LONG-TERM EFFECTS OF RODENT HERBIVORES ON TREE INVASION DYNAMICS ALONG FOREST–FIELD EDGES

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Abstract. Despite many observations of herbivores and granivores influencing the survival of tree seeds and seedlings, the net effects of these consumers on plant succession remain unclear. We used both experimental herbivore manipulations and observations of changes in vegetation cover to evaluate the longer-term impacts of small-mammal herbivores and granivores on woody plant invasion into old fields in New York State. Over a 5-yr period, we manipulated the density of meadow voles (*Microtus pennsylvanicus*) within partial enclosures replicated at five study sites. Average vole activity in enclosures with high vole density was significantly greater than that in enclosures with low vole density. In contrast, activity of competitively inferior white-footed mice (*Peromyscus leucopus*) was significantly greater within enclosures designated as low vole density. Colonization by tree seedlings, as well as shrubs and vines, was significantly greater in enclosures under the low vole density treatment. Further, tree seedling abundance was higher in shrub-dominated enclosures with low vole, but high mouse, activity. Five years of contrasting mouse and vole activity within adjacent enclosures revealed that seedling predation by voles had a greater net effect on changes in woody vegetation cover in old fields than did seed predation by mice, despite studies reporting higher rates of seed vs. seedling predation in these areas. We conclude that short-term measures of predation intensity may not accurately predict the longer-term effects of small-mammal herbivores on vegetation dynamics and suggest that voles may be a keystone herbivore in old-field succession.

Key words: granivory; herbivory; keystone species; Microtus pennsylvanicus; *New York State; old-field succession;* Peromyscus leucopus; *plant–herbivore interactions; rodents; seed vs. seedling predation; seedling establishment; tree invasion.*

INTRODUCTION

A growing number of studies suggest that herbivores can influence plant population and community dynamics (McNaughton 1979, Brown and Gange 1989, De Steven 1991*a, b,* Hulme 1994, Ostfeld et al. 1997). However, the nature of herbivore effects and the long-term impact of herbivores on vegetation change are still under considerable debate (Huntly 1991, Davidson 1993, Reader 1997). An important factor limiting generalizations about the effects of herbivores on plant succession is the relatively short time scale over which most herbivory experiments are conducted (Mittelbach and Gross 1984, Schupp 1988, Gill and Marks 1991, Myster and Pickett 1993, Holl and Lulow 1997, Ostfeld et al. 1997). Herbivory studies performed on the order of weeks to months may reveal considerable short-term variation not relevant to the net effects of herbivores in successional processes operating over time scales of years to decades.

Longer term studies, by integrating the effects of herbivory through time, hold more promise in illumi-

nating the role of herbivores vs. other factors in vegetation dynamics (Rankin and Pickett 1989, Brown and Heske 1990, Bowers 1993, Inouye et al. 1994). Such studies typically use selective herbivore exclosures (e.g., Bowers 1993) or make inferences about the role of herbivores based on natural recruitment and mortality patterns (Myster and Pickett 1992, Hill et al. 1995). In both cases, important information regarding changes in populations and communities of herbivores is often lacking (Ostfeld et al. 1997, Hämback et al. 1998, Manson and Stiles 1998), thus weakening the interpretative and predictive power of such experiments. Well-documented, long-term manipulations of herbivore communities, while clearly capable of demonstrating the net effects of herbivores on plant community dynamics (e.g., Brown and Heske 1990), are rare.

A key factor controlling the rate and trajectory of old-field succession is colonization by trees (Bard 1952, Pickett 1982). Although various factors can influence the establishment of trees in old fields (Pickett et al. 1987, Myster 1993), many studies have highlighted the potential importance of seed and seedling predation (Myster and McCarthy 1989, Gill and Marks 1991, Myster and Pickett 1993, Ostfeld and Canham 1993, Hill et al. 1995, Ostfeld et al. 1997). White-

FIG. 1. The experimental design used within enclosures at five study sites. Paired enclosures for maintaining vole density treatments extended 5 m into forests and 35 m out into old fields at each study site. Locations of 25 trap stations placed within each enclosure are marked by X's. We used seven 1.4 × 1.4 m, sampling quadrats (dashed open rectangles) along each of three transects running parallel to the forest edge to census natural patterns of tree seedling establishment within each enclosure. Transects were located 17.5, 25, and 32.5 m from the forest edge.
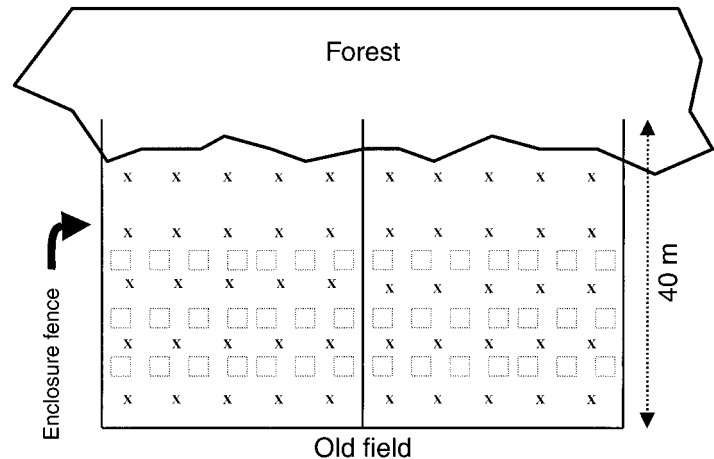
footed mice (*Peromyscus leucopus*) and meadow voles (*Microtus pennsylvanicus*) are the dominant tree seed and seedling consumers, respectively, in the northeastern United States (Gill and Marks 1991, Ostfeld et al. 1997, Manson et al. 1998). Mice prefer areas of high shrub cover and are more common along forest–field borders, whereas voles are more abundant in grass-dominated portions of old fields and avoid forests and forest edges (M'Closkey and Fieldwick 1975, Nupp and Swihart 1996, Manson and Stiles 1998, Manson et al. 1999). Both species exhibit dramatic, multiyear fluctuations in population density (Taitt and Krebs 1985, Batzli 1992, Ostfeld et al. 1996) that, combined with their distinct habitat preferences, may create contrasting temporal and spatial windows of opportunity for tree invasion in old fields. Meadow voles are competitively dominant over white-footed mice (Grant 1972) and thus can have both a direct negative impact on seedlings and an indirect positive influence on seed survival in old fields through the competitive suppression of white-footed mice (Ostfeld et al. 1997, Manson et al. 1998). This dual effect on tree propagule survival has led to the suggestion that voles, not mice, are keystone herbivores in old-field succession (Ostfeld et al. 1999). However, little direct evidence supports this conjecture.

We performed a series of experiments utilizing the competitive interactions and habitat partitioning exhibited by mice and voles to clarify their role in the invasion of trees and other woody vegetation into old fields. Specifically, we manipulated vole densities over five years within paired partial enclosures located along edges between forests and old fields. We simultaneously monitored patterns of activity of mice and voles, as well as changes in the abundance of tree seedlings and other woody vegetation within these experimental enclosures, to assess the relative and net effects of these herbivores on old-field succession. We predicted that the invasion of old fields by tree seedlings and other woody vegetation should be slower under high vs. low density of voles, and that greater tree seedling recruit-

ment should occur in microhabitats avoided by voles but favored by mice, such as near forest edges and in sites with high shrub cover.

METHODS

Study sites

We used five study sites located in or adjacent to the Institute of Ecosystem Studies (IES) in Millbrook, southeastern New York State, USA (41°50′ N, 73°45′ W). These sites were situated along relatively straight borders of forests and adjacent old fields that, depending on their topography, historically had been used as pastures or for row crops (Glitzenstein et al. 1990). Prior to this study, these fields were maintained in an early successional state by annual mowing to a height of 6–10 cm. Dominant herbaceous cover at these study sites included a mixture of grasses (*Schizachyrium scoparium* and *Bromus inermis*), forbs (*Solidago* spp., *Galium tincturum,* and *Centaurea maculosa*), and sedges (*Carex* spp.). Previous studies provide a more detailed description of herbaceous vegetation cover at these sites (Manson 1999).

Enclosures and trapping

In April–June 1994, we built two adjacent vole enclosures (each 40 × 40 m; Fig. 1, Plate 1) along the forest–field border at each of the five study sites, which were separated from one another by 2 km, on average. Three sides of each enclosure consisted of 0.9 m tall, 1.2-cm mesh galvanized hardware cloth fencing buried to a depth of ~0.4 m. The forest edge at each site functioned as the fourth side of the enclosures (Fig. 1), due to the strong avoidance by voles of forests and forest edges (Tamarin et al. 1984). Because voles also avoid open areas (Ostfeld and Canham 1993), a 0.5-m strip on either side of the fences was mowed every two weeks to enhance the effectiveness of enclosure fencing. In contrast, our experimental design allowed mice, known habitat generalists, to move freely between forests and adjacent old-field vegetation within each enclosure.

PLATE 1. Aerial photograph taken from a helium balloon showing one of 40×40 m vole density enclosures used during the present study. Observable are the enclosure fences, the forest edge, the trails created while checking Sherman live-traps, trap locations (marked by white squares), and the transitions between various vegetation types such as shrubs, grasses forbs, and vine cover. Also visible are repicated small-mammal exclosures and adjacent control plots used to assess annual rates of meadow vole (*Microtus pennsylvanicus*) herbivory (source: R. H. Manson).

In the summer of 1994, we randomly assigned one member of each pair of enclosures to a high-vole-density treatment, and the other to a low-vole-density treatment. Vole density differences between adjacent enclosures were maintained from 1994 until autumn of 1998 by transporting most juvenile or subadult voles captured in enclosures designated as low density to those designated as high density (524 individuals in total). An exception to this general practice was in 1996, when populations of voles were extremely low and vole density manipulations could not be carried out effectively. Voles were also occasionally captured in locations outside of the study sites and released in the high-density vole enclosures to help maintain differences between the vole density treatments.

A five by five array of live traps with 7.5 m between traps (Fig. 1) was established within each enclosure. This array was used to maintain the vole density treatments as well as to monitor changes in the distribution and abundance of mice and voles within enclosures at the five study sites. The only other species of small mammal captured consistently was the short-tailed shrew (*Blarina brevicauda*), which is insectivorous. Medium-sized Sherman traps ($5.1 \times 6.4 \times 15.2$ cm) (H. B. Sherman, Tallahassee, Florida) and Longworth traps (B. N. Bolton, Vernon, British Columbia, Canada) were used at alternating trap stations to control for the possibility that mice or voles might exhibit a preference for one type of trap over the other. No such preferences were found; because all enclosures had the same pro-

portion of each trap type, our small-mammal sampling was consistent and unbiased. Trapping sessions occurred at 2-wk intervals from early May until late November or early December of each year. Sessions spanned two consecutive days, with traps set in the afternoon and checked the following morning. All captured animals except shrews were given a numbered metal ear tag for identification and were identified to species before either being released at the point of capture or moved to a high-vole-density enclosure at another site.

Censuses of woody vegetation

To examine the effects of our vole density manipulations on natural patterns of tree seedling abundance, we counted seedlings within the field portion of the enclosures at each of the five study sites in August–September of 1998. Within each enclosure, we determined the total number and species composition of all seedlings found within a series of 1.4×1.4 m quadrats. Seven regularly spaced quadrats were used to sample undisturbed vegetation in each of three sampling transects (Fig. 1). Only seedlings <0.5 m high, with no signs of resprouting or vegetative reproduction, were sampled, to help ensure that they had established independently during our study.

We also measured the percent cover of vines and shrubs at four of the study sites. The fifth site was excluded from shrub and vine cover surveys because we thought that inadvertent damage to several shrubs in one of the enclosures at this site might bias the results. Five sampling transects were established within each enclosure in the summer of 1994. Transects were oriented parallel to forest edges at randomly determined distances. They were resampled when necessary to maintain a 2-m minimum spacing between transects, as well as to sample only undisturbed vegetation. All experiments within enclosures were conducted ≥1 m from transects. Transects were 38 m long, with 1 m left on either end for fence repair and maintenance. All transects were sampled once in the summer in 1994 and 1998. Sampling consisted of recording the start and stop distances (couplets) of each vine and shrub intersecting the transect tape, and identifying each plant to species.

Statistical analysis

We estimated mouse and vole activity by summing the number of captures of each species, at each trap station, within each enclosure over the duration of the 5-yr study period ($n = 25$ trap stations per enclosure). We expected that animal activity (the number of captures), rather than density, would best reflect local-scale predation pressure on seeds and seedlings. Differences in mouse and vole activity were examined using a split-factor ANOVA with the vole density treatment as the main-plot effect, distance from the forest edge as the subplot effect, and study sites as blocks (GLM pro-

cedure, SAS Institute 1993). Activity of mice and voles at individual trap stations was also used to calculate the average activity level for each species, within each enclosure, during the study. Subsequent linear regression analyses then compared these means with enclosure-specific tree seedling abundance as well as shrub and vine cover data to explore the nature and strength of the relationship between these variables (REG procedure, SAS Institute 1993).

As no tree seedlings were found in over two-thirds of sampling quadrats, these data could not be normalized. We performed a series of nonparametric Wilcoxon rank-sum tests and Kruskal-Wallis tests (NPAR1WAY procedure, SAS Institute 1993) to examine changes in tree seedling abundance ($n = 210$ quadrats) as a function of study site, vole density treatment, and distance from the forest edge. The number of tree seedlings found in each enclosure was regressed against the average activity of voles and mice ($n = 10$ enclosures) as a partial test of the hypothesis that tree seedling invasion should be greater in areas of low vole, but high mouse, activity.

We calculated the total cover of all vine and shrub species recorded along each sampling transect to generate a unique percent cover value for each combination of distance, enclosure, and census year ($n = 40$ transects per year). Although shrub and vine cover within enclosures was generally low to non-existent in 1994, transect surveys revealed that some shrub and vine growth had occurred since mowing in the fall of 1993 and before the start of vole density treatments the next year. Because of general absence of shrub and vine cover within enclosures in 1994, we used Wilcoxon and Kruskal-Wallis tests to determine whether pretreatment levels of shrub and vine cover in 1994 differed between vole density treatments, study sites, or distances from the forest edge. A similar analysis was performed on transect data in 1998 to facilitate comparison between years.

We estimated the rate of change in shrub and vine cover during our experiment by subtracting percent cover values for transects in 1994 from those in 1998 ($n = 40$ transects). A square-root transformation was used to normalize this variable prior to analysis. We tested for differences in rates of change in shrub and vine cover as a function of vole density treatment, distance from the forest edge, and study site using the split-plot ANOVA described previously. It was not possible to test distance × vole density treatment interactions using a split-plot ANOVA design. Therefore, additional regression analyses were used to examine how change in shrub and vine cover varied with distance from the forest edge under low vs. high vole density conditions ($n = 20$ for each regression). Tree seedling abundance within enclosures was regressed against average shrub and vine cover (combining the 1994 and 1998 transect censuses) to partially evaluate the hypothesis that tree seedling invasion should be

greatest in habitats avoided by voles but not by mice. Because shrub and vine cover change was independent of average shrub and vine cover over the 5-yr study period ($F_{1,7} = 1.33$, $P = 0.2931$, $r^2 = 0.044$), we performed additional regression analyses examining (1) the effects of average shrub and vine cover (independent variable) on mouse and vole activity within our experimental enclosures, and (2) how the change in shrub and vine cover within enclosures (dependent variable) varied as a function of average mouse and vole activity.

RESULTS

Animal activity

In total, 5256 small mammals were captured over the course of 27 250 trap-nights spanning five years of study. Of all species captured, meadow voles (*Microtus pennsylvanicus*) were by far the most active within our experimental enclosures, comprising 68.2% of all captures. White-footed mice (*Peromyscus leucopus*) were the next most abundant species (15.7% of captures), followed by short-tailed shrews (*Blarina brevicauda*, 11.6%), eastern chipmunks (*Tamias striatus*, 3.6%), and meadow jumping mice (*Zapus hudsonius*, 0.9%). Voles were significantly more active in the high-vole-density enclosures, whereas white-footed mice exhibited significantly higher activity within the low-vole-density enclosures (Table 1, Fig. 2A). Average vole and mouse activity also varied significantly with distance from the forest edge, but the activity of both species across sites was relatively constant (Table 1). Vole activity increased, whereas mouse activity decreased with distance from the forest edge (Fig. 2B). The activity of white-footed mice increased significantly within enclosures with higher average shrub and vine cover ($F_{1,7} = 49.8$, $P = 0.0004$); however, voles exhibited the reverse response and were less active within enclosures with more shrub and vine cover ($F_{1,7} = 9.0$, $P = 0.0238$; Fig. 2C).

Woody plant colonization

Altogether, 114 tree seedlings were encountered in sampling quadrats, yielding an average density of 0.27 seedlings/m² within enclosures. Significantly more tree seedlings established under low vole (81 seedlings) vs. high vole density (33 seedlings; $\chi^2 = 7.4$, df = 1, $P = 0.007$). The pattern of lower seedling colonization within high-vole-density enclosures was consistent at all sites except site number two, where this pattern was reversed; however, differences in tree seedling abundance between study sites were not statistically significant ($\chi^2 = 7.0$, df = 4, $P = 0.14$; Fig. 3A). Seedling abundance was significantly greater at distance classes farther from the forest edge ($\chi^2 = 7.2$, df = 2, $P = 0.027$). Regression analyses revealed that the number of tree seedlings within enclosures was significantly negatively correlated with the average activity of voles

TABLE 1. Split-plot ANOVA testing the effects of study site (block), vole density treatment (main-plot effect), and distance from the forest (subplots) on meadow vole (*Microtus pennsylvanicus*) and white-footed mouse (*Peromyscus leocupus*) activity, as well as the change in shrub and vine cover over the 5-yr study period.

Source of variation	df	MS	F
A) Vole activity			
Site	4	352.4	0.4
Density†	5	832.9	14.8***
Distance	4	1352.1	17.3***
Site × Distance	16	119.3	1.5
Density × Distance†	20	78.9	1.4
B) Mouse activity			
Site	4	7.1	0.7
Density†	5	107.8	6.5***
Distance	4	264.9	38.0***
Site × Distance	16	22.9	3.3**
Density × Distance†	20	6.96	0.4
C) Shrub and vine cover			
Site	3	6.9	2.9
Density†	4	2.4	3.5*
Distance	3	1.9	1.1
Site × Distance	8	2.5	1.4
Density × Distance†	5	1.7	2.5*

Notes: Random distances for shrub and vine cover transects were grouped into four distance classes (≤ 7.5 m, >7.5 m–≤ 15 m, >15 m–≤ 22.5 m, and >22.5 m) prior to analysis. The Type I mean squares for density treatment was used as the error term for site, whereas that for the density treatment × distance interaction was used in tests for significance of distance and the site × distance interaction.

  * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.
  † Factors nested within site during analysis.

($F_{1,9} = 7.7$, $P = 0.024$) and significantly positively correlated with the average activity of mice ($F_{1,9} = 10.6$, $P = 0.0115$; Fig. 3B). Further, the number of tree seedlings found within enclosures was positively correlated with the average shrub and vine cover present within enclosures during the study ($F_{1,7} = 7.4$, $P = 0.0348$; Fig. 3C). Of the 18 species of tree seedlings found within quadrats in our study sites, the most abundant were sugar maple (*Acer saccharum,* 17.5% of seedlings), white ash (*Fraxinus americana,* 13.2%), tree of heaven (*Ailanthus altisima,* 12.3%), choke cherry (*Prunus virginiana,* 11.4%), and American elm (*Ulmus americanum,* 9.6%). All of these species were common as adult trees along the forest edges at each site.

Differences in shrub and vine cover between study sites were highly significant at the start of the experiment in 1994 ($\chi^2 = 24.5$, df = 3, $P = 0.0001$), diminished slightly by 1998 ($\chi^2 = 19.0$, df = 3, $P = 0.0003$; Fig. 4A). There was no significant difference in pre-treatment levels of shrub and vine cover between the high- and low-vole-density enclosures ($\chi^2 = 2.1$, df = 1, $P = 0.1452$). However, by 1998, total shrub and vine cover was significantly lower in enclosures with the high- vs. the low-vole-density treatment ($\chi^2 = 3.9$, df = 1, $P = 0.0487$; Fig. 4B). We observed no significant differences in the amount of shrub and vine
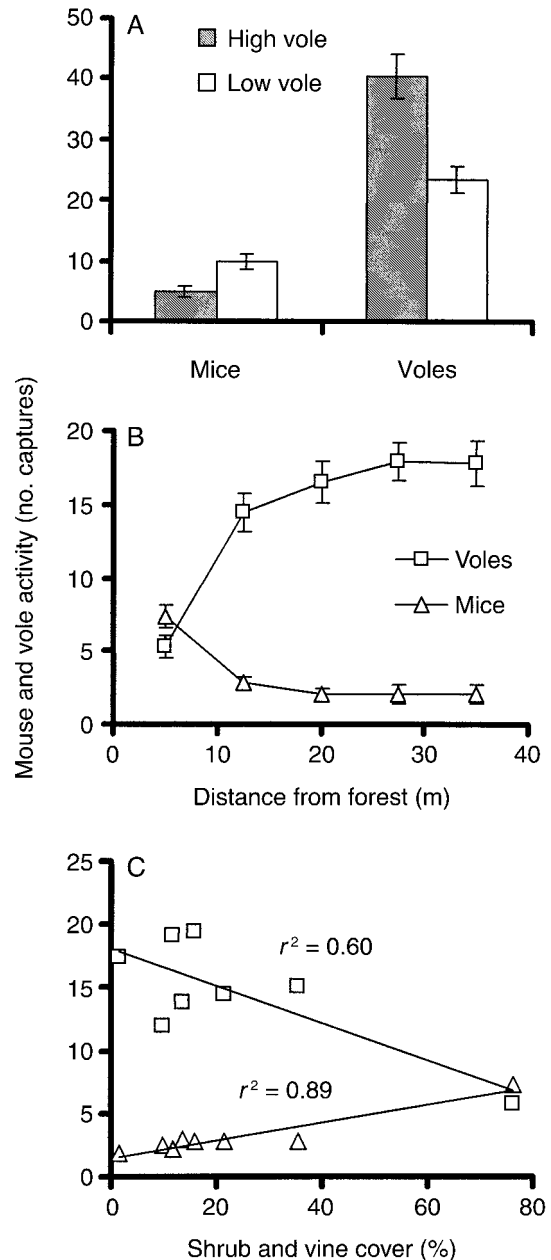

FIG. 2. Mouse and vole activity (mean ± 1 SE) as a function of (A) vole density treatment, (B) distance from the forest edge, and (C) the average amount of shrub and vine cover present within enclosures. Activity was determined by summing the captures of each species at each trap station within experimental enclosures and then calculating the mean of all trap stations for each vole density treatment, distance from the forest edge, or enclosure (n = 125, 50, and 25, respectively). Best-fit (P < 0.05) regression lines and adjusted r² values are provided for panel (C).

cover as a function of distance from the forest edge in either 1994 or 1998.

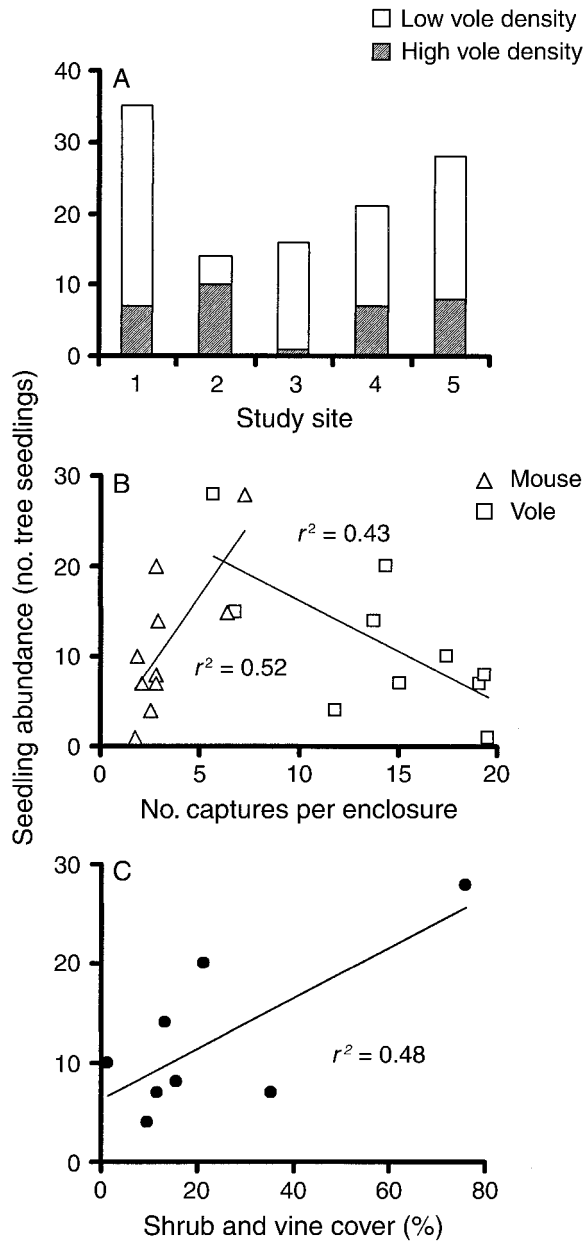The change in shrub and vine cover varied significantly between vole density treatments, but no varia-

FIG. 3. Abundance of tree seedlings (A) within the high-density and low-density vole enclosures at each study site, (B) within enclosures varying in mean mouse and vole activity, and (C) as a function of average shrub and vine cover present in enclosures during the study period. Best-fit ($P <$ 0.05) lines and adjusted r^2 values from linear regression are provided.

whereas no such distance effect was observed in high-vole-density situations ($F_{1,18} = 0.1$, $P = 0.81$; Fig. 5). The most common shrub and vine species establishing within the vole density enclosures were *Rubus flagellaris, Lonicera morrowi, Cornus racemosa, Rosa multiflora,* and *Rhus radicans.*

DISCUSSION

Evidence from this study supports the hypothesis (Ostfeld et al. 1999) that seedling predation by meadow voles (*Microtus pennsylvanicus*) plays a more important role than seed predation by white-footed mice (*Peromyscus leucopus*) in the invasion of trees into old fields in the northeastern United States. First, the number of tree seedlings naturally colonizing our study sites over a 5-yr period was significantly greater within enclosures with low vole density than in those with high vole density (Fig. 3A). Second, tree seedling abundance was negatively correlated with vole activity, but was positively related to mouse activity within experimental enclosures (Fig. 3B). Third, tree seedling abundance increased in enclosures with higher cover of shrubs and vines (Fig. 3C), where mice were more active and voles were less active, respectively (Fig. 2C). Previous work
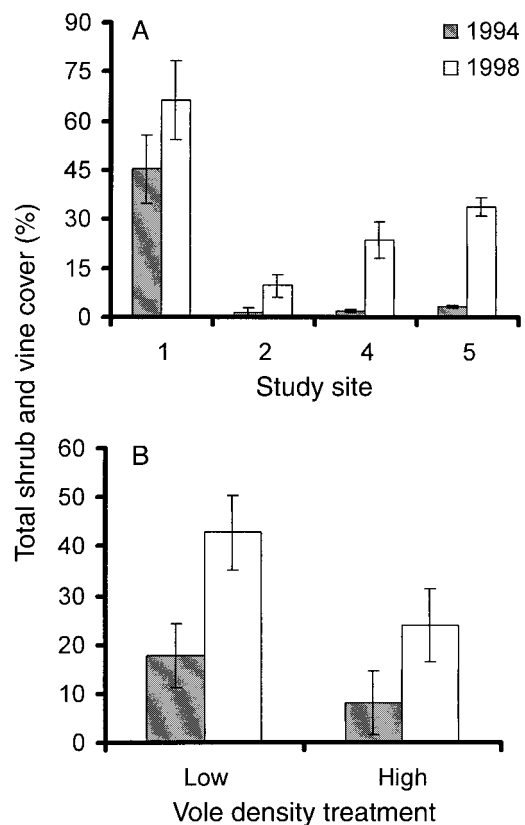

FIG. 4. Results of transect surveys of shrub and vine cover conducted in 1994 and again in 1998. Graphs show the percent cover (mean ± 1 SD) of shrubs and vines (A) across the study sites surveyed, and (B) under low- and high-density vole situations for each census year.

tion was observed with distance from the forest edge or across study sites (Table 1). Shrub and vine cover increased significantly faster within enclosures under the low- (increase of 25.1 ± 3.6%, mean ± 1 SE) than the high-vole-density treatment (15.8 ± 3.3%; Fig. 4B). Further, the invasion of shrub and vine cover decreased significantly with distance from the forest edge in low-vole-density enclosures ($F_{1,18} = 5.8$, $P = 0.0269$),
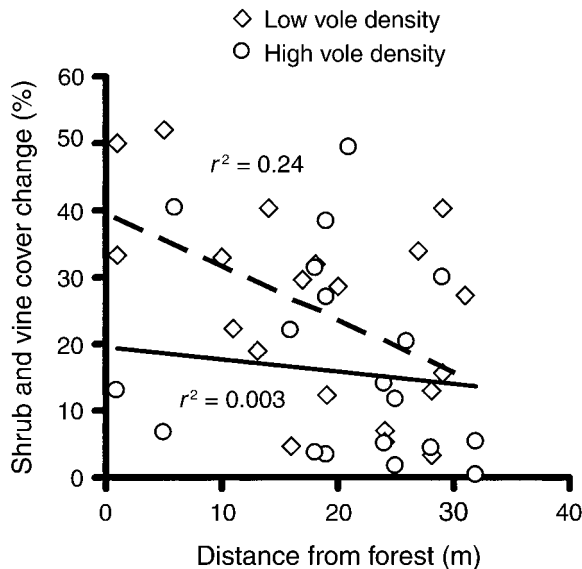
◇ Low vole density
○ High vole density

FIG. 5. Rate of change of shrub and vine cover within experimental enclosures as a function of distance from the forest edge under the low-density (dashed line) and high-density (solid line) vole treatments. Data points represent individual survey transects within enclosures. Best-fit ($P <$ 0.05) lines from linear regression and adjusted r^2 values are provided.

has also demonstrated preferences by voles for grass-dominated portions of old fields (M'Closkey and Field-wick 1975), which may help to explain differences in the relative rates of tree colonization observed in old fields with different amounts of shrub cover (Hill et al. 1995).

Apart from reducing the overall rate of tree invasion, voles may also influence the spatial pattern of tree seedling colonization of old fields. In contrast to predictions, seedling abundance was observed to increase with distance from the forest edge. This finding contradicts results from short-term herbivory studies suggesting that increasing vole activity in the interior of fields results in greater seedling mortality with distance from the forest edge (Ostfeld et al. 1997, Manson 1999), and observations that seedling density is typically highest adjacent to forest edges early in old-field succession (Hughes and Fahey 1988, Myster and Pickett 1992). Vole foraging, particularly at high population density, results in changes in the composition of herbaceous plant communities (Batzli and Pitelka 1970, Cockburn and Lidicker 1983). This, in combination with foraging by other small- to medium-sized mammalian herbivores, may reduce total herbaceous biomass in old fields (Bowers 1993). If such changes reduce the suppression of tree seedlings via competition from herbaceous species (Werner and Harbeck 1982), this could explain the higher tree seedling abundance that we observed in the interior of our old-field study sites.

A number of observations suggest that our results

may provide a conservative, but realistic, estimate of the potential impacts of voles on tree invasion into old-fields. First, significant differences in vole and mouse activity with distance from the forest edge (Fig. 2B) and within enclosures with different amounts of shrub and vine cover (Fig. 2C) suggest that our experimental vole density manipulations did not override the natural habitat preferences of these species. In addition, despite our vole density manipulations, vole density within our experimental enclosures varied substantially across years (Ostfeld et al. 1997, Manson 1999), mirroring the 3–5 yr population fluctuations that are typically observed for this and other *Microtus* species (Krebs and Myers 1974, Hansson and Henttonen 1988, Batzli 1992). Vole density manipulations during this experiment resulted in abundance (Ostfeld et al. 1997) and activity levels that were on the low end of the range typically observed for this species in old fields (Krebs and Myers 1974, Taitt and Krebs 1985, Ostfeld and Canham 1995). Finally, because vole density was manipulated only from spring through fall of each year, winter vole densities, and presumably the intensity of winter seedling predation, were allowed to equilibrate between vole density treatments. Such equilibration may have reduced the magnitude of the effects of changes in vole density on natural tree seedling establishment observable during this study.

In addition to inhibiting tree invasion, vole herbivory may also reduce the rate and modify the pattern of shrub and vine invasion into old fields. Previous studies suggest that vole herbivory on shrubs invading old fields may be high (Gill and Marks 1991). In the current study, the rate of increase of shrub and vine cover was significantly lower in enclosures with high vole density. Further, increases in shrub and vine cover were significantly lower farther from forest edges within enclosures under the low- but not the high-vole-density treatment (Fig. 5). High vole population density results in increased intraspecific antagonism and dispersal into less preferred habitats such as those near forest edges (Ostfeld 1992). Such density-dependent habitat use could explain why a negative relationship between change in shrub and vine cover and distance from the forest edge was only observed within low-vole-density enclosures.

If voles have a net negative impact on the rate of shrub and vine invasion in old fields, there may be a number of consequences for subsequent patterns of tree seedling invasion and old-field succession. Shrubs are often used as perches by birds. The defecation of tree seeds by birds on these perches appears to be a major mechanism accelerating tree colonization of old fields (McDonnell and Stiles 1983, Guevara et al. 1992), and is thought to explain the deterioration of the negative relationship between tree seedling density and distance from the forest edge that is typically observed as succession progresses (Myster and Pickett 1992, Myster 1993). On the other hand, by slowing seedling growth

and thus exposing seedlings to mortality agents for a longer period of time, shrub communities are thought to be an effective means by which tree invasion can be slowed in some old fields (Hill et al. 1995). The influence of shrub and vine cover on tree invasion dynamics in old fields, as well as the role of voles and other herbivores in shrub and vine invasion into these habitats, deserve more attention in future studies.

The negative impact of vole herbivory on the establishment of woody vegetation in old fields in this study corresponds with previous research demonstrating an inhibitory effect of herbivores on plant succession (Watt 1981, Brown 1982, Davidson 1993). However, as voles also appear to avoid woody vegetation cover, this study highlights the bi-directional nature of plant–vole interactions in old fields. Voles appear to be able to slow, but not stop, the invasion of woody species into old fields. Thus, as succession progresses in old fields and woody vegetation becomes more abundant, vole populations are expected to decline and their population fluctuations should become less pronounced (Lidicker 1988, Ostfeld 1992). This, in turn, should result in the highest predation rates on tree seedlings occurring earlier in succession, delaying domination by tree species, as well as decreasing tree seedling cohort structure through time. These predictions are consistent with long-term studies of tree invasion patterns in old fields (Buell et al. 1971, Pickett 1982, Rankin and Pickett 1989).

Power et al. (1996) defined a keystone species as one whose effect on community or ecosystem processes is greater than would be expected based on its relative biomass. Given the strong negative effects of voles on the rates of establishment of woody vegetation in general, and on tree seedling establishment in particular, as well as the relatively low biomass of this species in old fields (assuming 100 individuals/ha, and 40 g/vole, they contribute only 4 kg/ha), our findings support the contention that voles play a keystone role in tree invasion dynamics in old fields (Ostfeld and Canham 1993, Ostfeld et al. 1999).

Seed predation by white-footed mice had no apparent effect on rates of tree colonization within our experimental enclosures. Indeed, enclosure-specific activity of mice was positively correlated with tree seedling establishment after five years of study (Fig. 3B). This finding contrasts with the results of numerous studies that report levels of seed predation by mice that are consistently higher than rates of tree seedling predation by meadow voles (Mittelbach and Gross 1984, Gill and Marks 1991, Ostfeld et al. 1997, Manson et al. 1998, Manson 2000). Our results suggest that short-term measures of predation intensity may reveal little about the long-term net effects of small-mammal herbivores. A separate study of seedling predation by voles conducted at the same study sites suggests that vole seedling predation is continuous throughout the year and may ultimately reach levels of seed predation ascribed to mice

(71.4% of seedlings killed after one year; Manson 1999). In contrast, seed predation by white-footed mice, known dietary generalists (Baker 1968), may fluctuate with seasonal changes in the availability of other food types, and thus may not have the same effect as that of mammalian granivores in other ecosystems (Brown et al. 1979). Moreover, white-footed mice may, in some cases, facilitate seedling establishment by caching, rather than consuming, tree seeds (Abbot and Quink 1970). In addition to mice, substantial seed predation by invertebrate granivores has been noted in grasslands and old-field habitats (Mittelbach and Gross 1984, Hulme 1994, Reader 1997). Regardless of the particular seed predators involved, however, our results suggest that the process of tree invasion in old fields is less affected by seed than by seedling predation. Although the mortality of seeds may be extremely high (Cavers 1983, Fenner 1985, Reader 1997), a modest rate of seedling mortality may be more important in limiting tree invasion into old fields.

Vole herbivory on tree seedlings is one of many interacting factors that may influence old-field succession (Pickett et al. 1987). Previous studies (Livingston and Allessio 1968, Gill and Marks 1991) suggest that finding suitable conditions for germination is a major establishment barrier for trees in old fields. In addition, physical factors such as moisture availability (De Steven 1991b) and frost heaving (Buell et al. 1971) can readily influence the fate of newly germinated seedlings, as can competition with other old-field plants (Harper 1977, Rankin and Pickett 1989, De Steven 1991b). Finally, upon emerging from the herbaceous canopy, tree seedlings may be subject to browsing from other herbivores such as deer, which can exert powerful influences on plant communities (Waller and Alverson 1997). Although they describe only one of a number of ecological filters through which tree propagules must pass in order to successfully colonize old fields, our experiments demonstrate that herbivory by voles can be sufficient to influence the rate, and perhaps the pattern, of invasion by these woody species into old fields.

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