Depauperate Small Mammal Communities in Managed Pine Plantations in Eastern Virginia

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ABSTRACT

Loblolly pine (*Pinus taeda* L.) plantations of four different ages were examined to identify changes in the small mammal community in relation to changes in the vegetational community. Small mammals were evaluated during five seasons using two methods of trapping. Live traps accounted for 65% of captures and seven of nine species, whereas pitfall traps yielded eight species, of which two were not taken with live traps. For both trap types, catch rates averaged less than two per 100 trap-nights, very low even for pine forests. Both abundance and biomass of small mammals declined with increasing stand age, whereas species diversity increased with increasing stand age. The relative proportions of trophic groups changed after crown closure from mostly granivores and omnivores to mostly insectivores. However, after mechanical thinning of late-age stands, small mammals of forested habitats and of early successional habitats were found together. The numbers of trapped small mammals decreased progressively throughout the study. We speculate that weather events might have contributed to this pattern but the reasons are unknown.

INTRODUCTION

Small mammals of forests often show preferences for habitats differing in age and structure (Linzey and Linzey 1973, Kirkland and Griffin 1974, Dueser and Shugart 1978). Thus, the abundance and species of small mammals inhabiting recent clearcuts often differ greatly from those found in maturing forests. Furthermore, secondary succession sometimes is governed by attributes of the initial disturbance (Boring et al. 1981). For example, timber management practices such as site preparation and the use of herbicides, pesticides, fertilizers, and selective cutting can directly affect the composition of the plant community, and in turn indirectly affect small mammal communities.

Much research has evaluated changes in small mammal communities in relation

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to vegetation changes in hardwood forest systems in eastern North America (e.g., Kirkland 1977, McComb and Rumsey 1982, Martell 1983, Buckner and Shure 1985). However, fewer studies have been conducted on small mammals in pine plantations in the Southeast. Atkeson and Johnson (1979) and Mengak et al. (1989) studied small mammals in pine plantations in the piedmont regions of Georgia and South Carolina, respectively, and Mitchell et al. (1995) studied small mammals in pine plantations on cleared pocosins in coastal North Carolina. In contrast, our study examined small mammal communities in managed loblolly pine plantations on upland sites in the coastal plain of Virginia, a region in which commercial stands of such pines often locally comprise a majority of the forested landscapes.

To learn details of changes in the small mammal community in relation to age of pine stand, we chose pine plantations of ages 1, 8, 18, and 24 years. In eastern Virginia, most loblolly pine (*Pinus taeda* L.) plantations are harvested at ca. 30 years of age. Our objectives were to determine the relative abundance, biomass, and species diversity of small mammal communities in relation to the age of managed pine plantations, to examine seasonal changes in the small mammal communities of these stands, and to document the presence or disappearance of small mammal species with age of pine stand.

MATERIALS AND METHODS

Study sites, selected from holdings of The Union Camp Corporation, were located in Isle of Wight County, in the Southeastern Coastal Plain Region of Virginia. Pine trees had been planted at densities of 1042-1482 stems/ha using mechanical planters after stumps and debris had been pushed into windrows. We chose four age classes of pine plantations on sites in relatively close proximity (1-16 km apart) to minimize the effects of variation in local weather conditions. We had no control over the herbicide, pesticide, or thinning treatments applied to some forest stands; we sought replicate sites that were as similar as possible. We had three replicates of the 1- and 24-year-old stands, and two replicates of the 8- and 18-year-old stands.

We trapped during five seasonal periods: (1) 12 June - 26 July 1995, (2) 20 October - 3 December 1995, (3) 19 January - 3 March 1996, (4) 3 April - 17 May 1996, (5) 9 July - 22 August 1996. The interval between seasons was at least 30 days.

Small Mammal Trapping

Effective surveys of small mammals require two methods of trapping, one of them being removal trapping (e.g., Getz 1961; Wiener and Smith 1972). Because pine forests support low-density populations of most small mammal species (Mengak et al. 1989, Mitchell et al. 1995) and removal trapping can locally reduce population density, we chose to use four 0.25 ha grids separated from one another by at least 50 m rather than one large hectare grid at each site. This design produces twice as much edge as one large grid, enabling small mammals living on the margins to enter the 0.25 ha grids after pitfall trapping had reduced abundances within the grids, potentially allowing populations to recover quickly.

The 50 m X 50 m (0.25 ha) grids were established at each site, each with 25 trap stations 12.5 m apart. A minimum buffer zone of 50 m separated grids from both the edge of a site and from one another. One Fitch live trap (Rose 1994) and one # 10 can

pitfall trap were placed within 1 m of each grid coordinate. (Fitch traps are superior to Sherman traps in capturing two common rodents in this study, white-footed mice and hispid cotton rats (Rose et al., 1977)). Live traps were baited with birdseed, tended for nine consecutive days, followed by at least seven days of no trapping, and finally by seven consecutive days of pitfall trapping. All traps were checked daily. Pitfall traps were buried to ground level and ca. 5 cm of water was placed in each trap. Pitfall traps were turned over and thereby made non-functional, except during active pitfall trapping. When captured, each animal was identified, weighed, and painted with permanent marker so that it was counted only once for that season.

Assessment of Vegetation

All planting rates are from information provided by Union Camp personnel. Vegetation data were recorded in late spring 1996, thus allowing one-year-old pine stands to go through two complete growing seasons to give more meaningful assessments of the early plant community. We estimated the percent of ground-level vegetation cover using a 0.3-m^2 frame placed flat on the ground (modified from Brower et al. 1990). Heights (m) of pines and of understory shrubs and trees were assessed by using a reference pole (James and Shugart 1970). Leaf-litter depth was measured using a 10-cm rod marked at 1-cm intervals and coarse woody debris was classified into four categories: none, scattered, moderate, and extensive. Ten randomly selected pine trees in each grid were measured for diameter at breast height (dbh).

Analysis of the Small Mammal Community

Small mammal communities were characterized using five indices: success by type of trap, presence or absence, total captures, biomass, and species diversity (Shannon-Wiener Index (H')). The total number of captured individuals per species serves as a measure of relative abundance for each species (Mitchell et al. 1995). Biomass was determined by summing the masses of all individuals trapped during each season. Differences in total individuals, biomass, species diversity, and means of trap success were evaluated using a Model I, 1-Factor ANOVA at an alpha level of 0.05; trends in species distribution, total captures, and biomass were analyzed using a Runs Up-and-Down test (t_s); and bivariate correlations were determined for small mammal community indices and stand age using the Pearson's correlation coefficient (Sokal and Rohlf 1995).

RESULTS

Descriptions of Pine Stands

One-year-old stands had grass coverage that varied widely (0-100%) among grids and pine saplings averaging 2.5 m. Planting rates averaged 1359 stems/ha. Density of woody debris varied from none to moderate amounts. The understory, comprised primarily of blackberry (*Rubus allegheniensis* Porter), poison ivy (*Toxicodendron radicans* (L.) Kuntze), wild grape (*Vitis* spp.), dogfennel (*Eupatorium capillifolium* (Lamarck) Small), yellow jessamine (*Gelsemium sempervirens* St. Hilaire), broomsedge (*Andropogon virginicus* L.) and panic grass (*Panicum* spp.), was moderately open and included volunteer hardwood species (mostly sweet gum (*Liquidambar styraciflua* L.) and red maple (*Acer rubrum* L.) saplings.

Eight-year-old stands had complete crown closure, were devoid of grasses, had a 3.5 cm litter layer, and no woody debris. Pines averaged 9 m with a dbh of 15 cm and had a 90 % survival rate. Original planting rates averaged 1235 stems/ha. Volunteer hardwood trees were found primarily along the windrows of debris from previous logging activities. The understory, open below 0.5 m and moderately dense from 0.5-3.0 m, was comprised of highbush blueberry (*Vaccinium corymbosum* L.), sweet-pepperbush (*Clethra alnifolia* L.), wild grape, greenbrier (*Smilax rotundifolia* L.), Japanese honeysuckle (*Lonicera japonica* Thunberg), blackberry, poison ivy, and American cane (*Arundinaria gigantea* (Walter)).

Eighteen-year-old stands had little or no woody debris, no grasses, and a 3.7 cm litter layer. Pines averaged 12.5 m with an average dbh of 18.5 cm and had 91% survival for 1235 stems/ha. Understory plants, similar to those of 8-year-old stands, were dense from 0-2 m and moderately dense from 2-3 m.

The two unthinned 24-year-old stands averaged of 579 pine and 372 hardwood stems/ha. Litter averaged 4.6 cm deep; moderate amounts of woody debris but no grasses were present. Pines averaged 14 m and 26.75 cm dbh. The understory remained similar but American cane was now dominant.

The 24-year-old thinned stand had elements of both early and late vegetation communities. Before thinning, there were 1110 pine and 85 hardwood stems/ha. When trees were removed from every fifth row, an understory dense up to 1 m and similar in composition to that of 1-year-old stands was created. Unthinnned rows remained devoid of grasses with moderate amounts of woody debris and a 2.2 cm deep litter layer. Pines averaged 16 m and 23.5 cm in dbh. The understory, moderately dense from 0.5-3 m, was composed primarily of highbush blueberry and sweet-pepperbush.

Trapping of Small Mammals

In 67,950 trap-nights, 1,039 small mammals of nine species were captured (Table 1). This represents an overall catch rate of 1.53 small mammals per 100 trap-nights (one trap in place for one night equals one trap-night) for both trap types. In 39,600 trap-nights, 672 small mammals of seven species were captured in live traps, for a capture rate of 1.7 per 100 trap-nights, whereas during 28,350 nights of pitfall trapping, 367 small mammals representing eight species were captured (1.29 mammals/100 trap-nights). The capture rates per 100 trap-nights of both trap types combined declined progressively across the five seasons from 2.8, 2.0, 1.7, 1.2, to 0.6, respectively.

Our assessment of the composition of the small mammal community was influenced by trap type (Table 1). Least shrews (*Cryptotis parva* Pomel) and southeastern shrews (*Sorex longirostris* Bachman) were taken only in pitfall traps, whereas hispid cotton rats (*Sigmodon hispidus* Say and Ord) were captured exclusively in live traps. All other species were captured in both trap types, but with varied capture rates.

The Community of Small Mammals

The proportions of different shrew species were relatively constant in pine stands of different ages (Table 2). Short-tailed shrews (*Blarina brevicauda* Gray), significantly more numerous in 18-year-old stands than in other stands (F = 39.97, P < 0.001), were significantly more numerous than least shrews there (F = 11.98, P =

TABLE 1. Totals and percent of small mammals captured by trap type across all seasons and ages of pine stands combined.

Small Mammal Species	Total	% by live traps	% by pitfall traps
Short-tailed shrew			
Blarina brevicauda	73	56	44
Least shrew			
Cryptotis parva	38	0	100
Southeastern shrew			
Sorex longirostris	212	0	100
Pine vole			
Microtus pinetorum	61	66	34
House mouse			
Mus musculus	36	72	28
Eastern harvest mouse			
Reithrodontomys humulis	26	73	27
White-footed mouse			
Peromyscus leucopus	378	91	9
Golden mouse			
Ochrotomys nuttalli	130	91	9
Hispid cotton rat			
Sigmodon hispidus	85	100	0

0.037). Least shrews maintained relatively constant numbers in all stand ages. Southeastern shrews, captured in all but one stand, had significantly higher numbers than other shrews in the 24-year-old stands (F = 7.02, P = 0.027). The southeastern shrew also had a significantly higher abundance than the least shrew in 18-year-old stands (F = 12.04, P = 0.037). Despite these significant differences, mean numbers of shrews in each stand across the five seasons were small, usually <5 but sometimes as high as 12 and 13 per season.

Unlike shrews, the abundance of most rodent species varied considerably among pine stands of different ages (Table 2). Exceptions to this pattern were pine voles (*Microtus pinetorum* (LeConte)) and house mice (*Mus musculus* L.), which, except that the latter was absent in 18-year-old stands, had similar but low mean abundances in all stands. Eastern harvest mice (*Reithrodontomys humulis* (Audubon and Bachman)) were present only in 1- and 24-year-old stands. By contrast, white-footed mice (*Peromyscus leucopus* (Rafinesque)) dominated and had significantly higher numbers in the 1-year-old stands than in other age classes (F = 19.62, P < 0.001). White-footed mice were absent from both 8-year-old stands and one of the two 18-year-old stands; they reappeared in low numbers in 24-year-old stands.

By contrast, golden mice (*Ochrotomys nuttalli* (Harlan)) were captured in all except 1-year-old stands (Table 2). The golden mouse was significantly more abundant

Table 2. Mean numbers of animals (averaged across seasons, rounded to the nearest whole number) of small mammals in pine stands of ages 1, 8, 18, and 24 years. Grand means ($\bar{x}$) are for the same age classes combined, given to one decimal place. The asterisks (*) denote sites treated with herbicides and insecticides by the Union Camp Corporation. Common names are defined in the legend to Table 1.

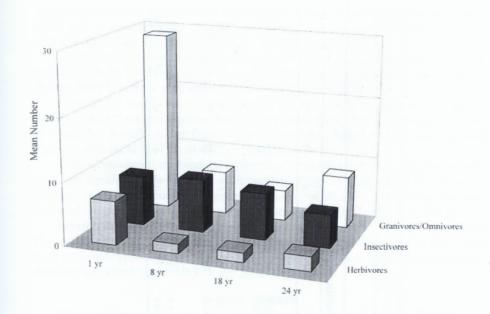| Species	Pine Stand Age													
	1	1*	$\bar{x}$	8	8	$\bar{x}$	18	18	$\bar{x}$	24	24	24	24	$\bar{x}$
Short-tailed shrew	1	1	1.0	1	1	1.0	3	4	3.5	1	1	1	1	1.0
Least shrew	7	0	2.3	1	1	1.0	1	0	0.5	1	1	1	1	1.0
Southeastern shrew	13	0	4.6	12	1	6.5	4	3	3.5	2	3	5	5	3.3
Pine vole	3	1	1.3	1	0	0.5	1	2	1.5	2	1	1	1	1.3
House mouse	1	4	3.0	2	0	1.0	0	0	0.0	0	0	1	0	0.3
Eastern harvest mouse	1	2	2.0	0	0	0.0	0	0	0.0	0	1	1	1	0.7
White-footed mouse	18	22	24.0	0	0	0.0	1	0	0.5	4	2	8	2	4.6
Golden mouse	0	0	0.0	7	5	6.0	5	4	4.5	2	5	1	1	2.7
Hispid cotton rat	10	2	5.6	1	1	1.0	0	0	0.0	0	1	2	1	1.0

FIGURE 1. Mean numbers of small mammals collected during the study in pine stands of four ages, based on the trophic group to which they belonged (similar to the expanded data in Table 3).

in 8- and 18-year-old pine stands (F=8.91, P= 0.013) and was significantly more abundant than other rodents in 8-year-old (F = 13.98, P = 0.003) and 18-year-old stands (F = 25.13, P < 0.001). The hispid cotton rat usually was captured in low numbers but it was absent in 18-year-old stands.

Trophic groups of small mammals

The proportions of trophic groups differed somewhat among age classes of pine stand (Table 3). Insectivores made up a significantly higher proportion of totals in the 18-year-old stands than other trophic groups (F = 23.22, P = 0.015). Granivores/omnivores (*Mus, Reithrodontomys, Peromyscus, Ochrotomys*) comprised a significantly higher proportion of small mammals than other trophic groups (Figure 1) in both 1-year-old (F = 8.56, P = 0.018) and 24-year-old stands (F = 38.15, P < 0.001).

No significant trends were found in herbivores (*Microtus* and *Sigmodon*). Abundances, biomasses, and diversity.

Despite using four 0.25-ha grids instead of one 1-ha grid in each stand (thus promoting the possibility of immigration from adjacent habitat onto each small grid), mean abundances for all sites declined progressively with each season (45, 27, 22, 16, 8 animals; not shown because these results are not directly relevant to composition changes of the small mammal community in relation to age of pine stands). All stands had declining capture trends over successive trapping seasons ($t_s = 3.74$, P = ≤ 0.05).

TABLE 3. Mean numbers of animals and percent of catch of trophic groups of small mammals for all seasons combined in pine stands of ages 1, 8, 18, and 24 years. Grand means ($\bar{X}$) are for same age classes combined, given to one decimal place. Insectivores include all three shrews, granivores/omnivores are defined as house, eastern harvest, white-footed, and golden mice, and herbivores are pine voles and hispid cotton rats. The asterisks (*) denote sites treated with herbicides and insecticides by the Union Camp Corporation.

Trophic Groups	Pine Stand Age													
	1	1*	1*	$\bar{X}$	8	8	$\bar{X}$	18	18	$\bar{X}$	24	24	24	$\bar{X}$
Insectivores														
Means	21	2	1	8.0	14	3	8.5	8	7	7.5	4	5	7	5.3
Percent	39	4	3	18.2	56	33	50.0	54	54	53.6	33	33	33	33.3
Granivores/Omnivores														
Means	20	39	28	29.0	9	5	7.0	6	4	5.0	6	8	11	8.3
Percent	37	85	88	65.9	36	56	41.2	40	31	35.7	50	53	52	52.1
Herbivores														
Means	13	5	3	7.0	2	1	1.5	1	2	1.5	2	2	3	2.3
Percent	24	11	9	15.9	8	11	8.8	7	15	10.7	17	13	14	14.6

The number of live-trapped small mammals (n = 268) was much higher in summer 1995 than in summer 1996 (n = 78), contributing to the significant differences in abundances among seasons (F = 3.40, p = 0.018).

Significantly higher abundances were observed in 1-year-old stands than in other stands (F = 6.49, P = 0.001; Table 4). A significant negative correlation was found for the number of captures with stand age (r = -0.517, P < 0.001).

Biomass of small mammals followed a pattern similar to number of captures (Table 4), namely it was significantly higher in 1-year-old stands than in other stands (F = 6.49, P = 0.001). A significant negative correlation was found for small mammal biomass with stand age (r = -0.481, P = 0.001).

Unlike abundance, the biomass differences between consecutive trapping seasons were not significant. However, as with number of captures, all stands had declining biomass trends over successive trapping seasons (t_s = 4.09, P = $\leq$ 0.05). Mean biomass declined progressively with each successive season (832, 677, 366, 216, 104 g).

Finally, differences in average species diversity of small mammals among age classes of pine stands (Table 4), as measured by the Shannon–Wiener index (H'), were not significant. However, a significant positive correlation was found between species diversity and stand age (r = 0.353, P = 0.019).

DISCUSSION

More small mammals were caught per 100 trap-nights for live traps (1.70) than per 100 pitfall trap-nights (1.29). These are very low catch rates for small mammals in forests (see beyond), especially for live traps. Live traps were more successful than pitfalls at catching granivores/omnivores and herbivores, probably due to the attraction of bait and the ability of some small mammals, such as adult hispid cotton rats, to escape from pitfall traps. Pitfall traps accounted for only 12% of all rodent captures (Table 1). However, pitfall traps were more effective than live traps at catching shrews, accounting for 87% of shrew captures (Table 1). Shrews are primarily insectivorous and therefore less attracted to baits used in live traps. Many investigators (e.g., Hudson and Solf 1959, Brown 1967, Briese and Smith 1974, Williams and Braun 1983) have also found pitfall traps to be more effective than live traps for capturing shrews.

Live traps failed to catch least shrews and southeastern shrews, and pitfall traps caught no cotton rats. Thus, two (or more) trap types are necessary to obtain the most accurate depiction of a small mammal community (Getz 1961, Wiener and Smith 1972).

Shrew Abundance and Distribution

Although the composition of the shrew community remained relatively constant in the four age stands (Table 2), shrew abundances varied somewhat among pine stands of the same age. Such variation is probably due to local site differences. Similar to Mengak et al. (1989), short-tailed shrews had greatest abundances in 18-year-old stands, likely due to the high density of American cane on those sites. However, these greater abundances may not be directly related to the American cane, but, as Getz (1961) suggests, to a response to the soil moisture conditions in which the American cane thrives.

By contrast, the southeastern shrew was uniformly most numerous, varying among

TABLE 4. Means of community parameters of small mammals found in four ages of pine stands for all seasons combined. Grand means ($\bar{x}$) are for all same-age classes combined. The asterisks (*) denote sites treated with herbicides and insecticides by the Union Camp Corporation.

Community parameter	Pine Stand Age													
	1	1*	1*	$\bar{x}$	8	8	$\bar{x}$	18	18	$\bar{x}$	24	24	24	$\bar{x}$
Abundance (no.)	54	46	32	43.8	25	9	17	15	13	14	12	15	21	15.9
Biomass (g)	1105	824	760	896	236	212	224	181	180	180	216	197	416	276
Species Diversity (H')	1.04	0.55	0.64	0.74	0.85	0.94	0.89	0.95	0.81	0.88	1.13	1.31	1.15	1.19

means of 3.3-6.5 per site (Table 2). The ability of the southeastern shrew to flourish in all stand ages is due in part to its ability to tolerate low soil moisture. Using pitfall traps on similar 0.25-ha grids, Rose et al. (1990) found southeastern shrews at dozens of locations in southeastern Virginia, ranging from boggy sites with peaty soils to those with dry mineral soils.

Rodent Abundance and Distribution

The rodent community varied among age classes of pine stand (Table 2), a response to the changing plant community (Atkeson and Johnson 1979, Mengak et al. 1989). Cotton rats, harvest mice, and house mice prefer oldfield habitats having a substantial amount of vegetative cover (Atkeson and Johnson 1979), such as was found in 1-year-old stands. Absent after crown closure, these rodent species reappeared in the 24-year-old stands, but at lower abundances (Table 2), associated with the reappearance of grasses and forbs in the more open thinned stand. Unlike other rodents, the semi-fossorial pine vole was found in all stand ages at relatively constant low abundances (Table 2).

Mengak and Guynn (2003), who also studied small mammals in loblolly pine forests, used discriminant function analysis to relate capture rates to habitat variables for the six species sufficiently numerous to merit analysis. In part because they used only snap traps, they caught too few least or southeastern shrews, house mice, or pine voles to include in their analyses. Nevertheless, some comparisons with our study are possible, such as the virtual disappearance of harvest mice and cotton rats by 8 years, the mutual patterns of abundance of these two species, and the importance of dense covering vegetation near ground level for both species. Other investigators, especially Cameron and his colleagues (Joule and Cameron 1975, Cameron 1977, Cameron et al. 1979), have published on this *Sigmodon-Reithrodontomys* association.

White-footed mice were numerically dominant only in the 1-year-old stands (Table 2), and although virtually absent in 8- and 18-year-old stands, more were captured in 24-year-old stands. Our results are similar to Atkeson and Johnson (1979), who found white-footed mice in greatest abundances in 1-year-old pine stands and decreasing with stand age thereafter. Its presence in 24-year-old stands is not surprising because white-footed mice are considered to be arboreal and well adapted to life in forests (Shure 1970, M'Closkey and Fieldwick 1975, Dueser and Shugart 1978, Kantak 1983, Rose and Walke 1988). However, as seen in our study, the white-footed mouse also is an excellent colonizer of early seral stages and usually rapidly increases in abundance immediately after clearcutting (Gashwiler 1959, Verme and Ozoga 1981).

Unlike other rodents, golden mice were found in all except 1-year-old stands (Table 2). Golden mouse numbers were highest in 8-year-old and 18-year-old stands, probably due to the presence of the dense intertwined understory they prefer and perhaps to the virtual absence of their close relative and potential competitor, the white-footed mouse, in these stands. The arboreal golden mouse is a habitat specialist, selecting habitats with an understory of vines and bushes (Barbour 1942, Goodpaster and Hoffmeister 1954, Linzey and Packard 1977). Atkeson and Johnson (1979) found peak abundances of golden mice at stand age 7, results similar to ours. Knuth and Barrett (1984) report that golden mice compensate for their habitats having low quality and widely dispersed food sources by having lower body temperatures and metabolic rates but higher assimilation

efficiencies than similar small rodents, such as white-footed mice.

Although both species were captured in the same 24-year-old stands, white-footed and golden mice were not captured in the same microhabitats (personal observation). Golden mice were captured most frequently in dense microhabitats, whereas white-footed mice were captured most often in more open microhabitats. Seagle (1985) suggests that competition between golden and white-footed mice is reduced by selection of different microhabitats and that disturbances such as thinning create a mosaic of microhabitats, thereby facilitating their coexistence.

Trophic Groups

Our finding that insectivores comprised a large proportion of small mammals in 8- and 18-year-old stands probably was due to the low numbers of rodents there. Because numbers of insectivores remained relatively constant in the stands of different age (5.3-8.5; Table 3), proportions were influenced more by abundances of other trophic groups than by changes in insectivore abundance. Mengak et al. (1989) report similar results for 18-year-old pine stands. Presence and abundance of insectivores may depend more on prey populations of invertebrates and the related soil moisture than on the nature and quality of plant communities. However, in some instances, the proportions of trophic groups differed more within same-age stands than among stands of different ages (Table 3). This was most apparent in 1-year-old stands, where differences likely were due to the use of insecticides, which probably reduced the invertebrate prey base of insectivores on the two treated sites.

The high abundances of granivores/omnivores in 1- and 24-year-old stands (Table 3) likely were due to suitable habitat to support large populations of seed plants, herbaceous vegetation, and their associated organisms. Kirkland (1977) also found granivore/omnivore abundances to be highest in recent clearcuts. The moderate abundances of granivores/omnivores in 8- and 18-year-old stands were due primarily to presence of golden-mice (Table 3).

Herbivore numbers were uniformly the lowest of all trophic groups and remained relatively constant across age classes, although herbivores were somewhat more numerous in 1-year-old stands, similar to Atkeson and Johnson (1979). Interestingly, no meadow voles (*Microtus pennsylvanicus* (Ord)) were collected in our study. Before the movement from the south of cotton rats into Virginia (Patton 1941), meadow voles were the largest and most abundant herbivorous rodents in oldfield habitats in eastern Virginia (Handley and Patton, 1947).

Small Mammal Abundance

Small mammal abundances were highest in young stands and declined with increasing stand age (Table 4), reflecting the significant negative correlation between number of animals and age of stand. Large numbers of small mammals in young stands are the result of diverse plant communities (Boring et al. 1981) that are high in ground cover, grass cover, weedy annuals, and perennials (Mengak et al. 1989), thus providing sufficient food and cover for many kinds of small mammals (McComb 1982). As pines grow, the associated plant community becomes more homogenous and nearly devoid of grasses and forbs, thus supporting fewer and often different kinds of small mammals

than younger plant communities (McComb 1982). McComb and Rumsey (1982) report clearcuts with 1.5 times more small mammals than uncut sites. Even with pesticide and herbicide treatments, our 1-year-old stands had 2-3 times more small mammals than maturing stands.

Unlike Mengak et al. (1989), we observed no increases in small mammal numbers during the breeding seasons of spring and autumn, only a progressive decline. This systematic decline over successive trapping seasons has not been noted in previous studies, either in pine plantations or in other types of forest communities. The observed systematic decline in small mammal abundances in our study, seen in all stands, likely was caused by two factors that would have had relatively equal effects in all stands: removal trapping (and low immigration rates of animals from nearby onto depopulated grids) and weather.

Stickel (1946), Getz (1961), Smith et al. (1974), Kirkland (1977), Atkeson and Johnson (1979), Mengak et al. (1989), and many others have conducted removal trapping on small plots without finding the same declining trend in numbers as we did. In fact, it has been suggested that it is nearly impossible to deplete a small mammal community with seasonal removal trapping due to the rapid immigration of animals into unoccupied habitat. Recently, Sullivan et al. (2003) reported significantly higher small mammal numbers in removal sites (due to rapid colonization) than in control sites. Therefore, we believe that removal trapping did not cause the systematic decline of captures through the five seasons in our study.

Instead we implicate climatological factors that affected three of five seasons. Extreme environmental conditions sometimes increase mortality rates of small mammals and their effects can continue through the following breeding season. In July 1995, temperatures averaged 5.6 °C above normal with 19 of 31 days having high temperatures above 32.2 °C (NOAA, 1995), and precipitation was 8.21 cm below normal, creating drought-like conditions.

During January 1996, temperatures averaged 14.4 °C below normal with 24 of 31 days having low temperatures of below 0 °C (NOAA, 1996). Precipitation was 5.4 cm above normal with 27.7 cm of ground-covering precipitation in the form of snow or ice. In January and February 1996, three significant ice storms had potentially detrimental effects on the biota. During extreme winter conditions, some species of small mammals (e.g., *Sigmodon hispidus*) can go through local extinctions (Slade et al. 1984, Sauer 1985). Schmidt-Holmes and Drickamer (2001) also speculate that unusually cold temperatures caused high winter mortality, thereby depressing usual densities in the next breeding season.

Finally, the second summer, temperatures averaged only 1.4 °C below normal, but the 29.5 cm above normal precipitation created flooding in most stands. As with the other two periods of extreme weather conditions, it is likely that reproduction failed or was reduced. Thus, we believe that the effects of drought, unusually cold winter conditions, and flooding may be primarily or partially to blame for the progressively declining numbers of small mammals across our study.

Biomass

Strongly related to number and body size, biomass peaked in young pine stands and

decreased with stand age (Table 4), as has been found by many others (e.g., Atkeson and Johnson 1979; Mengak at al. 1989). This finding is not surprising because the young plant community is diverse and supports numerous and often large-bodied small mammals, resulting in high biomass. Not proportional to declines in abundance, much of the biomass decline was due to the presence or absence of the cotton rat, a species 5-30 times larger than the other small mammals in this community.

Species Diversity (Shannon-Wiener Index)

Species diversity increased with increasing stand age (Table 4). The high diversity in the 24-year-old stands may be partially due to the moderately heterogenous plant communities of mixed pine and volunteer hardwood trees and areas of early successional habitat created by thinning. Although species diversity was highest there, all species were low in abundance. Our findings differed from those of Atkeson and Johnson (1979), who found species diversity to increase after clear-cutting and to attain highest values in stands of ages 1-4 years.

Pine Forests and Small Mammals

The moderately high diversity of the small mammal community of older pine plantations gives a false impression of quality. Overall, pine plantations support relatively low numbers of small mammals compared to other plant communities in eastern North America. Whether judged by live traps or pitfall traps, our catch rate averaged < 2 animals per 100 trap-nights across the study. Trap successes of 19 - 42% have been published for studies conducted in early successional (oldfield) habitats (McComb and Rumsey 1982, Buckner and Shure 1985, Healy and Brooks 1988), whereas somewhat lower trap successes (8 - 32%) are reported for hardwood and mixed forests (Kirkland and Griffin 1974, Healy and Brooks 1988, DeGraaf et.al. 1991). The lowest trap successes, of 1 - 5% (our study, Mengak and Guynn 1987, Mengak et. al. 1989, Mengak and Guynn 2003), were in pine plantations.

Although pine plantations live up to their nickname of "biological deserts," some timber management practices can create more suitable habitat for small mammals. For example, thinning every fifth row in 24-year-stands increased diversity of small mammals by creating favorable habitats as well as improving timber production. Windrows also enhance habitat quality for small mammals and other wildlife too.

Finally, although small mammals have no commercial value, they are important as the prey base for populations of many avian and mammalian wildlife, and probably in less well-studied subtle roles of soil mixing, distribution of important hypogeous fungi, consumption of insects, and dispersal of seeds. An understanding of how small mammals respond to different stages in pine growth can help forest managers and wildlife biologists manage pine plantations for mutual benefit, and by doing so, contribute to the conservation of biodiversity, as endorsed by the American Forest and Paper Association (2002).

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LITERATURE CITED

American Forest and Paper Association. 2002. Sustainable Forest Initiative® (SFI) Program: 2002-2004 SFI Standard and Verification Procedures. AFPA, Washington, DC.http://www.afandpa.org/content/navigationmenu/ environment_ and_recycling/ SFI/publications1/current_publications/current_SFI_ publications.htm.

Atkeson, T. D., and A. S. Johnson. 1979. Succession of small mammals on pine plantations in the Georgia Piedmont. American Midland Naturalist 101:385-393.

Barbour, R. W. 1942. Nests and habitat of the golden mouse in eastern Kentucky. Journal of Mammalogy 23:90-101.

Boring, L. R., C. D. Monk, and W. T. Swank. 1981. Early regeneration of a clear-cut southern Appalachian forest. Ecology 62:1244-1253.

Briese, L. A., and M. H. Smith. 1974. Seasonal abundance and movement of small mammals. Journal of Mammalogy 55:615-629.

Brower, J., J. Zar, and C. von Ende. 1990. Field and laboratory methods for general ecology, 3rd ed. Wm. C. Brown, Dubuque, Iowa. 237 pp.

Brown, L. N. 1967. Ecological distribution of six species of shrews and comparison of sampling methods in the central Rocky Mountains. Journal of Mammalogy 48:617-623.

Buckner, C. Z., and D. J. Shure. 1985. The response of *Peromyscus* to forest opening size in the southern Appalachian Mountains. Journal of Mammalogy 66:299-307.

Cameron, G. N. 1977. Experimental species removal: demographic responses by *Sigmodon hispidus* and *Reithrodontomys fulvescens*. Journal of Mammalogy 58:488-506.

Cameron, G. N., W. B. Kincaid, and B. A. Carnes. 1979. Experimental species removal: temporal activity patterns of *Sigmodon hispidus* and *Reithrodontomys fulvescens*. Journal of Mammalogy 60: 195-197.

DeGraaf, R. M., D. P. Snyder, and B. J. Hill. 1991. Small mammal habitat associations in poletimber and sawtimber stands of four forest cover types. Forest Ecology and Management 46:227-242.

Dueser, R. D., and H. H. Shugart, Jr. 1978. Microhabitat in a forest-floor small mammal fauna. Ecology 59:89-98.

Gashwiler, J. S. 1959. Small mammal study in west-central Oregon. Journal of Mammalogy 42:128-139.

Getz, L. L. 1961. Factors influencing the local distribution of shrews. American Midland Naturalist 65:67-88.

Goodpaster, W. W., and D. F. Hoffmeister. 1954. Life history of the golden mouse, *Peromyscus nuttalli*, in Kentucky. Journal of Mammalogy 35:16-27.

Handley, C. O., Jr., and C. P. Patton. 1947. Wild Mammals of Virginia. Virginia Commission of Game and Inland Fisheries, Richmond. 220 pp.

Healy, W. M., and R. T. Brooks. 1988. Small mammal abundance in northern hardwood stands in West Virginia. Journal of Wildlife Management 53:491-496.

Hudson, G. E., and J. D. Solf. 1959. Control of small mammals with sunken-can pitfalls. Journal of Mammalogy 40:386-391.

James, F. C., and H. H. Shugart, Jr. 1970. A quantitative method of habitat description. Audubon Field Notes 24:727-736.

Joule, J., and G. N. Cameron. 1975. Species removal studies: I. Dispersal strategies of sympatric *Sigmodon hispidus* and *Reithrodontomys fulvescens* populations. Journal of Mammalogy 56:378-396.

Kantak, G. E. 1983. Behavioral, seed preference and habitat selection experiments with two sympatric *Peromyscus* species. American Midland Naturalist 109:246-252.

Kirkland, G. L., Jr. 1977. Responses of small mammals to the clearcutting practices of northern Appalachian forests. Journal of Mammalogy 58:600-609.

Kirkland, G. L., Jr., and R. J. Griffin. 1974. Microdistribution of small mammals at the coniferous-deciduous forest ecotone in northern New York. Journal of Mammalogy 55:417-427.

Knuth, B. A., and G. W. Barrett. 1984. A comparative study of resource partitioning between *Ochrotomys nuttalli* and *Peromyscus leucopus*. Journal of Mammalogy 65:576-583.

Linzey, D. W., and A. V., Linzey. 1973. Notes on the food of small mammals from Great Smoky Mountains National Park. Journal of the Elisha Mitchell Scientific Society 89:6-14.

Linzey, D. W., and R. L. Packard. 1977. *Ochrotomys nuttali*. Mammalian Species, No. 75, 6pp.

Martell, A. M. 1983. Changes in small mammal communities after logging in north-central Ontario. Canadian Journal of Zoology 61:970-980.

M'Closkey, R T., and B. Fieldwick. 1975. Ecological separation of sympatric rodents (*Peromyscus* and *Microtus*). Ecology 56:119-129.

McComb, W. C. 1982. Forestry and wildlife habitat management in central hardwoods. Journal of Forestry 80:490-492.

McComb, W. C., and R. L. Rumsey. 1982. Response of small mammals to forest clearings created by herbicides in the central Appalachians. Brimleyana 8:121-134.

Mengak, M. T., and D. C. Guynn, Jr. 1987. Pitfalls and snap traps for sampling small mammals and herpetofauna. American Midland Naturalist 118:284-288.

Mengak, M. T., and D. C. Guynn, Jr. 2003. Small mammal microhabitat use on young loblolly pine regeneration areas. Forest Ecology and Management 173:309-317.

Mengak, M. T., D. C. Guynn, Jr., and D. H. Van Lear. 1989. Ecological implications of loblolly pine regeneration for small mammal communities. Forest Science 35:503-514.

Mitchell, M. S., K. S. Karriker, E. J. Jones, and R. A. Lancia. 1995. Small mammal communities associated with pine plantation management of pocosins. Journal of Wildlife Management 59:875-881.

NOAA (National Oceanic and Atmospheric Administration). 1995. Climatological data, annual summary, Virginia. Vol. 105, No. 13.

NOAA (National Oceanic and Atmospheric Administration). 1996. Climatological data, annual summary, Virginia. Vol. 106, No.13.

Patton, C. P. 1941. The eastern cotton rat in Virginia. Journal of Mammalogy 22:91.

Rose, R. K. 1994. Instructions for building two live traps for small mammals. Virginia Journal of Science 45:151-157.

Rose, R. K., and J. W. Walke. 1988. Seasonal use of nest boxes by *Peromyscus* and *Ochrotomys* in the Dismal Swamp of Virginia. American Midland Naturalist 120:258-265.

Rose, R. K., R. K. Everton, J. F. Stankavich, and J. W. Walke. 1990. Small mammals in the Great Dismal Swamp of Virginia and North Carolina. Brimleyana 16:87-101.

Rose, R. K., N. A. Slade, and J. H. Honacki. 1977. Live trap preference among grassland mammals. Acta Theriologica 22,21:296-297.

Sauer, J. R. 1985. Mortality associated with severe weather in a northern population of cotton rats. American Midland Naturalist 113:188-189.

Schmidt-Holmes, S., and L. C. Drickamer. 2001. Impact of forest patch characteristics on small mammal communities: a multivariate approach. Biological Conservation 99:293-305.

Seagle, S. W. 1985. Competition and coexistence of small mammals in an east Tennessee pine plantation. American Midland Naturalist 114:272-281.

Shure, D. J. 1970. Ecological relationships of small mammals in a New Jersey barrier beach habitat. Journal of Mammalogy 51:267-278.

Slade, N. A., J. R. Sauer, and G. E. Glass. 1984. Seasonal variation in field-determined growth rates of the hispid cotton rat (*Sigmodon hispidus*). Journal of Mammalogy 63:263-270.

Smith, M. H., J. B. Gentry, and J. Pinder. 1974. Annual fluctuations in small mammal population in an eastern hardwood forest. Journal of Mammalogy 55:231-234.

Sokal, R. R., and F. J. Rohlf. 1995. Biometry, 3rd ed. W. H. Freeman and Company, New York, New York. 887 pp.

Stickel, L. F. 1946. The source of animals moving into a depopulated area. Journal of Mammalogy 27:301-307.

Sullivan, T. P., D. S. Sullivan, D. B. Ransome, and P. M. F. Lindgren. 2003. Impact of removal-trapping on abundance and diversity attributes in small-mammal communities. Wildlife Society Bulletin 31:464-473.

Verme, L. J., and J. J. Ozoga. 1981. Changes in small mammal populations following clearcutting in Upper Michigan conifer swamps. Canadian Field Naturalist 95:253-256.

Wiener, J. G., and M. H. Smith. 1972. Relative effectiveness of four small mammal traps. Journal of Mammalogy 53:868-873.

Williams, D. F., and S. E. Braun. 1983. Comparison of pitfall and conventional traps for sampling small mammal populations. Journal of Wildlife Management 47:841-845.