understory neighborhood explained 26.1%; see *Results* for further explanation). Because the dependent variables were all count data and displayed nonlinear trends, we used nonlinear Poisson regression to fit an equation of the form $Y = AB^{(X-C)^2}$. We chose this equation because it has a flexible shape and the parameters are easy to interpret: A is the curve height, B determines the curve width, and C is the mode. We used simulated annealing (a global optimization procedure) to find the parameter

estimates for A, B, and C that maximized the likelihood of observing the data set (Goffe et al. 1994, Hilborn and Mangel 1997). The global optimization procedure was performed using software written in the Delphi programming environment (Borland Software 2001).

We used the nonlinear Poisson regression to estimate parameters for the small-mammal captures and seed survival data in 1995, and for small-mammal captures, seed survival, seed rain, and seedling recruitment in 1996. For the small-mammal data, the value of parameter A is the highest average capture rate. B is a measure of habitat breadth, ranging from 0, if captures were all in one habitat type, to 1, if the average capture rate did not vary across the PCA axis. C indicates the position along the axis at which the capture rate was highest. For seed survival, A is the maximum number of seeds surviving (with the maximum possible being 25 seeds); B is the size of the area where seeds survived; and C is the habitat where survival was greatest. The parameters for seed rain and seedling recruitment are similar to the seed survival values, except that there is no upper limit on A.

We used likelihood ratio tests to test hypotheses about differences among the Poisson regression models and to construct 95% asymptotic support intervals for parameter estimates (Hilborn and Mangel 1997). In particular, the likelihood ratio test for whether the parameter B was significantly less than a fixed value of 1 was used to test the hypothesis that there was significant variation in the response variable (mammal capture rate, seed survival, seed rain, or seedling establishment) along each axis. This is a direct test of the significance of the relationship between the ordination axis and a particular response variable (i.e., that the relationship differs from a flat line). There is no direct analogue to an R^2 statistic for goodness of fit of Poisson regression because the variance is equal to the mean for Poisson-distributed data. Thus, the relationship between observed and expected for a given data set is a unique function of the range of expected values in the data set, and the expected scatter in the residuals increases necessarily as the expected values increase.

We examined the distribution of body mass of captured animals to test whether variation between years in the distribution of small mammals among neighborhoods was associated with changing body condition. We divided both the canopy tree and understory PCA ordination axes into lower, middle, and upper sections and determined the average mass of captured animals for each area. We used ANOVA and Bonferroni pairwise comparisons to compare values among areas of the axis, using SYSTAT version 8 (Wilkinson 1998).

RESULTS

Canopy tree and understory neighborhoods

Principal components analysis identified three factors that explained ~50% of the variation in the canopy tree neighborhoods (Appendix A). Although these three factors were nearly equivalent statistically, which is unusual in analyses of this type, we choose to concentrate our analysis on the first factor. This factor discriminated between neighborhoods dominated by sugar maple and white ash on the left (negative) side of the axis, black cherry and red maple in the center of the axis, and red oak and beech on the right (positive) side (Fig. 1A). Other studies at Great Mountain Forest have shown that this axis reflects responses of the dominant tree species to fine-scale spatial variation in soil fertility, particularly the availability of calcium and other base cations (van Breemen et al. 1997, Bigelow and Canham 2002). We confined our analyses to the first factor for several reasons: (1) this factor was readily interpretable and ecologically meaningful; (2) this factor consistently displayed significant relationships between variables, whereas the analyses involving factors 2 and 3 had many nonsignificant regressions; and (3) this factor displayed variation shown to be important for other forest processes at GMF (van Breemen et al. 1997, Bigelow and Canham 2002).

Principal components analysis identified three factors that explained ~75% of the variation in understory neighborhoods, although again the three axes were nearly equivalent (Appendix B). We again chose to use only the first factor in our analyses because it was easily interpretable and displayed consistently significant relationships. This factor ranged from high amounts of woody debris on the negative side of the axis to high amounts of herbaceous vegetation on the positive side. The middle portion of the axis was a ''mixed'' understory habitat with high amounts of fern and woody vegetation (Fig. 1B).

Canopy tree and understory neighborhoods were largely independent of each other (correlation between the ordination scores for the first axes of the two PCAs = 0.056, $P = 0.13$). Examination of contour plots demonstrated that a wide range of understory neighborhoods occurred in each canopy tree neighborhood type (data not shown).

Seed rain

Total seed rain varied significantly among the three years (Schnurr et al. 2002). In 1994, seed rain was high for all species, including a moderate red oak crop of ~12 acorns/m². We observed a near-total seed crop failure in 1995 across all species. Subsequently, most species produced seed in 1996, with the notable exception of red oak.

The estimated 1996 seed rain was greatest in the mixed canopy tree neighborhoods, primarily because of a large seed crop by red maple, which had its greatest abundance in those neighborhoods (Figs. 1 and 2A). Seed rain by other tree species was similar across all canopy tree neighborhoods (Fig. 2A). Total seed rain and red maple seed rain across the understory neigh-
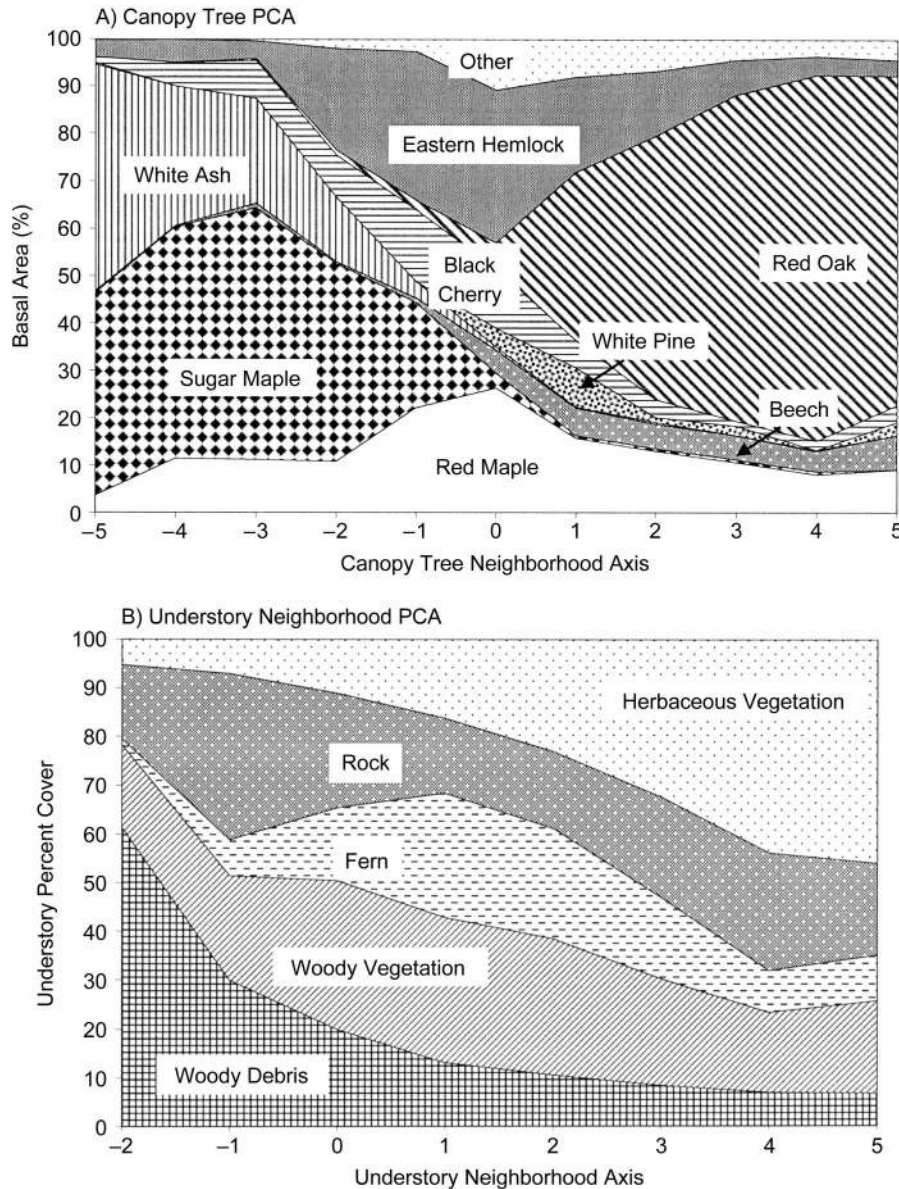
FIG. 1. (A) Basal area of tree species plotted against the first factor identified by the principal components analysis (PCA) of canopy trees. Note that the negative side of the axis is dominated by sugar maple and white ash, the middle is mixed, and the positive side is dominated by red oak and beech neighborhoods. (B) Percent cover of understory components plotted against the first factor identified by the understory PCA. Note that the negative side of the axis is dominated by woody debris, the middle is mixed, and the positive side is dominated by herbaceous vegetation neighborhoods.

borhoods was also greatest in mixed areas, but seed rain by other tree species was greatest in understory neighborhoods dominated by herbaceous vegetation (Fig. 2B). For the means and 95% support intervals for the parameter estimates for the curves in Figs. 2 and 4–6, see Appendix C.

Small-mammal distribution and abundance

1995, following a red oak mast in 1994.—In 1995, small-mammal population sizes were high, apparently in response to the red oak mast of 1994 (Schnurr et al.

2002). Because of the difficulty of distinguishing *Peromyscus* species in the field, as well as similar patterns displayed by each species in this and previous studies (Wolff et al. 1985, Schnurr et al. 2002), we combined the data for the *Peromyscus* species. Contour plots of the average capture rates of *Peromyscus* showed a very broad distribution across all canopy tree and understory neighborhoods (Fig. 3A). *Clethrionomys gapperi* were captured at the highest rates in red oak neighborhoods, and were widely distributed across understory neighborhoods (Fig. 3B). *Tamias striatus* occurred in neigh-
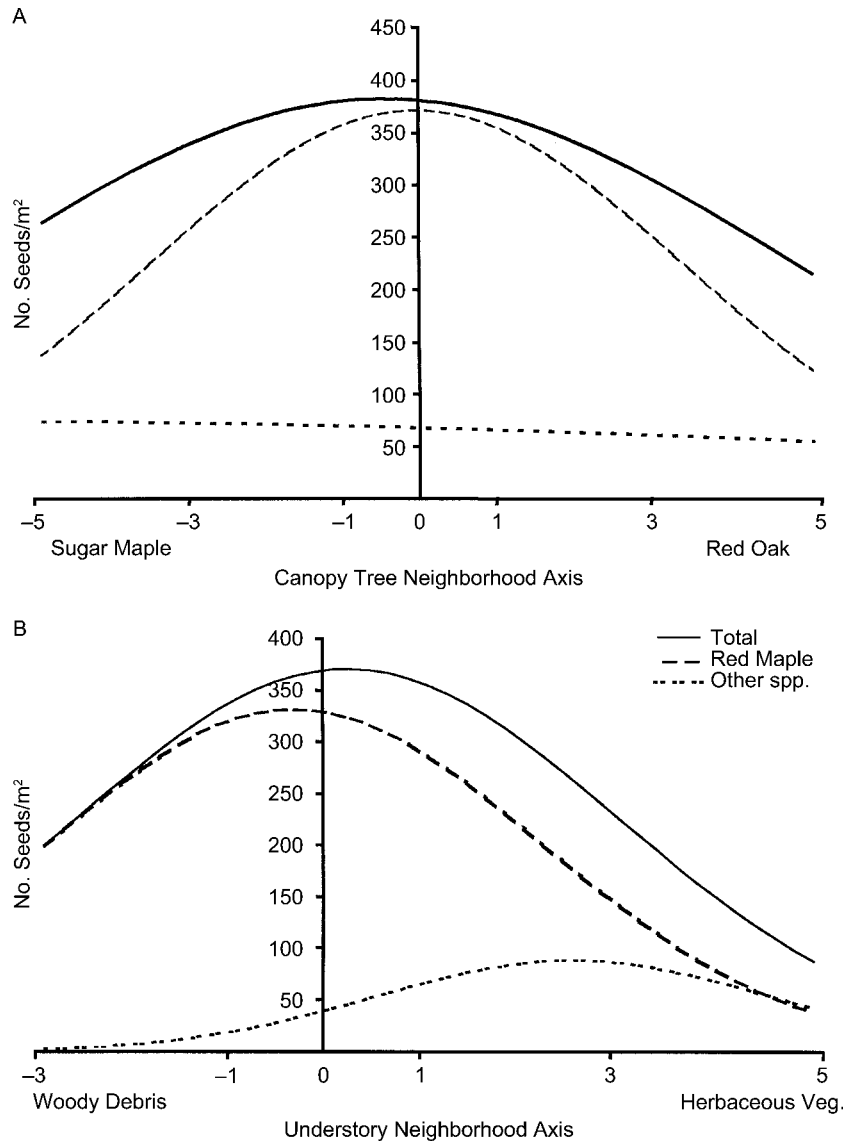
FIG. 2. Estimated 1996 seed rain across the neighborhood axes. The major PCA neighborhood type is identified to aid in interpretation. Note that the total seed rain contains seed rain by both red maple and other species. (A) Estimated seed rain across the canopy tree neighborhood axis; (B) estimated seed rain across the understory neighborhood axis.

borhoods similar to those where *C. gapperi* were captured (Fig. 3C).

Peromyscus had the highest predicted capture rate across the entire canopy tree neighborhood axis (Fig. 4A), with the greatest number of captures occurring in the mixed red maple–black cherry neighborhoods. Although the estimated curve for *Peromyscus* is shallow ($B = 0.98$), a likelihood ratio test (LRT) indicated that it was significantly different from a flat line, i.e., compared to a model with $B = 1$ (LRT, $\chi^2 = 7.961$, $P < 0.005$, df $= 1$). *C. gapperi* and *T. striatus* were most often captured in the red oak neighborhoods, although *C. gapperi* were captured at a much lower rate than *T. striatus*. Both *C. gapperi* and *T. striatus* had B values that were significantly different from 1 (for *C. gapperi*, $B =$

0.97; LRT, $\chi^2 = 17.34$, $P < 0.001$, df $= 1$; for *T. striatus*, $B = 0.96$; LRT, $\chi^2 = 45.68$, $P < 0.001$, df $= 1$).

Understory regression results were also consistent with the contour plots (Fig. 4B). In 1995, *Peromyscus* were captured at high rates across all understory neighborhoods, and the mode of the captures occurred in neighborhoods dominated by woody debris. Again, although the line was only slightly curved ($B = 0.99$), the likelihood ratio test indicated a significant difference from a horizontal line (LRT, $\chi^2 = 13.71$, $P < 0.005$, df $= 1$). *C. gapperi* were captured at a low maximum rate in areas dominated by woody debris, and were selective in their habitat occupancy ($B = 0.98$; LRT, $\chi^2 = 9.27$, $P < 0.005$, df $= 1$). *T. striatus* were more likely to be captured in mixed-understory neigh-
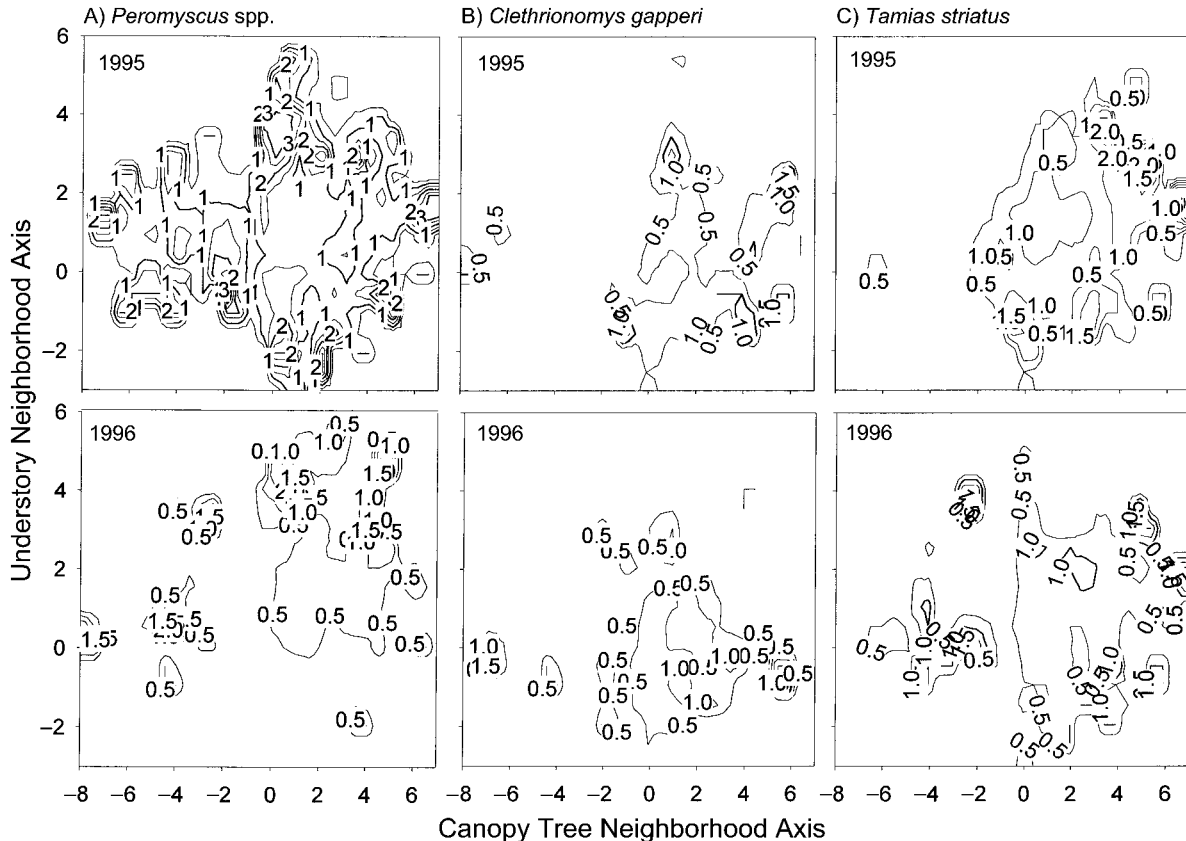
FIG. 3. Contour plots of the average capture rates of (A) *Peromyscus* spp. in 1995 and 1996; (B) *Clethrionomys gapperi* in 1995 and 1996; and (C) *Tamias striatus* in 1995 and 1996, across both the understory and canopy tree axes. The capture rate is the average number of animals caught within each neighborhood type. Canopy and understory axes are the same as those plotted in Fig. 1.

borhoods at an intermediate maximum capture rate and were selective in habitat occupancy ($B = 0.95$; LRT, $\chi^2 = 14.43$, $P < 0.005$, df = 1).

1996, following a low seed year in 1995.—Capture rates in 1996 were lower than in 1995, presumably in response to the limited seed rain in the fall of 1995 (Schnurr et al. 2002). *Peromyscus* captures were limited to red oak–beech neighborhoods, and the highest average capture rate occurred in understory neighborhoods dominated by herbaceous vegetation (Fig. 3A). *C. gapperi* were most often captured in areas dominated by woody debris, and were more likely found in neighborhoods of mixed canopy trees (Fig. 3B). *T. striatus* remained consistent in habitat occupancy from 1995 to 1996 (Fig. 3C).

Results of the regression of captures in canopy tree neighborhoods mirror those of the contour plots (Fig. 4A). *Peromyscus* were captured at a much lower rate in 1996 than in 1995, and they were captured more often in red oak–beech neighborhoods, reflecting a change in habitat from 1995. *Peromyscus* were selective in habitat type ($B = 0.99$; LRT, $\chi^2 = 7.44$, $P < 0.05$, df = 1). *C. gapperi* had an average capture rate similar to that of *Peromyscus*, and they selectively oc-

cupied more neighborhoods with mixed canopy trees ($B = 0.96$; LRT, $\chi^2 = 12.48$, $P < 0.005$, df = 1). *T. striatus* had fewer average captures than in 1995, but they remained consistent in habitat choice ($B = 0.98$; LRT, $\chi^2 = 22.45$, $P < 0.001$, df = 1) for red oak–beech neighborhoods.

We observed a striking pattern in habitat partitioning of understory neighborhoods in 1996, when capture rates of the three groups were roughly equal (Fig. 4B). *C. gapperi* were most likely to be captured in neighborhoods dominated by woody debris, *Peromyscus* were most likely to be captured in areas of high herbaceous vegetation, and *T. striatus* were most likely to be captured in mixed areas. This indicated a change in habitat between 1995 and 1996 for *Peromyscus*, but not for *C. gapperi* or *T. striatus*. All three species demonstrated strong habitat choice (for *Peromyscus*, $B = 0.96$; LRT, $\chi^2 = 17.56$, $P < 0.001$, df = 1; for *C. gapperi*, $B = 0.96$; LRT, $\chi^2 = 48.56$, $P < 0.001$, df = 1; for *T. striatus*, $B = 0.93$; LRT, $\chi^2 = 12.80$, $P < 0.005$, df = 1).

Body condition of *Peromyscus* varied among understory neighborhoods between 1995 and 1996. In the high population year of 1995, *Peromyscus* captured in
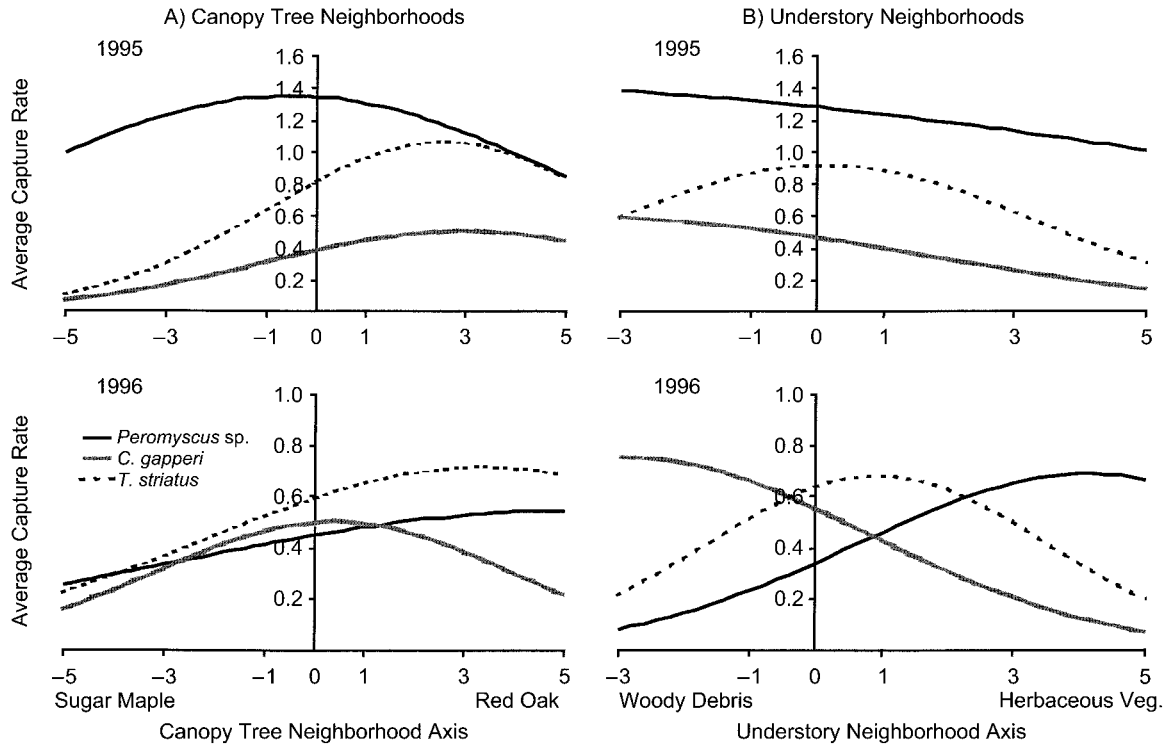
FIG. 4. Likelihood of capture for the three major small-mammal species based on (A) canopy tree neighborhood and (B) understory neighborhood for 1995 and 1996. Note the different scale on the y-axis between the two years, which reflects higher abundances in 1995.

neighborhoods dominated by woody debris were significantly smaller (mass 18.2 ± 0.3 g; mean ± 1 SE) than animals captured in areas dominated by herbaceous vegetation (mass 20.0 ± 0.5 g; $F = 4.713$, $P = 0.009$, df $= 2,616$). In 1996, *Peromyscus* body mass values were equal across all subsampled sections; however, values in 1996 were significantly higher than in 1995 (mass 21.5 ± 0.5 g; $F = 19.095$, $P < 0.001$, df $= 1,616$). There were no significant mass differences across canopy tree neighborhoods.

Seed removal

Canopy tree neighborhoods.—Seed survival was lower in 1995 than in 1996, most likely due to the large populations of *Peromyscus* in 1995. In 1995, red oak–beech neighborhoods had the largest number of seeds remaining of any canopy tree neighborhood. Although the line was only slightly curved ($B = 0.98$), it was a significantly better fit to the data than a horizontal line (LRT, $\chi^2 = 38.19$, $P < 0.001$, df $= 1$). Sugar maple neighborhoods had the greatest seed survival in 1996, and seed survival was much higher than in 1995. Again, there was a significant curve to the regression line ($B = 0.99$; LRT, $\chi^2 = 39.80$, $P < 0.05$, df $= 1$).

In 1995, removal of different species of seeds varied among neighborhood types (Fig. 5A). Red oak acorns consistently had the lowest survival overall, although they had significantly higher survival rates in the red

oak neighborhoods ($B = 0.98$; LRT, $\chi^2 = 5.134$, $P = 0.01$, df $= 1$). Sugar maple and white pine seeds experienced significantly higher survival when in mixed neighborhoods (for sugar maple, $B = 0.95$; LRT, $\chi^2 = 4.74$, $P = 0.02$, df $= 1$; for white pine, $B = 0.97$, LRT, $\chi^2 = 2.02$, $P = 0.045$, df $= 1$). Seeds of black cherry ($B = 0.99$; LRT, $\chi^2 = 1.6$, $P = 0.065$, df $= 1$) and red maple ($B = 0.98$; LRT, $\chi^2 = 1.12$, $P = 0.07$, df $= 1$) displayed marginally nonsignificant variation in survival across canopy tree neighborhoods.

In 1996, all seed species displayed a similar trend across canopy tree neighborhoods (Fig. 5A). Sugar maple neighborhoods had significantly higher survival rates (LRT for all seed species, $\chi^2 > 2.5$, $P < 0.05$, df $= 1$), and red oak neighborhoods had the lowest. White pine seeds had the lowest survival of all species.

Understory microhabitat neighborhoods.—In 1995, overall rates of seed removal did not vary significantly as a function of understory neighborhood ($B = 1.0$; LRT, $\chi^2 = 0.821$, $P = 0.25$, df $= 1$). Seed survival in 1996 was highest in a small range of understory neighborhoods ($B = 0.86$; LRT, $\chi^2 = 86.0$, $P < 0.001$, df $= 1$). The lowest seed survival occurred in the areas where *C. gapperi* and *Peromyscus* were most active, i.e., in areas dominated by woody debris and herbaceous vegetation. The highest seed survival occurred in the interstitial area between those supporting the maximum capture rates of *T. striatus* and *Peromyscus*.
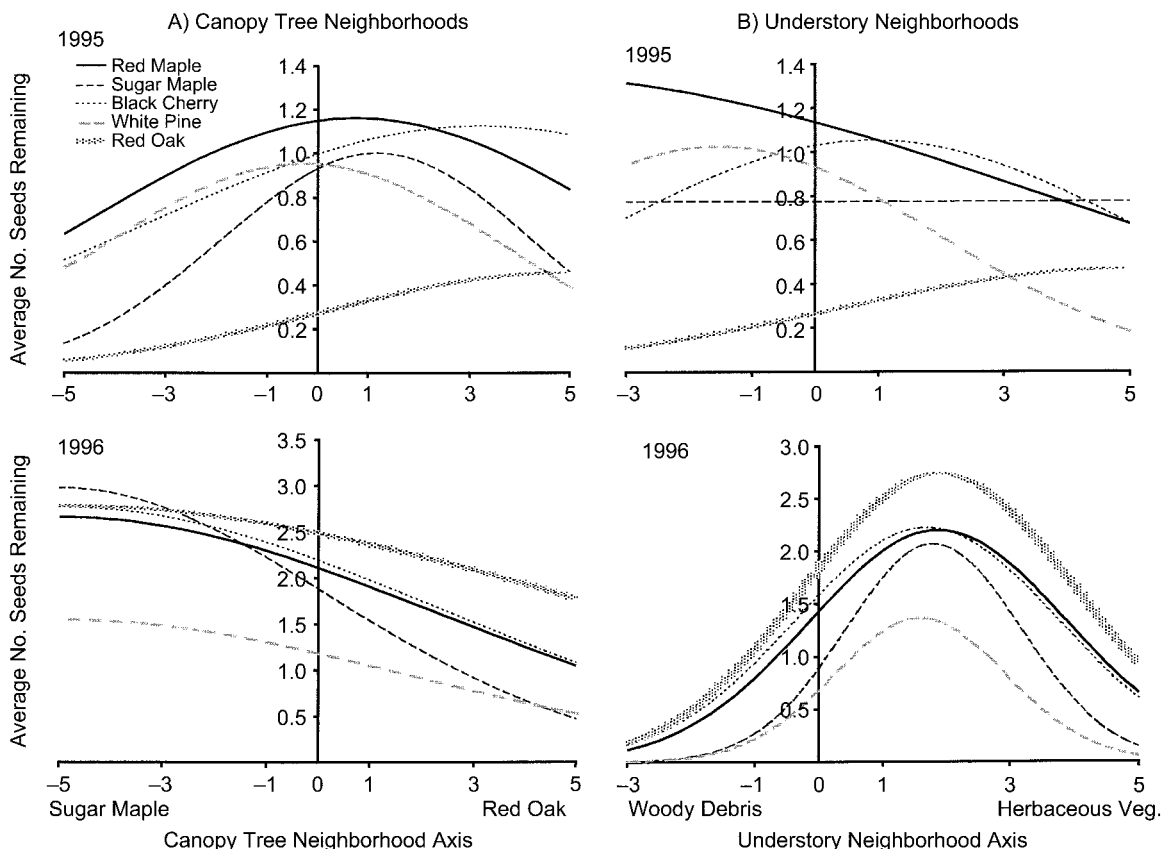
FIG. 5. Species-specific seed survival along the (A) canopy tree neighborhood axis and (B) understory neighborhood axis for 1995 and 1996. Note the different scales on the *y*-axes, reflecting higher seed survival in 1996.

Survival patterns of individual species of seeds varied between 1995 and 1996 in understory neighborhoods (Fig. 5B). In 1995, red oak acorns experienced equal survival across all neighborhoods ($B = 0.98$; LRT, $\chi^2 = 0.79$, $P = 0.36$, df $= 1$), as did red maple seeds ($B = 0.99$; LRT, $\chi^2 = 0.63$, $P = 0.44$, df $= 1$), black cherry seeds ($B = 1$; LRT, $\chi^2 = 0.891$, $P = 0.25$, df $= 1$), and sugar maple seeds ($B = 1$; LRT, $\chi^2 = 0$, $P = 1$, df $= 1$). More white pine seeds survived ($B = 0.96$; LRT, $\chi^2 = 2.47$, $P = 0.03$, df $= 1$) in the mixed understory neighborhoods. In 1996, all species displayed a similar pattern, with significantly increased survival (LRT for all species, $\chi^2 > 1.92$, $P < 0.05$, df $= 1$) in mixed understory neighborhoods.

Seedling establishment

Canopy tree neighborhoods.—Seedling establishment was greatest in canopy tree neighborhoods where seed production and seed survival were both favorable (Figs. 2A and 6A). The maximum number of seedlings of all species occurred in the sugar maple neighborhoods (Fig. 6A). Red maple seedlings were the most numerous of the new germinants, and had maximum recruitment nearer to neighborhoods of the mixed canopy trees, where red maple was a canopy dominant, than did seedlings of other species (Fig. 6A).

To assess the correlation between seed rain and seedling establishment, we plotted the proportion of seeds that germinated as a function of the canopy tree neighborhoods. If seed rain were solely responsible for seedling emergence, the proportion of seeds that germinated should be constant. A greater proportion of the total seed rain germinated in the sugar maple neighborhood types (Fig. 7AI), as did a greater proportion of species other than red maple (Fig. 7AIII). Red maple seedling establishment was lowest in the areas of highest red maple seed production (Figs. 2A and 7AII).

Understory microhabitat neighborhoods.—Total seedling recruitment (across all species) was not highest in understory neighborhoods that had the greatest overall seed survival in our seed removal trials (Fig. 6B). Although seed survival was highest in the areas dominated by herbaceous vegetation, total seedling recruitment was greatest in areas dominated by woody debris. Similarly, red maple seedling recruitment was greatest in neighborhoods dominated by woody debris. However, the greatest recruitment of species other than red maple occurred in neighborhoods with the most herbaceous vegetation, which was also where the greatest seed survival occurred.

The proportion of seeds that germinated in different understory neighborhoods was not as easily interpret-

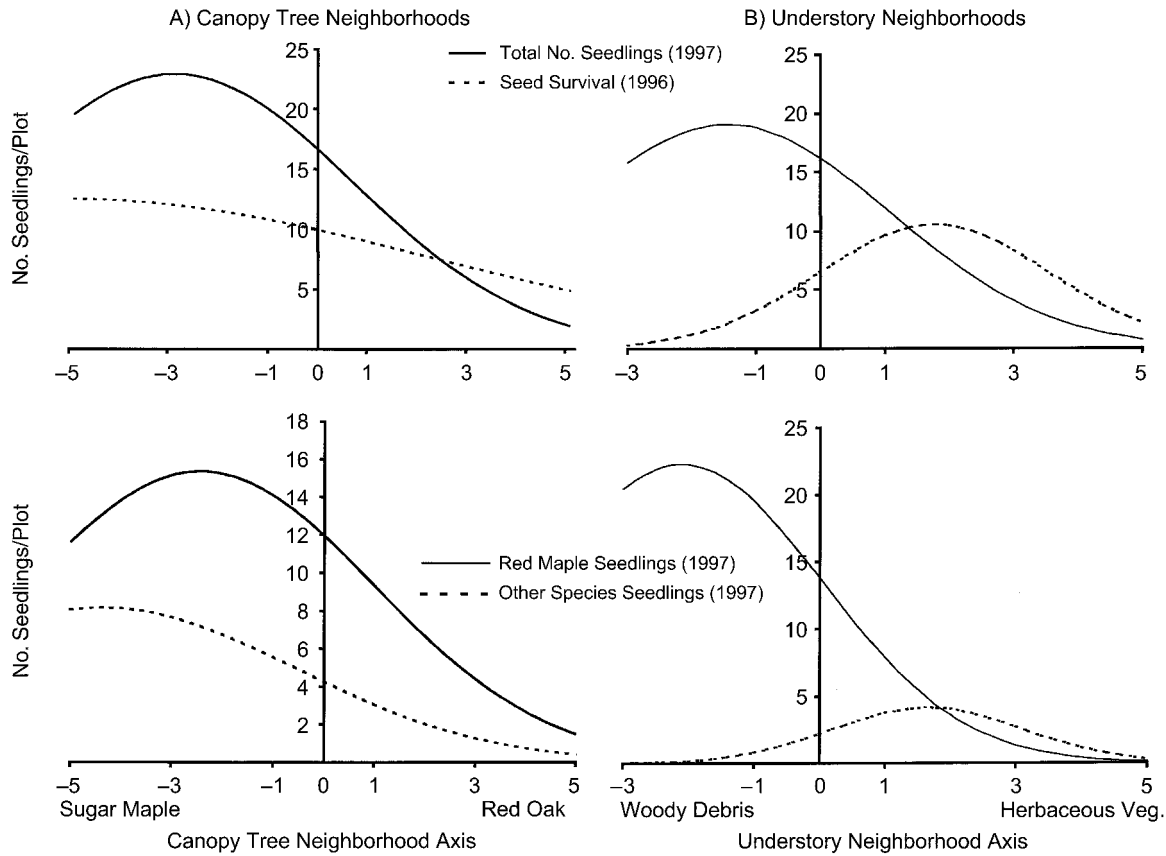A) Canopy Tree Neighborhoods   B) Understory Neighborhoods

FIG. 6.   Upper panels: Seedling recruitment of all species and seed survival in the previous fall along the (A) canopy tree neighborhood axis and (B) understory neighborhood axis. Lower panels: Recruitment separated into red maple seedlings and seedlings of other species along the (A) canopy tree neighborhood axis and (B) understory neighborhood axis.

able as in the canopy tree neighborhoods (Fig. 7B). A consistent, low proportion of the total and red maple seed rain germinated across all understory neighborhoods. However, both total seeds and red maple seeds showed a slight trend for an increase in the proportion that germinated in the neighborhoods dominated by woody debris. The proportion of other seeds that germinated was highest in the mixed-understory neighborhoods.

DISCUSSION

We found that the distribution and activity of a guild of small mammals was predictable on the basis of the distribution of canopy trees in neighborhoods ($\sim$100–200 m^2 areas) that represent both individual adult tree canopies and small-mammal home ranges. The distribution of the granivorous small mammals, in turn, was a good predictor of the intensity of predation on experimentally introduced seeds. Neighborhoods in which seed predation was lowest were characterized by the highest natural rates of seedling recruitment. If the seedling recruitment signal persists into the sapling and adult tree stages, then canopy trees would appear to be influencing their own neighborhood-specific pop-

ulation dynamics indirectly via their impacts on seed predators. Our study encompassed a year of light seed production and a year of heavy seed production, and we correlated this variation with the population sizes of rodent seed predators. In addition, small-mammal species responded differently to: (1) species-specific tree seed production, and (2) neighborhoods characterized by canopy trees vs. those characterized by understory features. These complexities, which both enrich and complicate the interpretation of our results, will be discussed.

Neighborhood analyses of the distribution and activity of small mammals

Much attention has been devoted to describing patterns of small-mammal abundance and distribution as a function of habitat variables in deciduous forests of eastern North America. The earliest studies of this type looked at coarse-scale aspects of the environment, such as correlating vegetation type and density with capture locations (M'Closkey and LaJoie 1975, Miller and Getz 1977). We selected the neighborhood level of analysis a priori because we expected that heterogeneity at the scale of tens of meters would be representative of both
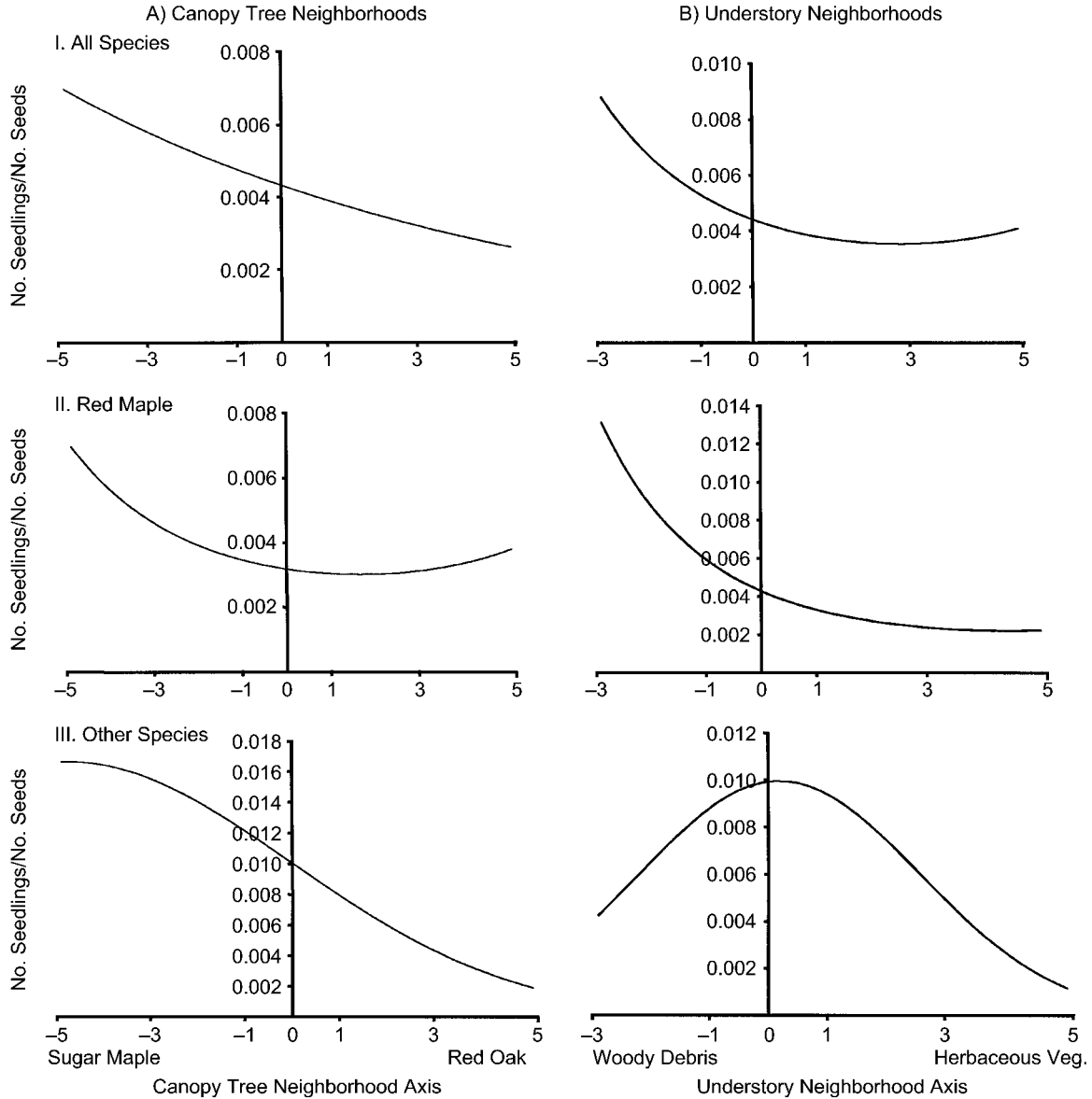
FIG. 7. The proportion of seeds that germinated across the (A) canopy tree neighborhood axis and (B) understory neighborhood axis for (I) all species, (II) only red maple, and (III) only other species.

local tree seed inputs (a critical food resource) and individual small-mammal home ranges. In our analyses, conducted over years of high and low mammal abundance, we incorporated both the more traditional understory habitat features (e.g., Kitchings and Levy 1981, Vickery 1981, Yahner 1982, Parren and Capen 1985, Seagle 1985) and the neglected overstory habitat features. To incorporate suspected nonlinear relationships between small mammals and neighborhood composition, we developed a new nonlinear Poisson regression approach, which, combined with maximum likelihood statistics, allowed us to quantify and visualize activity densities.

We found that small-mammal responses to overstory and understory composition were dramatically different. In the year of low rodent abundance (1996), much overlap occurred among all three groups (*Peromyscus* spp., *Clethrionomys gapperi*, and *Tamias striatus*) in neighborhoods dominated by red oak overstory. However, in the year of high rodent abundance (1995), *Peromyscus* was captured most frequently in mixed neighborhoods or those dominated by sugar maple, whereas the other two species maintained their occupancy of oak-dominated neighborhoods. This pattern is in marked contrast to our analyses of understory neighborhoods, which demonstrated almost perfect micro-

habitat complementarities at low rodent abundance (Fig. 4B, 1996) and considerable microhabitat overlap when rodent abundance was high (Fig. 4B, 1995). Thus, it appears that the small-mammal species at our site segregated neighborhood types by overstory (but not understory) when densities were high, but segregated by understory (but not overstory) when densities were low.

Peromyscus shifted overstory occupancy from mixed or maple-dominated neighborhoods at high abundance to red oak neighborhoods at low abundance, whereas the other two species shifted only modestly. Similarly, *Peromyscus* shifted from extreme nonselectivity of understory neighborhoods at high density to the strong selection of herbaceous-dominated neighborhoods at low density, whereas the other two species maintained similar understory occupancy in both years. The stronger interannual shifts in neighborhood occupancy by *Peromyscus* compared to the other two species might have resulted from the apparently stronger numerical response of the former species to the acorn mast in 1994 (Schnurr et al. 2002), as indicated by high modal values of capture rates in 1995 (Fig. 4).

Source–sink dynamics can alter the spatial structure of a population in a heterogeneous and temporally varying environment by allowing individuals the chance of reproducing in a ''poor'' habitat (Van Horne 1981, Pulliam 1988, Pulliam and Danielson 1991, Morris 2002), as well as maintaining coexistence between species by changing dispersal rates among species (McPeek and Holt 1992). At our sites, the largest change in *Peromyscus* capture rate occurred in the understory neighborhoods dominated by high woody debris (Fig. 4B). In the year of low population density (1996), few mice used this microhabitat type, suggesting that it is of low quality. When population size was greater in 1995, neighborhoods dominated by woody debris became occupied by smaller individual mice, which may have dispersed to these poorer areas during a phase of population growth following the red oak mast of 1994. Mice were larger in the preferred neighborhoods high in herbaceous vegetation (Elkinton et al. 1996, Ostfeld et al. 1996, Wolff 1996, McCracken et al. 1999).

Implications for tree population dynamics

Our results indicate that spatial variation in capture rates of small rodents in live traps correlates well with spatial variation in predation rates on seeds, mirroring the results of prior studies examining effects of rodent abundance on tree invasion of old fields (Ostfeld et al. 1997, 1999, Manson et al. 1998, 1999, 2001, Schnurr et al. 2002). In 1995, when *Peromyscus* were captured at high rates across all canopy tree and understory neighborhoods (Fig. 4), seed survival was low everywhere (Fig. 5). In 1996, when small-mammal abundance was lower, all of the rodent species were captured most frequently in red oak neighborhoods, and seed

survival was lowest in those areas (Figs. 4 and 5). Small mammals strongly partitioned understory neighborhoods in the year of low abundance (1996), and tree seed survival was highest in the interstitial areas between the neighborhoods where *Peromyscus* and *T. striatus* were most frequently captured (compare Fig. 4B with Fig. 5B).

Temperate deciduous forests typically display very low seedling recruitment rates (Shibata and Nakashizuka 1995, Clark et al. 1998, Houle 1998). Clark et al. (1998) found that both lack of seed and suitability of microsites limited seedling recruitment in southern Appalachian forests. We suspect that some of the variability in seedling establishment observed by Clark et al. (1998) was also due to the activity of seed predators. Increased seedling recruitment after a mast-seeding event is well known (Jensen 1985, Schupp 1990, Beckage et al. 2000, Connell and Green 2000, Vila and Lloret 2000), and is often interpreted as an illustration of the importance of seed predation and predator satiation for seedling recruitment. Seedling recruitment was correlated with seed rain (Fig. 7A), as well as with seed survival (Fig. 6A) in canopy tree neighborhoods. Thus, our results support the work of others in that the only successful seedling recruitment occurred in areas with sufficient seed rain (Shibata and Nakashizuka 1995, Clark et al. 1998, Houle 1998). However, we have also shown that seed predation by small mammals can be a major control on the suitability of microsites and rates of seedling recruitment.

Temporal variation in seed rain of trees has long been known to translate into temporal variation in seed predator abundance and changes in rates of tree seed predation and seedling recruitment (Janzen 1970, Hubbell 1980, Jensen 1985, Nilsson 1985, Schupp 1990, Elkinton et al. 1996, Ostfeld et al. 1996, Wolff 1996, McCracken et al. 1999, Connell and Green 2000, Vila and Lloret 2000, Schnurr et al. 2002). Our data show that the temporal variation in animal abundance is accompanied by fine-scale variation in the *spatial* pattern of seed predation. Predation risk for seeds is not spread uniformly across stands: a seed that falls in a neighborhood where small mammals are actively foraging will experience high predation risk, but that risk will change through time based on the spatial patterning in the abundance and activity of the small-mammal community. Other researchers have found similar results: spatial patterns of seed removal display yearly variation, making prediction of safe sites difficult (Webb and Willson 1985, Whelen et al. 1991, Houle 1992). Our data indicate that incorporating the yearly variation in seed rain, along with its effect on the spatial pattern of seed predation by foraging rodents, will allow us to better predict the spatial pattern and abundance of seedling recruitment over time.

Our results contribute to the growing evidence for the pervasive ecological effects of red oak mast in northeastern U.S. forests (Elkinton et al. 1996, Ostfeld

et al. 1996, Wolff 1996, McCracken et al. 1999, Schnurr et al. 2002, Schmidt and Ostfeld 2003). Mast years produce subsequent increases in *Peromyscus* numbers and distribution across canopy and understory neighborhoods, decreasing seed survival in all neighborhoods (Fig. 5). Tree species that produce seeds in a high mouse year (i.e., the year following a mast crop) will experience high rates of seed predation (Schnurr et al. 2002) that will decrease seedling recruitment. Mouse abundance typically declines in years following low acorn abundance (Schnurr et al. 2002), and our results indicate that mouse distribution and activity become concentrated in red oak neighborhoods. This should result in higher seed survival and seedling establishment for species that produce seed in a year with low *Peromyscus* numbers, but the rates of seedling establishment should still vary among canopy tree and understory neighborhoods.

Our results suggest that there is an ''associational risk'' for trees of species other than red oak that occur in neighborhoods dominated by red oak: throughout the mast cycle, their seeds should experience higher seed predation and lower probability of seedling establishment than seeds produced away from red oaks. Similar ''associational'' risks have been documented in seed removal studies, where less-preferred species experience higher removal when found with highly preferred species (Veech 2000; C. D. Canham, *unpublished data*). This result may help to explain the spatial segregation of red oak and sugar maple neighborhoods: maples present in oak stands will face higher predation risk, integrated over time, than maples locate away from oaks. Thus, sugar maples may be better able to establish in sugar maple neighborhoods, whereas red oaks can have increased seedling recruitment in red oak neighborhoods because of increased seed survival due to predator satiation after a mast (Janzen 1970, Hubbell 1980, Jensen 1985, Nilsson 1985, Schupp 1990, Elkinton et al. 1996, Ostfeld et al. 1996, Wolff 1996, McCracken et al. 1999, Connell and Green 2000, Vila and Lloret 2000, Schnurr et al. 2002).

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APPENDIX A

A table showing principal components factor loadings for the sum of the canopy tree (dbh > 10 cm) basal areas found within a 10-m radius from each trap location is available in ESA's Electronic Data Archive: *Ecological Archives* E085-018-A1.

APPENDIX B

A table showing principal components factor loadings for the understory variables based on the average value for the 625 m^2 surrounding each trap location is available in ESA's Electronic Data Archive: *Ecological Archives* E085-018-A2.

APPENDIX C

A table showing maximum likelihood parameter estimates for all estimated curves using the equation $Y = AB^{(X - C)^2}$ is available in ESA's Electronic Data Archive: *Ecological Archives* E085-018-A3.