

Interactions Between Meadow Voles and White-Footed Mice at Forest–Oldfield Edges: Competition and Net Effects on Tree Invasion of Oldfields

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Introduction

When farmers in New England and New York abandoned fields wholesale during the mid-1800s to mid-1900s, either due to economic depression, urbanization, or when seeking more fertile fields in the Ohio Valley and midwestern prairies, they unwittingly initiated an ecological experiment of gigantic proportions. Fields abandoned from agriculture were invaded initially by herbaceous plants and later by woody species such as shrubs and trees. The result 50–150 years later is a regionwide landscape mosaic that consists of a matrix of forests within which are embedded oldfields still dominated by herbaceous or shrubby vegetation. Some oldfields have resisted invasion by trees over this period due to either active management (e.g., mowing for hay, grazing) or slow rates of succession. Outside urban and suburban areas, the process of reforestation of land surrounding oldfield patches has resulted in a massive proliferation of edges between forest and field. These edges are zones of tension between the dominant vegetation types on either side, and they are the sites of most rapid changes in plant communities due to the ongoing process of invasion by woody species. The “experiment” that commenced with abandonment from agriculture has allowed ecologists to ask, What *landscape patterns* result from differential rates of succession, and what *processes* are responsible for the existence of these landscape patterns? This chapter is concerned with some cryptic but fundamental processes that influence the ability of trees to invade oldfields, the species composition of tree invaders, and the spatial pattern of tree invasion.

Ecologists appear to be highly polarized on the role of animals in landscape patterns and processes. In one arena, the paradigm of landscape ecology (Forman and Godron 1986, Turner 1989) often assumes that landscape features, (e.g., the spatial arrangement and connectedness of habitat patches) are

fixed entities that simply provide the template within which organisms live, die, and move about. Under this paradigm, it is assumed that landscape structure and function are determined by human disturbance, interactions among plants, and interactions between plant communities and the physical environment, which together determine the types of species assemblages (habitats) that comprise the various patches. Animals are assumed to be affected by, but not to alter, the landscapes in which they live. Thus, in a patchy landscape, mobile animals are expected to respond behaviorally and demographically to features such as patch size, shape, and connectedness, but they are not expected to influence the landscape itself.

On the other hand, the paradigm of community ecology is more sympathetic to the view that animals may play a major role in structuring plant communities via disturbance, herbivory, or ecosystem modification (e.g., Coppock et al. 1983, Naiman et al. 1988, Cantor and Whitham 1989, Brown and Heske 1990, Huntly 1991, Jones et al. 1994, Johnston 1995), potentially changing the very nature of the landscape itself. Studies of the effects of animals on plant communities, however, generally focus on processes that occur within patches and ignore effects of animals on larger-scale issues, such as landscape structure and function. We support an integrated view of interactions between landscapes and animals and explicitly examine both the ways in which animals respond to landscape features and the means by which animals influence these features.

In this chapter, we will describe our ongoing research on the role of small mammals in plant community dynamics at forest–oldfield edges. Land-use history and current management practices have resulted in the proliferation of forest–field edges throughout our region. Such edges are critical features of eastern U.S. landscapes, and they influence wildlife habitat quality (Litvaitis 1993, Heske 1995), regional biodiversity of plants and animals (Marks 1983), and both predation and brood parasitism of nesting passerine birds (Yahner and Scott 1988, Rudnický and Hunter 1993). We will begin by describing the nature of these edges and their influence on the small-mammal communities on either side. We will then describe the importance of meadow voles (*Microtus pennsylvanicus*) as tree-seedling predators and of white-footed mice (*Peromyscus leucopus*) as tree-seed predators. Both the magnitude of the effects of these consumers and their tendency to select propagules of different species of trees are described. We will then discuss how both habitat selection and interspecific competition influence the spatial distribution of voles and mice in the vicinity of forest–oldfield edges, and how that translates into differential effects of the two species on survival of tree propagules at the edges and within the oldfields. Finally, we will create a conceptual model of how the interactions between mice and voles may influence the patterns of tree invasion of oldfields, how that process of invasion may affect the nature of the landscape for the rodents, and thus how animal consumers and landscape processes are linked in a feedback loop.

Plant and Rodent Communities at Forest-Oldfield Edges

Our studies are conducted at the Institute of Ecosystem Studies in Millbrook, Dutchess County, New York. This site is representative of many postagricultural rural landscapes of eastern New York and southern New England. The landscape consists of a mosaic of three primary patch types: (1) forests dominated by oaks, particularly red oaks (*Quercus rubra*) and black oaks (*Q. velutina*), that were formerly woodlots and pastures, respectively; (2) forests dominated by sugar maples (*Acer saccharum*), red maples (*A. rubrum*), and white pines (*Pinus strobus*) that were abandoned from row crops; and (3) shrub- and herb-dominated oldfields that were more recently abandoned from agriculture (Glitzenstein et al. 1990).

We selected oldfield sites that spanned the range of vegetation types within our region and which represented a spectrum of entirely herbaceous to shrub-dominated habitats. Herbaceous sites contained high coverage of grasses (*Schizachyrium scoparium*, *Bromus inermis*, and *Phleum pratense*), forbs (*Galium tinctorum*, *G. mollugo*, *Solidago juncea*, *S. rugosa*, *Vicia cracca*, and *Centuria maculosa*), and sedges (*Carex* spp.). Mixed herbaceous/shrubby sites contained honeysuckle (*Lonicera morrowii*), gray dogwood (*Cornus racemosa*) and multiflora rose (*Rosa multiflora*); shrub-dominated sites contained large clones of gray dogwood.

In herbaceous patches within this landscape, the meadow vole (*Microtus pennsylvanicus*) is the most abundant small-mammal species (Rose and Birney 1985, Ostfeld et al. 1997). Meadow voles are largely restricted to herbaceous habitats, and use forests only when dispersing (Tamarin et al. 1984, Kirkland 1990). Meadow voles tend to undergo dramatic seasonal and multiannual fluctuations in population density that may be cyclic (Krebs and Myers 1974, Tamarin et al. 1984, Batzli 1992) or erratic (Taitt and Krebs 1985, Batzli 1992). Some evidence suggests that voles occupy a restricted range of habitat types when density is low, and increasingly invade suboptimal habitats as density increases (reviewed by Ostfeld 1992a). Theoretical studies suggest that the tendency to undergo fluctuations in optimal habitats is affected by landscape features, particularly the ratio of optimal-to-marginal patch area (ROMPA; Lidicker 1988, 1991, Gaines et al. 1991, Ostfeld 1992b).

The white-footed mouse (*Peromyscus leucopus*) is the dominant small mammal in many forested habitats of eastern North America (Baker 1968, Wolff 1985, Dueser and Porter 1986, Morris 1991). Similar to voles, mouse populations often fluctuate dramatically, with population peaks in forests following years of good acorn production (Ostfeld et al. 1996, Wolff 1996). White-footed mice are more generalized than are meadow voles in their habitat use. In addition to forests, they occupy large gaps, clearcuts, and open fields (M'Closkey and LaJoie 1975, Drickamer 1976, Buckner and Shure 1985, Kirkland 1990). Several lines of evidence suggest that, like voles, white-footed mice disperse into suboptimal habitat types when density increases (Morris 1991, Ostfeld et al. 1996). Use of some open habitat types by white-

footed mice, however, appears to be inhibited by the presence of meadow voles (Grant 1972, Bowker and Pearson 1975, M'Closkey and Fieldwick 1975, Kaufman and Kaufman 1989). As a result, use of oldfields by white-footed mice tends to be concentrated in shrub-dominated patches, which are generally avoided by voles. Our prior studies have shown that meadow voles are the principle predator on tree seedlings in oldfields (Ostfeld and Canham 1993, Ostfeld et al. 1997), whereas white-footed mice are the primary predator on tree seeds in both forests and oldfields (Ostfeld et al. 1994, 1997, Manson and Stiles 1998).

Experimental Approach

Most of our experiments are carried out at edges between oldfields and both oak-dominated and maple-dominated forests. Our general approach is to simulate population fluctuations of voles by manipulating their population density inside enclosures either within oldfields or at forest-oldfield edges. We then determine the influence of meadow vole density on: (1) overall magnitude of predation on tree seedlings; (2) spatial pattern of predation on seedlings; (3) differences among tree species in intensity of seedling predation; (4) population density of white-footed mice; (5) magnitude and spatial pattern of predation on tree seeds by mice; and (6) differences among tree species in intensity of seed predation by mice.

We have employed two types of enclosures. In the first type, complete enclosures were constructed within herbaceous oldfields. In 1990 we built nine 40 × 40 m enclosures within which we maintained vole populations at three different densities (low, medium, high), with three replicates of each (Fig. 11.1A). In the second type, six pairs of U-shaped enclosures were erected in 1994 at forest-field edges, with fences extending 5 m into the forest and 35 m into the adjacent oldfield. The forest edge of the enclosures was not fenced in order to allow rodents to travel freely across the forest-field edge (Fig. 11.1B). We expected that white-footed mice would enter and exit the enclosures freely, whereas voles would perceive the edge as a barrier and maintain populations largely within the enclosed oldfields (Tamarin et al. 1984). We use a regular live-trapping protocol to census and manipulate small mammals within each enclosure. Due to consistently high capture probabilities for both voles and mice, we estimate population density of rodents as the minimum number known alive.

For the partial enclosures, we randomly designated one enclosure of each pair as a high-vole-density treatment and the other as a low-vole-density treatment. This manipulation allows us to examine the direct effects of vole density on survival of tree seedlings as well as the indirect effects of voles on seed survival via their effects on white-footed mice. To maintain differences between the two vole-density treatments, we removed selected numbers of voles from low-density enclosures and then released them into nonadjacent, high-density enclosures.

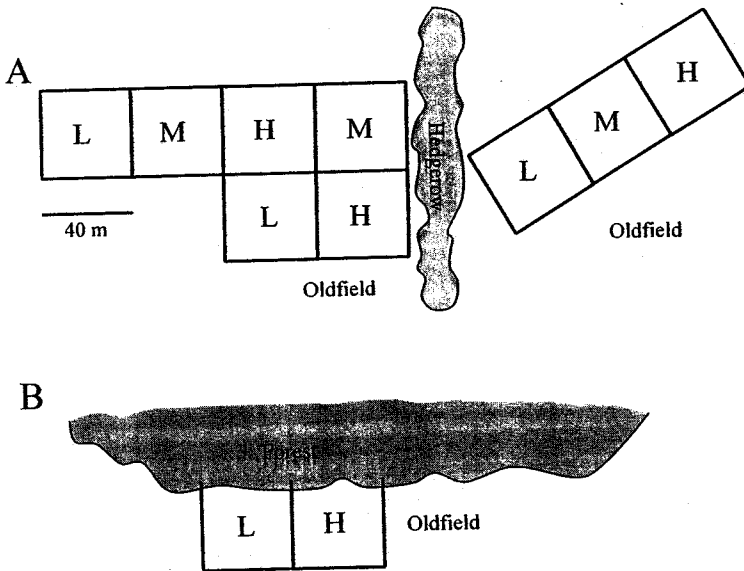


FIGURE 11.1. Diagram of the two types of study designs at the Institute of Ecosystem Studies. In (A) we show the nine 40×40 m enclosures used in our studies of the effects of meadow vole density on survival of tree seedlings, during which vole populations were maintained for 22 months at either low (L), medium (M), or high (H) density (see Ostfeld and Canham 1993). The diagram in (B) represents the design of our more recent studies in which we constructed six pairs of enclosures at forest-oldfield edges. One such pair is shown in the figure. Enclosure walls were again 40-m long, but they extended 5 m into the forest and 35 m into the oldfields in this design, and were unfenced on the forest side. Vole densities were maintained at either low (L) or high (H) levels. Each enclosure had a 5×5 grid of live traps with 7.5 m spacing between trap stations. Trapping was used both to estimate and to manipulate population density. In these studies (see Ostfeld et al. 1997) we examined effects of both meadow voles and white-footed mice on survival of both tree seeds and seedlings. Specific experiments are described in the text.

Predation by Rodents on Tree Seeds and Seedlings

To examine predation by rodents on tree seeds and seedlings, we introduce these propagules into our experimental enclosures in replicated stations at least 5 m apart, and monitor their fates over the ensuing several months to a year. In the majority of cases of killed or missing propagules, we are able to attribute the cause of removal to voles, mice, or other consumers by examining patterns of clipping or excision of the seed, and by signs such as runways, diggings, or feces at or near the station (Gill and Marks 1991, Ostfeld and Canham 1993, Ostfeld et al. 1997).

Effects of Voles on Tree Seedlings

We have found that meadow voles are voracious consumers of tree seedlings, and that their effects on seedling survival are strongly dependent on vole density. When vole density reaches levels characteristic of population peaks, cohorts of seedlings are virtually eliminated (Ostfeld and Canham 1993). However, when vole density is at levels characteristic of population troughs, 50–80% of seedlings survive (Fig. 11.2). Voles tend to prefer tree species such as red maple, white ash (*Fraxinus americana*), and tree of heaven (*Ailanthus altissima*), and they tend to avoid oaks, white pine, and eastern hemlock (*Tsuga canadensis*) (Ostfeld and Canham 1993, Ostfeld et al. 1997). In addition, predation by voles is most intense on seedlings that are less than 1 year old and decreases considerably on 2–3-year-old seedlings. For instance, small (0.5–1.5-mm stem diameter) white ash seedlings were 3.5 times more likely to be killed by voles than were larger (2.0–5.0 mm) seedlings (Ostfeld et al. 1997).

To integrate these results, we have argued (Ostfeld and Canham 1993, Ostfeld et al. 1997) that vole population dynamics are a keystone process in oldfield succession, whereby the magnitude of population peaks and the duration of low phases between peaks may have profound effects on the ability of trees to invade. The vast majority of seedlings that germinate immediately before or during vole

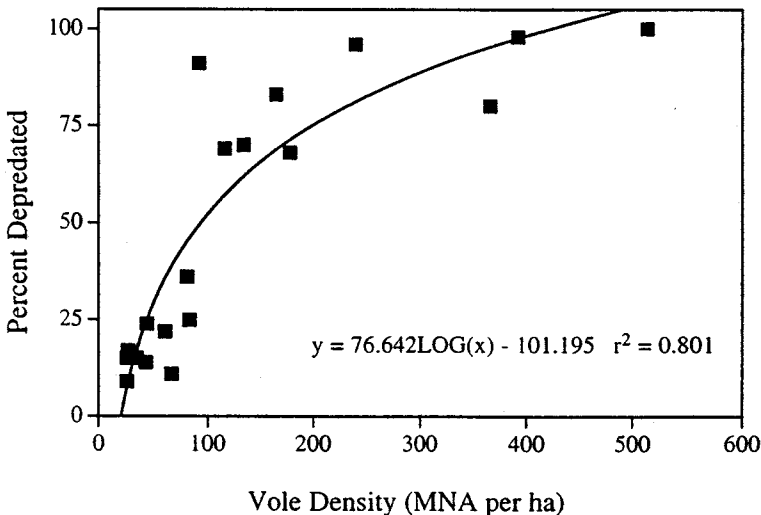


FIGURE 11.2. Percentage of young (<2-year-old) seedlings depredated by meadow voles as a function of vole density. Each data point represents the combined average for a specific enclosure of the total percentage of seedlings depredated and the density of voles over the time seedlings were censused. Data points near the origin represent experiments run in partial enclosures (see Fig. 11.1B and Ostfeld et al. 1997), during which vole density did not exceed 100 individuals/ha. Other data points are from the earlier experiments run inside total enclosures in fertile, lowland fields, where vole density generally was higher (see Fig. 11.1A and Ostfeld and Canham 1993).

peaks are doomed due to extremely high rates of predation, and we expect nearly complete failure of seedling cohorts appearing in those years. Seedlings establishing during low phases in vole population fluctuations have a much higher probability of surviving, but remain highly susceptible to vole herbivory until they reach a stem diameter of about 2.0–5.0 mm (Ostfeld et al. 1997). The rate at which this size is achieved depends on species of tree and on both biotic and abiotic factors in the oldfield (Hill et al. 1995). Under typical conditions at our field sites, seedlings need 2–4 years to grow to a size at which their probability of being killed by voles is substantially reduced. Thus, seedlings that establish early in the low phase of a vole cycle have a higher probability of surviving than do those establishing 1–2 years later, but the duration of the low phase in vole density will be critical to the probability of survival. When vole populations remain chronically high or reach peaks every second year, tree invasion may be prevented indefinitely, but when voles reach peaks only after 2–5 years of low density (a common pattern; Krebs and Myers 1974), cohorts of seedlings may survive, grow, and ultimately reduce habitat quality for voles by transforming oldfield vegetation from herbaceous to woody structure.

Effects of Mice on Tree Seeds

White-footed mice are avid consumers of tree seeds, and predation intensity varies with fluctuating mouse density in both forests and in oldfields (C.D. Canham and R.S. Ostfeld, unpubl. data). When mouse density reaches levels of about 25 individuals per hectare, which represents high density in oldfields but moderate density in forests (Ostfeld et al. 1996, 1997), 75% to well above 90% of tree seeds we experimentally introduced into forest or oldfield plots were removed over the several-month period of vulnerability from autumn through winter (Ostfeld et al. 1994). Rates of seed predation dip below 50% over winter only when mouse density is below about 10 individuals per hectare. Several studies (Pucek 1993, Ostfeld et al. 1996, Wolff 1996) have shown that the density of forest mice (*Peromyscus* spp. and *Apodemus flavicollis*) fluctuates with production of hard mast by species such as oaks, reaching peaks the summer or autumn following mast production and crashing to very low numbers after 2–3 consecutive years of mast failure. Many masting species produce acorn crops at intervals of 3–5 years (Sork et al. 1993), which often results in mouse populations that crash between mast years and are at low density when abundant acorns are produced. This mechanism would facilitate predator satiation and potentially result in periodic recruitment of seedlings followed by several years of recruitment failure when mouse density recovers.

Our studies also show that the intensity of seed predation by small mammals varies with species of seed. For example, red oak acorns and white pine seeds are highly preferred, whereas white ash and maple seeds are of intermediate preference, and tree of heaven seeds are strongly avoided (Ostfeld et al. 1997). Note that the species preference rankings of mice for seeds are almost exactly the reverse of those of voles for seedlings.

Spatial Distribution of Vole and Mouse Activity

Meadow voles and white-footed mice segregate spatially along at least two axes: a gradient of herb-dominance to shrub-dominance within oldfields, and a gradient of distance from the forest edge. We will address these two axes in turn. Voles tend to be more abundant and to have stronger effects on seedling mortality in herbaceous than shrub-dominated oldfields. Among our six oldfield sites, the highest vole densities are observed in enclosures with high percentage cover of grasses and herbaceous dicots, whereas the lowest vole densities occur in the site with the highest percentage cover of shrubs. The proportion of tree seedlings killed by voles varies significantly among these sites as well, exactly paralleling the patterns of vole density (Ostfeld et al. 1997). In marked contrast, intensity of seed predation tends to be highest in shrub-dominated sites and lowest in herbaceous sites (Fig. 11.3). This pattern of increased seed predation with increasing oldfield shrubbiness corresponds closely with the pattern of higher mouse density in shrub-dominated sites. Thus, voles and mice exert their strongest effects on mortality of tree propagules in different oldfield types.

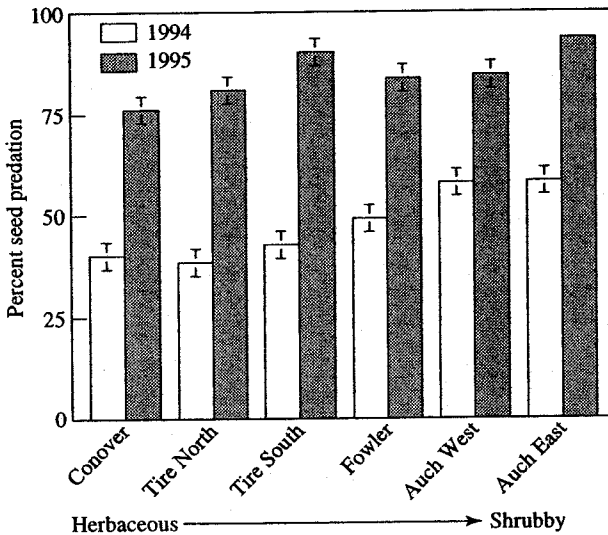


FIGURE 11.3. Average (± 1 SE) percentage of seeds depredated as a function of the relative degree of shrub cover in oldfields. Data are presented for both 1994, when density of white-footed mice was moderate to low, and 1995, when mouse density was high.

Voles are substantially more likely to kill seedlings introduced 10 m away from the forest edge than those planted <10 m from the edge or within the forest (Ostfeld et al. 1997). This spatial pattern parallels activity patterns of voles. Our capture records over 3 years of trapping reveal that voles tend to avoid (or experience high mortality within) the zone extending from the forest–field edge to about 10 m into the field (Fig. 11.4). In contrast, intensity of seed predation is generally high throughout the gradient from 5 m into the forest to 20 m into the oldfield, but is highest in the zone avoided by voles; seed predation is typically more intense at distances 5–10 m from the forest edge than at greater distances (Ostfeld et al. 1997). Seed predation was unexpectedly high 5 m into the forest interior only in 1 year of our study (1995), when mouse density was high, but not in 1994, when mouse density was moderate (Ostfeld et al. 1997). Seed predation rates are comparatively low at the forest–field edge itself (Fig. 11.5). This spatial pattern of seed predation contrasts somewhat with the pattern of mouse activity as revealed by our trapping records. Mice are captured at greatest frequencies in the zone extending from the edge to about 10 m into the field (Fig. 11.5). Thus, although

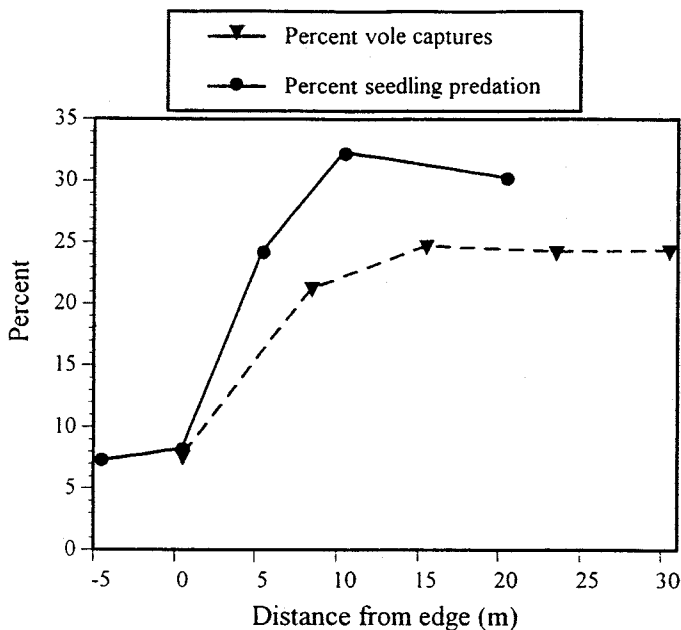


FIGURE 11.4. Relationship between activity of meadow voles and seedling predation as a function of distance from the forest edge. Percentage of vole captures refers to the total percentage of captures of voles in all grids combined for 1994 and 1995 combined, demonstrating gross patterns of distribution with distance from the forest edge. Percentage of seedling predation refers to the total percentage of all small (≤ 2 -year-old) seedlings of all species killed by voles, over both 1994 and 1995 combined.

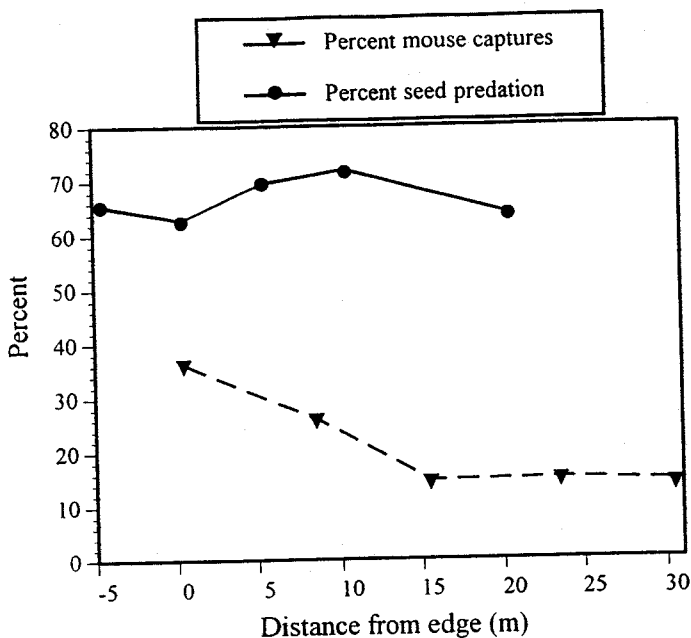


FIGURE 11.5. Relationship between activity of white-footed mice and seed predation intensity as a function of distance from the forest edge. Percentage of mouse captures refers to the total percentage of captures of mice in all grids combined for 1994 and 1995 combined, demonstrating gross patterns of distribution with distance from the forest edge. Percentage of seed predation refers to the total percentage of all seeds of all species killed over both 1994 and 1995 combined.

mice are captured frequently at the edge, they apparently are not lingering there to forage, but perhaps are in transit to or from the adjacent 10-m-wide zone, where they exert their strongest effects on seeds. Voles and mice clearly exert their strongest effects on mortality of tree propagules at different distances from the forest edge.

Effects of Seed and Seedling Density

When tree propagules exist in dense aggregations, they may experience either increased or decreased probability of being killed by a small mammal. Where propagules are aggregated, individual seeds or seedlings may have a high probability of surviving if the local food supply is sufficient to satiate predators that use the area. On the other hand, an aggregation of propagules may attract predators, resulting in a lower per capita probability of surviving than would occur in areas where propagules are more sparsely distributed. The Janzen–Connell escape hypothesis (Connell 1971, Janzen 1971) postu-

lates that tree propagules have a higher probability of surviving when they occur sparsely at a distance from the parent tree. It is widely accepted that this model helps explain why conspecific trees in tropical forests are often widely spaced rather than clustered in dense stands. In both tropical and temperate forest trees, seed-dispersal distances are extremely limited (Ribbens et al. 1994, Schupp and Fuentes 1995), and high densities of seeds tend to occur directly beneath parent trees. Gradients of decreasing density occur with increasing distance from parent tree (Houle 1995).

To test the applicability of the Janzen–Connell model to temperate oldfields, we mimicked the exponential decline in propagule density with distance from a seed source by introducing both red maple seeds and black birch (*Betula lenta*) seedlings at three different densities in small plots within our oldfield sites. Both of these species are common early invaders of oldfields in our region (Glitzenstein et al. 1990). For black birch seedlings, we used densities of 25, 10, and 5 seedlings/m² within adjacent 2 m² plots. For red maple seeds, we used densities of 750, 375, and 75 seeds/m² in adjacent 2 m² plots, and included an additional low-density plot (75 seeds/m²) 10 m from the group of three plots to mimic the tail of a leptokurtic distribution. During our experimental monitoring, vole densities were moderate on average, whereas mouse densities were high. We observed that seedlings in the high-density plots experienced a significantly lower per capita rate of predation than did those in medium- and low-density plots, which suggests that voles were satiated by plots of high seedling density (Manson et al., 1998). In contrast, proportion of seeds depredated was uniformly high (ca 99%) in the three adjacent plots irrespective of density, but predation was significantly reduced in the isolated, low-density plots (ca 89%) (Manson et al., 1998).

We suggest that, on a local scale, white-footed mice are unlikely to be satiated by high densities of seeds, especially when mouse densities are high. Seeds that are dispersed to greater distances from a locally dense seed source (i.e., away from the parent tree) are much more likely to escape predation by mice and to germinate. Thus, at the local scale, foraging by mice is consistent with the Janzen–Connell escape hypothesis. Because seed survival is higher farther away from parent trees, mouse foraging should tend to favor overdispersed distribution of conspecific trees and, thereby, favor high tree species diversity within local areas. We expect dense local aggregations of seedlings only in years following low mouse density, or when masting results in seed–predator satiation over large areas. Seedlings within dense local aggregations are more likely to escape predation by voles than are those occurring more sparsely, consistent with the predator–satiation hypothesis. The cause of differences between voles and mice in response to aggregation of tree propagules is unknown, but it may be related to species-specific functional responses (Ims 1990). The outcome, however, is that foraging by mice should tend to favor overdispersion, and that by voles should favor aggregation of tree propagules.

Synthesis: Does It Matter Whether Voles or Mice Predominate in Oldfields?

The results we described previously demonstrate that meadow voles and white-footed mice clearly are not functionally redundant in their effects on tree invasion of oldfields. Meadow voles prey on seedlings of maples, white ash, and tree of heaven most heavily, and they tend to avoid seedlings of red oak, white pine, and eastern hemlock. In contrast, white-footed mice prefer seeds of red oak and white pine, avoid tree of heaven, and have intermediate impacts on maples and ashes. Seedling predation by voles is most intense in herbaceous fields, whereas seed predation by mice is heaviest in shrub-dominated fields. Voles have their strongest effects on seedling mortality in sites >10 m away from forest edges, whereas seed predation by mice is strongest in the zone within 10 m of the forest edge. Finally, herbivory by voles may favor aggregations of seedlings, whereas granivory by mice may favor overdispersion of seeds. Thus, whether meadow voles or white-footed mice occupy an oldfield will have profound effects on several key features of tree invasion from adjacent forests. These features include the species of tree most likely to invade, oldfield type most easily invaded; rate of expansion of the edge; and patchiness of tree invaders.

Which of these two common species of rodent occupies an oldfield depends on features of the field (herbaceousness vs. shrubbiness) as well as on competitive interactions between the species themselves. Our results confirm prior suggestions that meadow vole and white-footed mouse populations interact within oldfields, and that their interaction is asymmetrical (Grant 1972, Bowker and Pearson 1975, M'Closkey and Fieldwick 1975). Oldfields comprise optimal habitat types for meadow voles (Getz 1985), although several studies suggest that shrub-dominated oldfields are of poorer quality than are herbaceous fields (Bowker and Pearson 1975, M'Closkey and Fieldwick 1975). It is possible that shrub-dominated oldfields comprise dispersal sinks (Lidicker 1975) for voles, supporting relatively high vole density only when colonized by dispersers from herbaceous fields during population peaks. On the other hand, oldfields in general are a suboptimal habitat type for white-footed mice (Lackey 1978, Linzey and Kesner 1991), and mice with home ranges near forest-field edges may enter oldfields opportunistically, remaining predominantly within the forest habitat when conditions in the oldfield are unfavorable. Our results show that two principal variables affect the favorability of oldfields for mice: (1) vole density (negative effect) and (2) shrub density (positive effect). Although vole density tends to be lower in areas of high shrub density, our experimental manipulations of vole density in various oldfield types show that vole density and shrub density clearly have independent effects on mouse density (Ostfeld et al. 1997).

Our results suggest that herb-dominated oldfields of the northeastern United States will tend to be occupied predominantly by meadow voles, but that vole density will fluctuate dramatically among years. Mice, we suggest, will

readily invade herbaceous oldfields either when density of voles is low (e.g., in the years between population peaks), or when dispersal pressure of mice is high (e.g., in the years that follow heavy mast production in adjacent oak-dominated forests). We expect that shrub-dominated oldfields of the northeastern United States will tend to be occupied predominantly by white-footed mice, and that their colonization of these suboptimal habitats types will fluctuate with mouse density within, and, thus, dispersal pressure from, adjacent forests, which are more favorable habitat types. Moreover, if vole populations in shrub-dominated fields reach high density due to dispersal from optimal patches, then mice will be inhibited from colonizing. One key issue that remains to be studied is whether voles and mice fluctuate synchronously or independently.

Our studies as well as others (Mittelbach and Gross 1984, De Steven 1991, Bowers 1993, Hulme 1996) have shown that seed and seedling predation by small mammals are often the most important mortality factors for these life stages of trees; thus, small mammals may have a profound effect on plant community dynamics. Based on the differential effects of meadow voles and white-footed mice on tree invasion processes, and their differential dynamics in herbaceous and shrub-dominated oldfields, we can make the following—as yet untested—predictions.

1. Herbaceous oldfields will tend to be invaded most readily by conifers (e.g., pines) and oaks, whereas shrub-dominated oldfields will be invaded most quickly by *Ailanthus*, maples, and ash. Note that this prediction assumes that oldfields of both types have similar seed pools invading from adjacent forests, and that these seed pools include all major tree species, which is an assumption that will rarely be true. Thus, a corollary of this prediction is that herbaceous oldfields adjacent to conifer- or oak-forests will be invaded more quickly than will those adjacent to maple-dominated forests. Shrubby oldfields adjacent to conifer- or oak-dominated forests will similarly be invaded more slowly than will those adjacent to maple-dominated or *Ailanthus*-dominated forests.
2. When herbaceous oldfields *are* invaded by maples and ashes, the cause will be either (a) seedling establishment that occurs early in a prolonged low phase in vole population dynamics, or (b) seedlings establishing in dense aggregations due to particularly heavy seed production, and satiation of vole seedling predators.
3. Tree invasion in herbaceous oldfields will tend to be concentrated within 10 m of the forest edge, whereas invasion in shrub-dominated fields will be more common at distances further into the interior of the oldfield.
4. Herbaceous oldfields will tend to be invaded by small patches of trees with a clumped distribution, whereas invading trees in shrub-dominated oldfields will have a more uniform distribution.

5. Herbaceous oldfields will tend to be colonized by trees exhibiting a cohort structure, often with 3–5 years between cohorts, reflecting fluctuations of vole density. In the case of shrub-dominated oldfields, cohorts will tend to occur only for masting species colonizing from adjacent forests. If outbreak densities of voles invade shrubby oldfields and suppress mouse populations therein, then we would expect to see periodic cohorts of *Ailanthus*, maples, and white ash that disperse seeds during the vole peak.

Interactions Between Rodents and Landscapes as a Feedback Loop

A great deal of attention has been focused on the ways in which landscape features, such as degree of fragmentation, patch size and shape, and patch connectivity, influence small mammals at the level of individuals and populations (Harper et al. 1993, Diffendorfer et al. 1995a,b, Bowers et al. 1996a,b, Collins and Barrett 1997). Our primary purpose in this chapter is to point out that the interaction between landscapes and small mammals is bidirectional. Small mammals clearly have the potential to influence the landscapes they inhabit by altering the interactions between plant community types both at edges and in the interiors of patches (Fig. 11.6). Thus, although lag times of years to decades may be involved, the effects of small mammals on plant communities may alter the degree of fragmentation, the size and shape of patches, and the degree to which patches are connected. Although small mammals respond to habitat edges in various ways that may influence their population dynamics (Lidicker and Peterson, Chapter 10), small mammals also affect the nature of those edges, a process that ultimately may feed back into animal population dynamics. Small mammals and landscapes are intimately connected in a feedback loop.

Great strides have been taken in describing how small mammals respond to experimentally altered landscapes (e.g., see Chapters 3, 4, and 6–9 in this volume). These experimental landscapes, which have been concocted largely by mowing to create habitat islands surrounded by a sea of less suitable space, have shown the potential for rodent populations to respond to landscape features at relatively small scales. The responses by small mammals to these carefully created landscapes, however, provide only a model of how the animals may respond to patchiness or fragmentation in the real world. Thus, these experimental model systems are more useful at providing clear, quantitative predictions about small mammals in patchy landscapes than they are at providing tests of those predictions. Two major challenges remain: (1) to determine whether experimentally contrived landscapes are indeed good model systems that mimic the real world; and (2) to begin to look for feed-

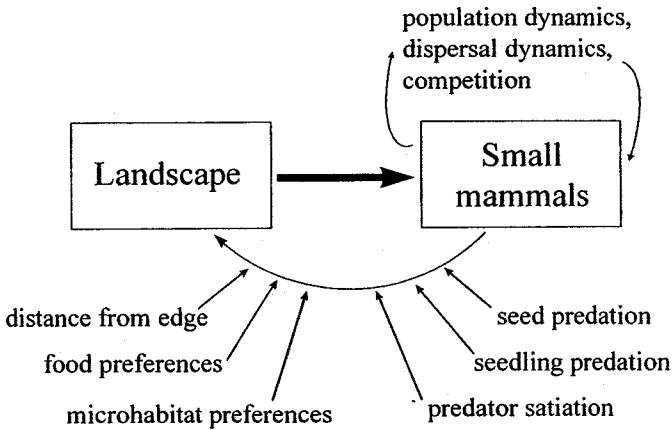


FIGURE 11.6. Schematic diagram of proposed two-way interaction between landscapes and small mammals. The thickness of the arrow from “landscape” to “small mammals” represents the predominant focus of attention on the influence of landscape patterns on small mammals. The thin reverse arrow indicates that the effects of small mammals on landscapes have received far less attention. Six factors impinging on the thin reverse arrow indicate some primary processes that influence the pattern of small mammal effects on some landscape features, which are described in the text. Curved arrows leaving and entering the “small mammals” box indicate some primary processes that influence the composition and dynamics of small mammal communities, which in turn influence many aspects of their impact on landscapes (see text for further description).

back loops in both contrived and real landscapes, and determine the factors that influence the effects of small mammals on these landscapes.

Applications for Management at the Landscape Scale

Interactions between rodents and tree propagules have two principal implications for landscape management. If the desired management endpoint is tree regeneration in oldfields, clearcuts, or other disturbed habitats, then rodent populations must be controlled either directly or indirectly through habitat management. In herbaceous habitats dominated by meadow voles, white pine and other species not preferred by this herbivore are most likely to survive, whereas seedlings occurring in dense clumps are most likely to satiate seedling predators. Seedlings introduced near forest edges are most likely to persist. In shrub-dominated habitats occupied by white-footed mice, *Ailanthus* and very small-seeded species are most likely to survive, but clumps of seeds will be unlikely to satiate predators. Seeds introduced far from forest edges have the best chance of persisting. If the desired endpoint is the management of open space, then rodent populations should be encouraged. If patches of

open space are small or isolated from similar patches by inhospitable matrix, corridors may be necessary to maintain viable populations of rodents. Management of rodent populations and their habitats is a poorly explored enterprise. Because many possible benefits of such management exist, we urge managers and ecologists to investigate methods and outcomes of rodent management.

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