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"Rodens & Spatium IV"				

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THE ROLES OF SMALL RODENTS IN CREATING PATCHY ENVIRONMENTS

Most research on the interaction between small rodents and patchy environments assumes that the rodents respond to, but do not affect, patchiness. We describe several modes by which voles and mice may create or destroy patchiness in plant communities. The modes include runway construction, selective foraging on herbaceous plants, predation on tree seedlings in old fields, and predation on both seeds and seedlings in forests. The spatial scales of the effects of rodents on plant communities are considered. We suggest that the interactions between rodents and patchy habitats be considered as a dynamic feedback, rather than a one-way relationship.

Key words: Small rodents, patchy environments, effects of rodents on plant communities.

1. INTRODUCTION

Current paradigms regarding the population ecology of microtine (= arvicolid) rodents were established in the "golden age" of field studies (1960s and 1970s). Most research was directed at what many considered the central problem to be explained: why do vole populations fluctuate cyclically through time? (Krebs et al. 1973). In order to document cyclic fluctuations and understand their causes, the predominant approach was to establish live-trapping grids in areas of prime

vole habitat, where voles could be expected to reach high densities. This approach permitted ecologists to make the simplifying assumption, often tacitly, that the causes of cyclic fluctuations could best be discovered from processes occurring within areas of homogeneous habitat quality. Although earlier discussions of the importance of habitat heterogeneity to rodent population dynamics had been published (e.g., Elton 1942, Naumov 1972), apparently they were not strongly influential.

During the 1970s and 1980s, the existence and role of habitat heterogeneity were rediscovered and incorporated into a series of conceptual models of the influence of patchy landscapes and dispersal on rodent population dynamics (e.g., Lidicker 1975, Hansson 1977, Anderson 1980, Lomnicki 1980, Stenseth 1980). These models emphasized the notions that (1) vole populations inhabit landscapes composed of a series of more or less discrete habitat patches, (2) these patches differ in quality, particularly in the length of time (seasonally) that they are suitable, and (3) density dependent dispersal among patch types should influence the stability of the subpopulations in each patch as well as the population occupying the entire mosaic. It often was assumed that the relevant scale of heterogeneity is on the order of hectares. Empirical studies and more formal modelling efforts have supported the hypothesis that patchiness at this scale affects vole population dynamics (reviewed by Ostfeld 1992a, 1992b).

In the 1980s ecologists began to recognize that heterogeneity on smaller spatial scales (i.e. 1–100 m²) may also affect vole populations, primarily through its influence on the behavior of individuals (e.g., Cockburn and Lidicker 1983, Ostfeld, Lidicker and Heske 1985, Ostfeld 1985, Stenseth 1986, Ims 1988). However, studies of small-scale heterogeneity focused more on the evolution of behavioral strategies, such as territoriality, and less on implications for population regulation (Cockburn 1988). Because spatial heterogeneity occurs along a continuum of scales, it is important to integrate the effects of small and larger scale heterogeneity on population processes in voles.

It is clear that major habitat discontinuities (e.g., forest-field edges) result in discontinuities in the composition of rodent communities (e.g., Grant 1972). However, the role of more subtle heterogeneity in rodent community dynamics is poorly understood. The importance of habitat heterogeneity in the structure of rodent communities is well demonstrated in desert and forest systems (e.g., Brown 1975, Kotler and Brown 1988), but not in grassland and tundra communities.

Much work remains to be done to understand the implications of spatial heterogeneity for processes occurring at the levels of individual, population, and community. Moreover, integration of the effects of heterogeneity at different spatial scales will be a key task for the 1990s and beyond. However, it is critical to recognize that small rodents not only respond to heterogeneity, but also create it. Thus, there may be a dynamic feedback between rodents and plant communities mediated by spatial heterogeneity. The purpose of this paper is to explore several mechanisms by which small rodents may create and destroy

patchiness in plant communities, and key consequences of that patchiness to the rodents themselves (i.e. the feedback).

Much of our discussion will concern the effects of rodents, especially voles, on plant heterogeneity, rather than on patchiness per se. If the heterogeneity the voles produce occurs as more or less discrete variation in plant species composition, architecture, or physical structure, then by definition (Ostfeld 1992a) it constitutes patchiness.

2. SCALE

Just as voles are affected by heterogeneity across a range of spatial scales, they may also influence heterogeneity on scales of square meters to many hectares. The activities (e.g., foraging, burrowing) of individual rodents will have their primary effects at scales of $< 1 \text{ m}^2 - 100 \text{ m}^2$, which encompass typical home range sizes for many species. The effects of populations, of course, must be scaled up to reflect the collection of individual home ranges in a population. Whether or not the effects of vole populations can be viewed accurately as simply the sum of effects of individuals comprising the population is an open question.

The spatial scale at which voles affect plant heterogeneity will be critical in determining the nature of any feedback that exists between plants and animals. If the major effects of voles on plant heterogeneity are at the scale of square meters, then the activities of voles should primarily affect behavioral strategies of individuals rather than population dynamics. However, if voles can enhance or reduce heterogeneity at the hectare scale, then their activities should feedback upon population dynamics.

In what follows, we will discuss several modes and contexts in which small rodents, especially voles, affect heterogeneity in plant communities. In each case we will discuss the relevant spatial scale(s) of the effects. Given the preliminary nature of most research in this area, we will also suggest questions for future research.

3. HETEROGENEITY OF HERBACEOUS PLANTS

Voles can affect the distribution of herbaceous plants primarily by two means: foraging and runway construction. Foraging can affect plant heterogeneity whenever plants are selected nonrandomly by species or spatial position. Ample evidence indicates that voles, although dietary generalists, have preferences for certain species of plants (Batzli 1985, Bergeron and Jodoin 1987). At high population densities, voles are known to virtually eliminate some preferred plant species, at least on small spatial scales (Batzli and Pitelka 1971, Cockburn and Lidicker 1983). Thus, when preferred plants have a patchy distribution, the effect of high vole density should be to reduce heterogeneity by destroying small patches. However, since some preferred species (e.g., *Trifolium* spp., *Medicago sativa*, *Rumex acetosella*) create buried seed banks inaccessible to voles (Rice 1989), the elimination of these species is temporary.

Given the ability of some plants to escape vole predation via seed banks, it is likely that the pattern of vole population dynamics will determine whether or not patchiness will be permanently affected. If voles undergo multiannual cycles, small patches of preferred plant species may escape permanent destruction via relaxed predation resulting from low vole density in most years. Indeed, the sustained existence of these plant species suggests such an escape in time. The role of vole population dynamics in the persistence of small herbaceous patches requires further study.

When voles are unevenly distributed in heterogeneous landscapes, patterns of patch occupancy often are related to nutritional quality of the patches (Cole and Batzli 1979, Ostfeld and Klosterman 1986). Preferred patches potentially could be degraded due to sustained high rates of herbivory by voles, which would reduce the abundance of the preferred species. On the other hand, relaxed herbivory in nonpreferred patches may allow invasion by plants of high food quality. These processes would serve to homogenize the landscape.

Long-term studies are necessary to test this scenario. The few studies carried out for at least several years indicate that large-scale patch structure in meadows persists despite occupation by both cyclic and noncyclic vole populations (Cockburn and Lidicker 1983, Ostfeld, Lidicker and Heske 1985, Ostfeld and Klosterman 1986). These results underscore the need to determine the relative importance of vole herbivory vs. such factors as plant competition, edaphic characteristics, and history, in determining the causes of patch structure (Pickett and White (Eds.) 1985).

In addition to foraging, voles can affect survival and reproduction of herbaceous plants via runway construction and maintenance. Voles construct a series of ramifying and anastomosing runways, typically < 5 cm in width, within which plant shoots are regularly clipped. Recent evidence indicates that meadow voles (*M. pennsylvanicus*) select for runways microsites in which the litter layer is thickest, and consequently light penetration to the surface is minimal (Lewin 1993). Both the total number and species diversity of herbaceous plant seedlings are lower in runways than at reference points outside runways (Fig. 1). Moreover, those plants that are able to persist in runways tend to be species that spread vegetatively. Runway construction and maintenance therefore has the potential to affect the distribution of safe sites for germination, and hence the distribution of plant species in herbaceous communities (Lewin 1993).

Again, patterns of vole population dynamics are likely to influence the long term effects of runways on plant heterogeneity. Runways tend to be constructed during population increases and are abandoned at high rates during population declines. Changes in physical characteristics (e.g., light penetration, humidity) in runways following abandonment probably are important in determining patterns of reinvasion by plants, but these factors and interactions have not been studied. Whether new runways tend to be constructed at sites that formerly had runways, or at different sites, also is not known.

It seems likely that voles will alter the very characteristics that cause them to select certain microsites for runway building. Runway sites, being in areas

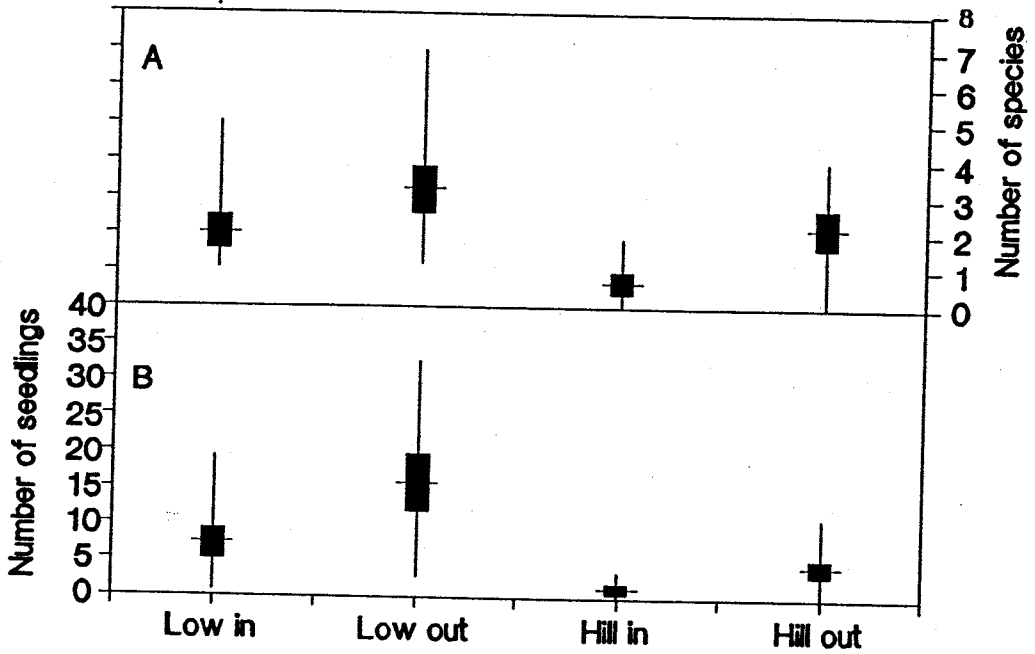


Fig. 1. Number of plant species (A) and total number of seedlings (B) both inside and at reference sites outside vole runways at two sites in southeastern New York, USA. "Low" and "Hill" refer to a lowland and hillside site, respectively, and "in" and "out" refer to runway position. Horizontal lines are means, rectangles are 95% confidence intervals, and vertical lines are ranges

of thick litter, and being maintained by clipping, should tend to experience low microsite productivity and biomass accumulation. As litter at runway sites decomposes, it will tend not to be replaced rapidly, compared to reference sites in which light penetration is higher and vole clipping is less intense. After a time lag, these reference sites may then provide the best microhabitats for runway construction due to the accumulation of litter. Thus, we predict that there will be a constant spatial shifting of sites receiving the heaviest impact from vole runways, leading to spatial heterogeneity that is transient and dynamic. If this prediction is correct, voles may play a critical role in generating or maintaining high species diversity of plants in herbaceous habitats, potentially counteracting competitive interactions that would cause local extinctions.

4. HETEROGENEITY OF WOODY PLANTS IN HERBACEOUS COMMUNITIES

Invasion of oldfields by trees is an essential process in oldfield succession, and an important generator of spatial heterogeneity (e.g., Pickett 1982). Several recent studies have revealed that voles are important predators of tree seedlings in oldfield communities (Myster and McCarthy 1989, Rousi, Henttonen and Kaikusalo 1990, De Steven 1991, Gill and Marks 1991, Ostfeld and Canham 1993). Ostfeld and Canham (1993) used

a randomized block design to determine experimentally the effects of meadow vole density on survival of tree seedlings in oldfields. They found that when population density of voles was high, they eliminated virtually all young tree seedlings within several months to a year, but when vole density was lower, seedlings had a somewhat higher probability of surviving (Fig 2). However, the probability of surviving vole predation was not random with respect to spatial position.

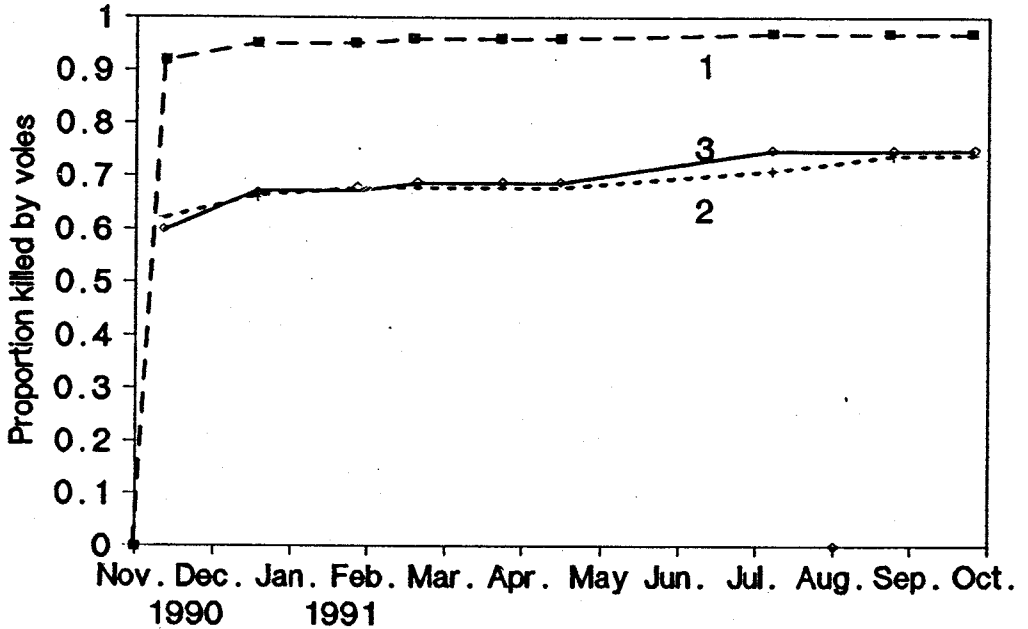


Fig. 2. Mean proportion of red maple seedlings (*Acer rubrum*) killed by voles as a function of vole density (low, medium, or high) in southeastern New York, USA. Seedlings were planted under intact vegetation. See Ostfeld and Canham (1993) for descriptions of site and methods
1 - high, 2 - medium, 3 - low

Several factors influenced spatial heterogeneity in seedling predation rates. First, within enclosures with low and medium vole density, some groups of seedlings were destroyed at the same rate as those in high-density enclosures, but other groups experienced low predation rates. A follow-up study showed that heterogeneity in seedling predation rates was associated with heterogeneity in the intensity of space use by voles (Price 1993; Fig. 3). At low to medium vole density, voles use space more unevenly than at high density, probably leading to more variable encounter rates between voles and seedlings. Because this variability was detected within the 40 m by 40 m enclosures used in these studies, the relevant spatial scale is on the order of tens of square meters.

Second, in most of Ostfeld and Canham's (1993) experiments, a significant block effect (where each block is a group of one low, one medium, and one high density treatment) on seedling predation was detected, indicating

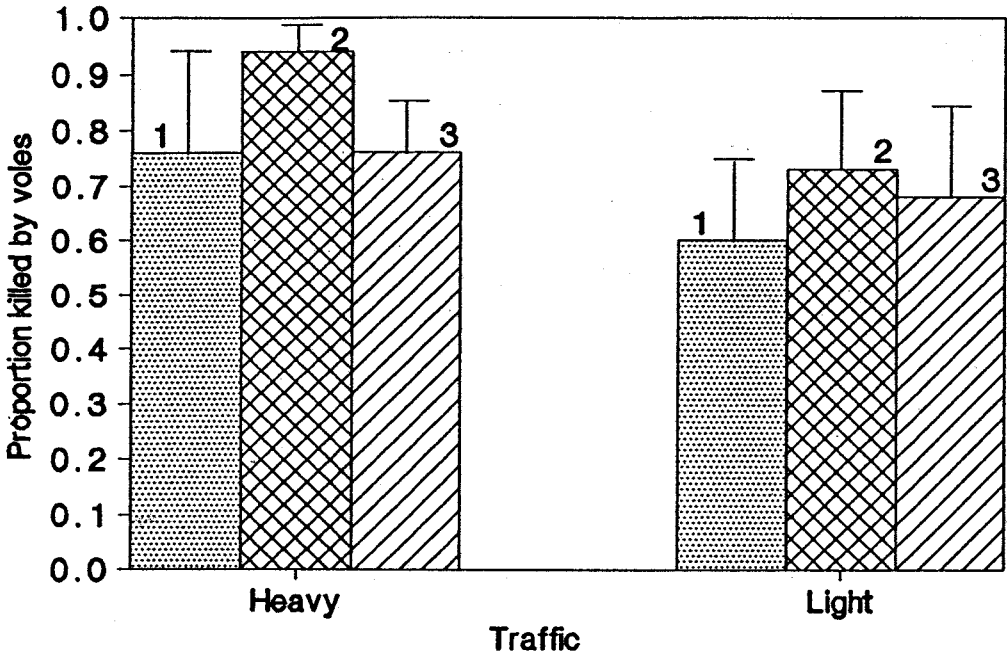


Fig. 3. Proportion (mean \pm 1 SE) of red maple seedlings killed by voles in areas of heavy and light use (traffic). Heavy traffic areas were overlapped by home ranges of ≥ 3 voles, and light traffic areas were used by ≤ 2 voles, as revealed by radiotelemetry. Different bar shadings represent different replicate enclosures:
1 – grid G, 2 – grid H, 3 – grid I

that replicates of each density treatment manifested different levels of seedling predation. In each case where a block effect occurred, the same block (block 1) had strongly elevated seedling predation relative to the other two. Differences among blocks in herbaceous plant communities appeared not to account for this effect. The block effect persisted for at least nine months, during which there was a 75% turnover of individuals in the vole populations, leading Ostfeld and Canham (1993) to suggest that voles in this block were intrinsically more aggressive toward tree seedlings. Because blocks were separated by up to 150m, we suggest that the relevant spatial scale of the block effect is on the order of hundreds of square meters.

Finally, Ostfeld and Canham (1993) introduced seedlings into 60 cm by 330 cm areas from which all aboveground and overhanging vegetation had been removed. Seedling predation rates were markedly lower in these small clearings than in areas of intact vegetation (Fig. 4). There was virtually no predation on seedlings in clearings except in block 1. The relevant spatial scale of the effect of these disturbances is $< 1 \text{ m}^2$. We conclude that spatial patterns of predation by voles on tree seedlings may produce heterogeneity at a continuum of scales from $< 1 \text{ m}^2$ to hundreds of square meters.

Finally, vole herbivory on seedlings may result not only in heterogeneity in the sites of tree invasion, but also may affect the species composition

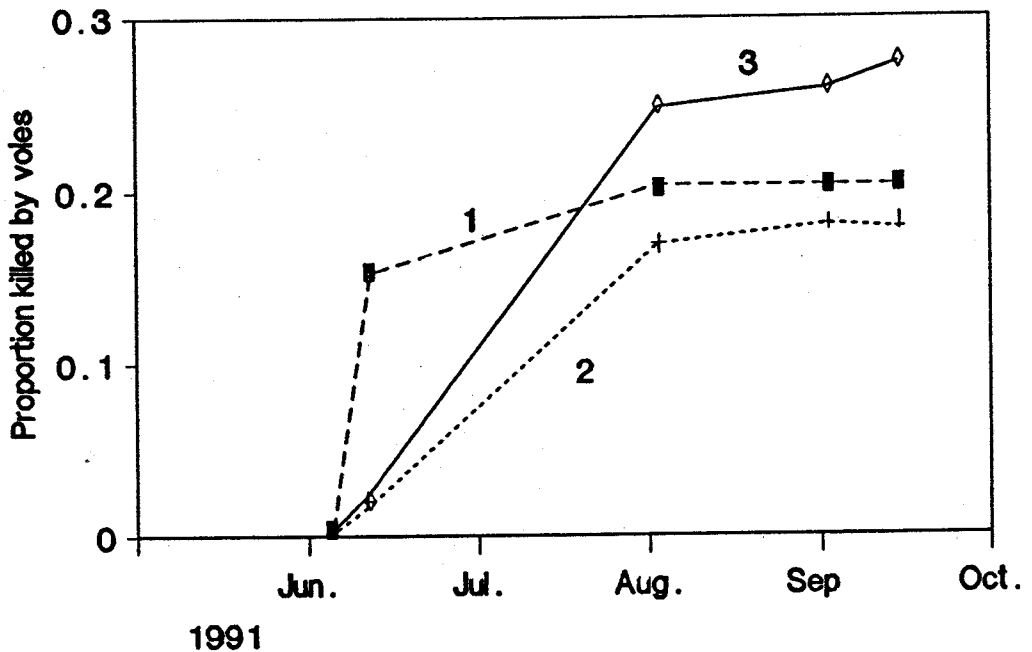


Fig. 4. Mean proportion of red oak (*Quercus rubra*) seedlings killed by voles as a function of vole density (low, medium, or high) in southeastern New York, USA. In contrast to the red maple seedlings in Figure 2, these red oak seedlings were planted in a line down the middle of experimental clearings 60 cm by 330 cm
1 – high, 2 – medium, 3 – low

of successful tree invaders. In Ostfeld and Canham's (1993) experiments, voles showed distinct preferences for certain species (e.g. white ash, *Fraxinus americana*, and red maple, *Acer rubrum*), and were somewhat less voracious on others (red oak, *Quercus rubra*, and eastern hemlock, *Tsuga canadensis*).

5. HETEROGENEITY OF WOODY PLANTS IN FOREST COMMUNITIES

The primary effects of voles and mice on woody plants in forests are as agents of seed and seedling mortality. If patterns of seed and seedling consumption are spatially nonrandom, then this may affect heterogeneity in the distribution of saplings and adult trees. In addition, rodents may cause clumping of seedlings by caching seeds in sites in which the probability of germination is high. Because sciurids, rather than arviculids, seem to be primarily responsible for caching seeds in such sites (Vander Wall 1990), we will not discuss the effects of seed caching here.

Although voles are known to destroy tree seedlings in forest communities (Kanervo and Myllymäki 1970; Larsson 1975; Pigott 1985; Bucyanayandi, Bergeron and Menard 1990), there is little

information on the spatial pattern of their herbivory. Some evidence indicates that voles avoid certain species and provenances of seedlings due to chemical defenses and nutritional composition (Pigott 1985, Hansson 1986, Bucyanayandi, Bergeron and Menard 1990). Due to limited dispersal capabilities of many forest trees, species and provenances of young seedlings are likely to be spatially clumped (Pacala, Canham and Silander 1993). Selective predation by voles may act to protect patches of certain genotypes, while destroying others. The net effect on heterogeneity is difficult to predict, and requires further study.

Perhaps more important than rodent predation on seedlings is their consumption of tree seeds. Although seed predation by rodents in tropical forests and deserts has received some attention (e.g., Janzen 1971, Hay and Fuller 1981, Schupp 1988), surprisingly little research has focused on rates and patterns of seed predation in temperate forests.

A study was undertaken at two sites in a transition oak-northern hardwood forest in northwestern Connecticut, in which the predominant rodents are mice (*Peromyscus leucopus* and *P. maniculatus*) and southern red-backed voles (*Clethrionomys gapperi*). Seeds of red maple, one of the most common tree species in eastern North America, were introduced in quadrats at varying distances from parent trees. Within these quadrats, red maple seedlings were counted in order to determine whether variation in intensity of seed predation was correlated with variation in seedling density (Schnurr 1993).

More than 95% of the 3600 seeds introduced were removed within one week. Tracks on smoked plates placed near the seeds indicated that rodents were the primary seed predators: < 8% of sites where seeds had been removed showed no small mammal tracks. For each of the two sites, seed predation rate was low or absent only at sites not directly under parent tree canopies, where the density of seeds is expected to be low. This result suggests that spatial variation in seed predation by rodents may produce spatial variation in the density of seedlings.

This hypothesis was tested by examining the relationship between seedling density and (1) seed predation rate, and (2) seed density. Although there was no statistically significant correlation among quadrats between seedling density and seed predation rate, the highest seedling densities were in locations with the highest seed predation rates, a pattern opposite the one predicted (Schnurr 1993). This result indicates that rodent predators probably were being satiated by seed production, despite their extremely high predation rates. However, the surprising lack of correlation between seedling density with seed density indicates that elevated predation rates at locations with high seed density in fact erode spatial heterogeneity in seedling density. By concentrating their foraging activities beneath mature tree canopies, rodents may be creating safe sites for those seeds that disperse farther from the parent tree. This finding reinforces the notion that the tail of the seed density by distance curve is critical to spatial pattern of forest trees (Portnoy and Willson 1993).

6. CONCLUSIONS

Studies of the effects of small rodents on patchiness in plant communities are just beginning, but the evidence suggests that voles and mice may play a key role. Voles in herbaceous communities appear to affect the distribution of herbaceous plants as well as woody plant invaders, via herbivory and runway construction. Voles and mice in forests appear to affect spatial pattern in recruitment of trees. Moreover, the effects of these rodents are density dependent, reflecting the density-dependent nature of their space use. Because many rodent populations fluctuate in density, the effects of an oscillation between heterogeneous and more homogeneous herbivory must be determined. We suggest four broad questions for future research. First, how general is the effect of rodent herbivory on plant heterogeneity? Second, what are the relationships between rodent herbivory, plant competition, and variation in physical substrate in determining patchiness? Third, over what spatial scales do rodents have their primary effects, and how do effects propagate across scales? Last, what is the nature of the feedback between rodent population dynamics and patchiness in plant communities?

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