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Small-mammal responses to pine regeneration treatments in the Ouachita Mountains of Arkansas and Oklahoma, USA

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Abstract

We compared the initial effects of four forest regeneration treatments (single-tree selection, group selection, shelterwood, and clearcut), and unharvested controls (mature, second-growth forest) on relative abundance of small mammals and small-mammal habitat throughout the Ouachita Mountains of western Arkansas and eastern Oklahoma. We compared small-mammal capture rates in 20 forest stands (4 replicates of 5 treatments) for 2 years prior to harvest treatments, and 1.5, 3.5, and 5.5 years after treatment. We also examined relationships among small mammals, treatments, and habitat conditions. Before harvest, all stands where characterized by high basal areas (BA), little understory vegetation, and low small-mammal capture rates. Compared with pre-harvest numbers, the number of individuals captured increased nearly five-fold in treated stands 1.5 years after harvest. After harvest, capture rates for all taxa combined were significantly greater in harvested stands (regardless of treatment) than in unharvested controls. Fulvous harvest mice (*Reithrodontomys fulvescens*) capture rates were greatest in clearcuts. Fulvous harvest mice, cotton rats (*Sigmondon hispidus*), and pine voles (*Microtus pinetorum*) were associated with abundant herbaceous vegetation in the understory and low BA. Eastern woodrats (*Neotoma floridana*), golden mice (*Ochrotomys nuttalli*), and *Peromyscus* spp. were associated with moderate to dense woody vegetation in the understory and intermediate BA levels. No taxon of terrestrial small mammal was captured exclusively in unharvested stands; most taxa we captured appear to be either disturbance-adapted or tolerant to disturbances from timber harvest.
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1. Introduction

From the 1940s until the 1980s, forest management and research throughout the southeastern U.S. (the Southeast hereafter) focused on wood production (Kessler et al., 1992; National Research Council, 1990). However, in the early 1990s, the U.S. Forest

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Service began to emphasize a more ecological approach to management, an approach that continues wood-product output while emphasizing biological diversity (Sharitz et al., 1992). In the early 1990s, public opposition to clearcutting in the Ouachita Mountains led the U.S. Forest Service to begin studying the social, economic, and environmental effects of alternative regeneration treatments (Baker, 1994). Since then, the U.S. Forest Service has reduced the use of clearcutting in the Southeast and now relies more on natural-regeneration systems of even- and uneven-aged management. Because clearcutting was among the dominant methods for regenerating pine (*Pinus* spp.) forests on national forests in the past (and is still the dominant regenerating method on timber industry lands in the Southeast), substantial information exists on the ecological effects of clearcutting (e.g., Kirkland, 1990). However, little information is available on the effects of alternative regeneration treatments on biotic communities. As an important part of an adaptive forest management program that integrates ecologically based decisions, land managers need to know how timber harvesting affects biological communities, habitats, and individual species.

The importance of maintaining species diversity in forest ecosystems is widely recognized (Salwasser, 1990; Millar et al., 1990). Small mammals play important ecological roles in forest ecosystems. They serve as primary prey for many species of raptors, snakes, and furbearers, and consumption of tree seeds by small mammals can affect forest regeneration (Smith and Aldous, 1947; Pank, 1974). Fossorial species may affect hydrological processes on forested watersheds (Ursic and Esher, 1988). Small mammals consume the larvae and pupae of forest insect pests, which may reduce the severity of insect outbreaks (Hanski, 1987).

Effects of clearcutting on small-mammal communities are well documented in North America. Kirkland (1990) reviewed 21 published studies documenting these effects; most of these studies found small-mammal abundance and diversity increased initially after clearcutting. In regions of North America other than the Southeast, studies that examined the effects of alternative regeneration treatments or thinning have found individual species may respond differently to each treatment type (e.g., Cambell and Clark, 1980; Ramirez and Hornocker, 1981; Martell, 1983; Von Trebra et al., 1998). In the Southeast, most studies examining the effects of forest management on small mammals have focused on small-mammal responses to short-rotation, intensively managed pine plantations (e.g., Atkeson and Johnson, 1979; Langley and Shure, 1980). Few studies have been conducted in naturally regenerated pine–hardwood forests, and we are unaware of any studies comparing small-mammal responses to a diversity of timber harvest and regeneration methods in this region.

As part of a large scale, multidisciplinary research initiative examining the social, economic, and ecological effects of timber harvest in the Ouachita Mountains of Arkansas and Oklahoma, we examined the effects of different stand-level forest-regeneration treatments on small-mammal capture rates. We compared winter small-mammal capture rates in mature, unharvested forest stands, and stands under four regeneration treatments (single-tree selection, group selection, shelterwood, and clearcut). We also examined relationships between habitat components and small mammals, and how timber harvest affected those habitat components.

2. Methods

2.1. Study areas

We conducted the study in the Ouachita Mountains of west-central Arkansas and east-central Oklahoma, throughout the Ouachita National Forest and the southern-most district of the Ozark-St. Francis National Forest. The Ouachita Mountains region is dominated by a series of east–west ridges and valleys where elevations range from 152 to 853 m. Throughout the region, mean annual precipitation ranges from 111.8 to 137.2 cm and mean annual temperatures range from 13.9 to 16.1 °C (Skiles, 1981).

We randomly selected 20 mature, second-growth, mixed pine–hardwood stands from those available within randomly selected townships and ranges. Five stands were selected from four physiographic blocks (5 stands/block; Baker, 1994). Selection criteria for candidate stands were tree age ≥60 years, aspect =

south or west, area >13 ha, slope < 20%, pine basal area (BA) of 13.8–25, and hardwood BA of 4.6–11.5. Further, candidate stands had no recent history of fire or extensive grazing and all stands were blocky in shape to minimize edge effects. Thus, our study stand ages in 1991 were 59–69 years old (average 64.5), and sizes were 13.0–28.3 ha (average 17.5). Mean total BA was 26.0 m^2/ha (S.E. = 1.0); of this, 17.6 m^2/ha (S.E. = 0.9; range = 13.8–27.5) was pine and 8.4 m^2/ha (S.E. = 0.6; range = 4.2–11.5) was hardwood. The most abundant tree species within study stands was shortleaf pine (*P. echinata*). For all stands as a group, the most abundant hardwood species were post-oak (*Quercus stellata*), white oak (*Q. alba*), sweetgum (*Liquidambar styraciflua*), and hickories (*Carya* spp.; Guldin et al., 1994). Prior to harvest, there were no differences among future treatment groups (including controls) in pine or hardwood BA, or any of our habitat variables (Thill et al., 1994). Further details on stand selection procedure and stand conditions prior to treatment can be found in Baker (1994), Guldin et al. (1994), and Thill et al. (1994).

2.2. Treatments

Within each of the four physiographic blocks, we randomly assigned one of five treatments to each stand; thus, each treatment was replicated four times. Each block contained four harvest treatments, plus an unharvested control. Harvesting was conducted between late-May and mid-September of 1993; site preparation occurred the following winter. The overall goal of harvest was to regenerate shortleaf pine. The four silvicultural treatments were:

1. *Pine–hardwood single-tree selection*: some overstory pines and hardwoods were removed uniformly throughout the stand (Table 1), using basal area–maximum diameter-q (BDq) methods (Baker et al., 1996).
2. *Pine–hardwood group selection*: most pines and hardwoods were removed in 3–10 openings that ranged from 0.04 to 1.9 ha in size; these openings constituted 6–14% of the stand area (Table 1). Pines within the matrix (remainder of the stand not included in openings) were thinned, but no hardwoods were harvested within the matrix. Thus, group selection stands consisted of two distinct habitat types: small open areas and the surrounding woodlands.
3. *Pine–hardwood shelterwood*: from 49 to 99 of the largest pines and hardwoods per hectare were retained uniformly throughout the stand (Table 1). All other pines and hardwoods (≥5 cm dbh) were harvested or felled and left on site.
4. *Clearcut*: all merchantable pines and hardwoods (except a few scattered trees retained for wildlife den, mast, and perch trees) were harvested (Table 1).

Site preparation was identical in single-tree selection stands, shelterwoods, and the group openings of group selection stands. Site preparation consisted of felling all hardwoods 5–15 cm dbh with chainsaws. Site preparation in clearcuts consisted of injecting all non-merchantable trees (except retained wildlife trees which were primarily oaks and hickories) with herbicide. Two of the four clearcut stands were ripped with a bulldozer the following

Table 1
Basal area (BA; m^2/ha) range, mean, and standard error (S.E.) for pines and hardwoods in 20 stands under five treatments ($n = 4$ stands per treatment) in the Ouachita Mountains of Oklahoma and Arkansas immediately following harvest treatments in 1993

Treatment	Pine BA			Hardwood BA			Total BA		
	Range	Mean	S.E.	Range	Mean	S.E.	Range	Mean	S.E.
Unharvested	19.4–27.5	22.7	1.7	4.2–9.8	6.6	1.3	24.4–31.7	29.4	1.7
Single-tree selection	10.1–14.4	12.4	0.9	1.7–5.3	3.1	0.8	14.5–16.2	15.5	0.4
Group selection									
Openings	0–0.7	0.3	0.2	2.4–4.9	3.9	0.5	2.4–5.6	4.1	0.7
Matrix	9.6–17.4	14.2	1.6	3.9–10.8	6.2	1.6	18.3–22.2	20.3	0.8
Shelterwood	6.4–9.3	8.3	0.7	2.6–4.4	3.1	0.4	9.0–12.9	11.4	0.9
Clearcut	0–1.0	0.3	0.2	0.7–1.6	1.2	0.2	0.7–2.6	1.4	0.4

summer (1994); rips were 3 m apart and 15–20 cm deep. Two of the clearcuts were not ripped because of problems obtaining contractors. Ripped clearcuts were hand planted with shortleaf pine at 2.4-m intervals within the rips and non-ripped clearcuts were hand planted on a 2.4 m × 3 m grid. Using *t*-tests, we found no difference ($P > 0.05$) in capture rates (each taxon each year, and all taxa combined each year) between ripped and non-ripped clearcuts. Therefore, we included both ripped and non-ripped clearcuts in the analysis as one treatment.

All stands contained ephemeral stream drainages. Unharvested, 30-m wide buffer strips (or greenbelts) were established for water-quality protection around each drain. The total percentage of each stand retained as greenbelt ranged from 4 to 20% and averaged 10.9% across all 16 harvested stands. Because greenbelts represented habitats that differed in structure from adjacent treated stands, small mammal and habitat data from greenbelt and greenbelt edge plots were not included in the analyses. Cutting prescriptions for all harvest treatments retained a residual component of overstory hardwoods (mostly oaks and hickories) for aesthetics and wildlife (Table 1).

2.3. Small-mammal sampling

In each stand, we established 100 permanent sampling stations at 15-m intervals along 4–9 parallel transects (Thill et al., 1994). Transects were 30–95 m apart, ran perpendicular to stand slope, and were >50 m from stand edges. We randomly selected 80 of these 100 stations for small-mammal trapping. Stations located in greenbelts and greenbelt edges (plots <15 m from the greenbelt boundary) were removed from the analysis, reducing the total number of trap stations to an average of 66.5 stations (±1.7S.E.) in treated stands. The same stations were sampled throughout the study.

We trapped small mammals for 2 years prior to harvest (1991 and 1992) and 1.5 years (1995), 3.5 years (1997), and 5.5 years after harvest (1999). In 1991, we placed a single Sherman live trap (7.6 cm × 8.9 cm × 22.9 cm) at each station. We increased our sampling effort to two traps per station thereafter. Traps were placed within 5 m of the station center. Small mammals were trapped for seven consecutive nights during winter (December–January); all stands were trapped concurrently. We trapped during winter because small-mammal trapping success tends to be highest during winter in the mid-south U.S. (personal observation; Whiting et al., 1983). In addition, fire ants (*Solenopsis invicta*), which are attracted to bait, are less active during this period. We baited traps with horse feed in 1991–1992. Although other studies used grains or seeds as bait in Sherman traps (e.g., Seagle, 1985; Loeb, 1999), we decided the potential existed for large grains to jam the trap mechanisms. Thus, in 1995–1999 we used rolled oats, which were less likely to affect trap mechanisms. We found no difference in total capture rates between pre-harvest stands (mean = 2.13 captures/100 trap nights, S.E. = 0.38) and post-harvest controls (mean = 1.66 - captures/100 trap nights, S.E. = 0.32) using a *t*-test ($t = 0.64$, d.f. = 50, $P = 0.522$), indicating changes in bait likely contributed little to increases in post-harvest captures. We followed mammal handling protocols of the ad hoc Committee on Acceptable Field Methods in Mammalogy (1987).

Captured small mammals were identified to species (with the exception of *Peromyscus* spp.) and marked by toe-clipping before release. Accurately differentiating some species of *Peromyscus* based solely on external characteristics is unreliable because measurements of external physical characteristics overlap in most species and this genus is known to hybridize (McCarley, 1954; Larem and Boone, 1994; Rich et al., 1996; Barko and Feldhamer, 2002). Further, biochemical markers may be the only reliable methods for distinguishing living specimens of white-footed mice (*P. leucopus*) and deer mice (*P. maniculatus*) in some areas (Rich et al., 1996). Therefore, we combined all *Peromyscus* into a single group. This group included four potential species that occur in the Ouachita Mountains: the white-footed mouse, the deer mouse, the Texas mouse (*P. attwateri*), and the cotton mouse (*P. gossypinus*; Montgomery, 1984; Sealander and Heidt, 1990).

2.4. Habitat measures

At the beginning of the study, we randomly chose 30 of the 100 sampling stations in each stand to use for habitat measures throughout the study. At each station, we established three adjacent 4-m^2 plots, each with a nested 1-m^2 plot. We also established a 5-m-radius, semicircular plot where down logs were measured.

Before timber harvest, all plots were permanently monumented with steel rebar to ensure the same areas were remeasured after harvest.

In each 1-m^2 plot, we estimated percent cover of rock, bare ground, litter, graminoids, and forbs using ocular estimates. Litter depth was measured in each 1-m^2 plot and assigned to a 2-cm increment class (0.0–1.9, 2.0–3.9, etc.). Within each 4-m^2 plot, we estimated percent cover of all down wood $\geq$2.54 cm diameter and percent cover of woody vegetation using ocular estimates. Within the 5-m radius semicircle, we measured the volume of each log with an average diameter $\geq$10 cm using Smalian's cubic volume estimate (Avery and Burkhart, 1994). We measured hardwood and pine BA at the center of each trap station using a 10-factor English prism; these data were converted to metric values. We estimated horizontal vegetation density using a 0.25-m^2 density board (Nudds, 1977; Thill et al., 1994). At a fixed distance of 15 m, observers estimated the percentage of these boards obscured by vegetation at three heights (from ground level to 0.5 m above the ground [VegDen1], 0.75–1.25 m above the ground [VegDen2], and 1.75–2.25 m above the ground [VegDen3]).

Habitat measures were collected in early March of each sample year (following small-mammal trapping) with the exception of horizontal vegetation density, which was measured in June. Thus, cover estimates for woody vegetation included only evergreen and tardily deciduous woody plants, and cover estimates for graminoids and forbs included only those plants that were green during late winter. Because most understory shrubs were deciduous, we used density board measures taken during summer to better characterize understory habitat available during approximately nine months of the year. Because changes in structure and understory composition occur slowly in mature, second-growth pine–hardwood stands, we conducted a single pre-treatment habitat survey in all stands during 1992.

2.5. Statistical analyses

We used new captures per 100 trap nights as an index of small-mammal abundance (e.g., Carey and Johnson, 1995; Carey and Wilson, 2001). We adjusted available trap nights by subtracting empty sprung traps; traps containing recaptured animals were also deemed unavailable. Because pseudoreplication likely exists when individual plots or substations within the same stand are used as the sample unit, we used individual stands as the sample unit. We compared the mean capture rates of small mammals among treatments and years using analysis of variance (ANOVA) on repeated measures in a randomized complete block design (RCBD), where stands were the sample units repeated over years. Fixed effects for treatment, time, and treatment × time interactions were tested for significance. We used separate repeated measures analyses for the pre-harvest and post-harvest data. For the pre-harvest analysis, stands were grouped by future treatment and tested for significant differences in time (2 sample years), future treatment, and whether a treatment × time interaction existed; analysis of individual taxa was not conducted in this analysis. For the three post-harvest samples, we conducted separate repeated measures analyses for each of the mammal taxa and for all species combined. Because we captured only two least shrews (*Cryptotis parva*) and one eastern chipmunk (*Tamias striatus*), we did not include these species in the analyses. For all repeated measures analyses, we used Bonferroni adjustment to separate the least squared means and considered physiographic block a random variable (Littell et al., 1996; SAS Institute Inc., 2000). For the covariance matrix structure, we used the variance components option (VC) in PROC MIXED (SAS Institute Inc., 2000; Littell et al., 1996). We used a log transformation ($\ln[x+1]$) and a Kenward–Roger degrees of freedom adjustment to adjust for unequal variances (PROC MIXED; Littell et al., 1996). We set statistical significance for all tests at alpha $\leq$0.05.

We used principal components analysis (PCA) in an exploratory analysis to quantify relationships among habitat variables, study stands, and treatments using CANOCO Version 4.5 (ter Braak and Šmilauer, 2002). We included pre- and post-treatment measures for each stand in the analysis; all years and treatments were analyzed simultaneously. Treatments were included in the ordination as passive (supplementary) variables. To ensure that each habitat variable was weighted equally and to adjust for different units of measure among habitat variables, we performed the eigenanalysis on the correlation matrix (ter Braak and Šmilauer, 2002).

We used canonical correspondence analysis (CCA) to examine the relationship between small-mammal capture rates (by taxa) and habitat variables using CANOCO Version 4.5 (ter Braak and Šmilauer, 2002). We used Monte-Carlo permutation tests (499 permutations) to determine significance of all CCA axes (ter Braak and Šmilauer, 2002). Species data were square-root transformed, and we included all pre- and post-harvest measures in the analysis.

3. Results

3.1. Treatment effects on overall small-mammal captures

Over the 5 sample years, we captured 3939 individual small mammals of 10 taxa during 83,704 adjusted trap nights (Table 2). An additional 304 individuals and 8374 adjusted trap nights, from greenbelt portions of harvested stands, were not included in the analysis. No taxon was exclusive to greenbelts. Although pre-treatment trapping effort in 1992 was twice that in 1991, we captured approximately a third the number of small mammals in 1992 compared with 1991. After harvest, overall number of individuals captured each sample year was nearly five times greater than average pre-harvest numbers. Captures increased for five of the 10 taxa after harvest. In general, numbers of small mammals declined after peaking in 1995 (1.5 years after harvest).

During the 2 pre-harvest years, there were no differences in the capture rates of small mammals (all taxa combined) among stands when grouped by future treatment (Table 3; Tappe et al., 1994). We found no significant treatment effect or treatment × year interaction ($F = 0.39$; d.f. = 4, 27; $P = 0.817$); however, we found a significant year effect between the 2 pre-harvest years ($F = 33.62$; d.f. = 1, 27; $P < 0.0001$). Overall, small-mammal capture rates were almost six times greater in 1991 (mean = 3.65, S.E. = 0.60) than in 1992 (mean = 0.62, S.E. = 0.09).

After harvest, we found no significant year ($F = 0.97$; d.f. = 2, 45; $P = 0.388$) or treatment × year interaction ($F = 0.37$; d.f. = 8, 45; $P = 0.931$) during the 3 sample years. However, we found significant differences in treatment effects (Table 3). After harvest, overall small-mammal capture rates did not differ among harvest treatments but capture rates were four to six times greater in harvested stands (regardless of treatment) than in unharvested controls. Clearcuts consistently had the highest capture rates, but we found no statistically significant differences among the four harvest treatments.

Table 2

Total small-mammal captures (by taxa) of new individuals and total adjusted trap nights (adjusted for sprung traps and recaptures) in 20 stands before treatment (1991 and 1992) and after four harvest treatments were imposed in 1993 in the Ouachita Mountains of Arkansas and Oklahoma

Taxon	Sample year					
	1991	1992	1995[a]	1997[a]	1999[a]	All years
Southern short-tailed shrew[b]	127	31	101	90	102	451
Least shrew	0	0	0	2	0	2
Southern flying squirrel	3	2	1	0	11	17
Pine vole	2	1	5	31	28	67
Eastern woodrat	8	5	73	66	95	247
Golden mouse	51	9	116	47	61	284
Peromyscus spp.	170	83	789	614	556	2212
Fulvous harvest mouse	5	1	264	209	139	618
Cotton rat	1	0	19	8	5	33
Eastern chipmunk	0	0	0	1	0	1
Unknown	1	1	5	0	0	7
Total	368	133	1373	1068	997	3939
Adjusted trap nights	10267	21346	17717	17928	16446	83704

[a] Captures and adjusted trap nights from unharvested portions of treated stands (greenbelts) not included.

[b] Scientific names presented in text.

Table 3
Mean capture rates (captures/100 trap nights; adjusted for sprung traps and recaptures) of new individual small mammals compared among five treatments ($n = 4$ stands per treatment; 20 stands total) sampled for 2 years before harvest (pre-harvest; 1991 and 1992; all taxa combined) and 3 years (1995, 1997, and 1999) after harvest (post-harvest; by taxa and all taxa combined) in the Ouachita Mountains of Arkansas and Oklahoma

Taxa	Treatment										*F*-value[a]	*P*-value
	Unharvested		Group selection		Single-tree selection		Shelterwood		Clearcut			
	Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.		
Pre-harvest												
All taxa	2.54	0.83	2.18	0.93	2.69	1.00	2.41	1.09	0.85	0.23	1.41	0.257
Post-harvest[b]												
Southern short-tailed shrew	0.21	0.06	0.89	0.22	0.69	0.22	0.66	0.22	0.50	0.14	2.18	0.088
Pine vole	0.00	0.00	0.05	0.03	0.20	0.09	0.27	0.16	0.20	0.11	1.55	0.205
Eastern woodrat	0.06A[c]	0.03	0.40AB	0.16	0.43AB	0.11	0.86BC	0.29	0.72BC	0.25	4.20	0.006
Golden mouse	0.28	0.11	0.38	0.13	0.21	0.06	0.77	0.21	0.52	0.42	1.63	0.186
Peromyscus spp.	1.00A	0.18	4.68B	1.16	4.00B	0.55	5.04B	0.62	4.85B	0.65	13.52	<0.001
Fulvous harvest mouse	0.02A	0.07	0.22A	0.07	0.82AB	0.35	1.49B	0.34	3.77C	0.73	20.45	<0.001
Cotton rat	0.00	0.00	0.05	0.03	0.02	0.01	0.15	0.07	0.13	0.06	2.84	0.036
All taxa	1.66A	0.32	6.67B	1.27	6.36B	1.02	9.26B	1.18	10.71B	1.33	19.58	<0.001

[a] RCBD ANOVA on repeated measures (treatments repeated over years); pre-harvest (2 year) and post-harvest (3 years) analyses were conducted separately. Data were log-transformed [$\ln(x + 1)$] prior to analysis.

[b] Stands were harvested during summer 1993.

[c] Within rows, means followed by like letters (A–C) were not different ($P > 0.05$) using Bonferroni adjustment for multiple comparisons.

3.2. Treatment effects on small-mammal taxa

For all seven of the most-captured taxa, we found no significant effects for year or treatment × year interaction during the 3 sample years after harvest. Capture rates for short-tailed shrews (*Blarina carolinensis*), golden mice, and pine voles did not differ among treatments (Table 3). However, there were significant differences among treatments for eastern woodrats, fulvous harvest mice, hispid cotton rats, and *Peromyscus* spp. Harvest mice capture rates were greatest in clearcuts, intermediate in shelterwoods and single-tree selection stands, and lowest in group selection stands and unharvested controls. Few fulvous harvest mice were captured in unharvested areas. Year effects for harvest mice were borderline significant ($F = 3.19$; d.f. = 2, 42; $P = 0.051$). Capture rates for harvest mice were greatest in 1995 but declined steadily in 1996 and 1998 in most harvested stands; however, they remained relatively consistent in clearcuts over the three sample periods. *Peromyscus* spp. capture rates were greater in harvested stands than in unharvested controls (Table 3). Eastern woodrat capture rates were greatest in clearcuts and shelterwoods, intermediate in single-tree selection stands and group selections, and lowest in unharvested controls. For cotton rats, the overall F-value for treatment effects was significant; however, Bonferroni adjustments rendered multiple comparisons among treatments insignificant.

3.3. Treatment effects on habitat conditions

Principal components analysis between habitat variables and treatments resulted in axes 1 and 2 explaining 59.8% of the variation in the habitat data (Fig. 1A). Principal component 1 explained 43.5% of the variation in the habitat data and represented a gradient from high BA to low BA and a greater density of stumps. Principal component 2 explained an additional 16.3% of the total variation in habitat data. Axis 2 appeared to represent a gradient from understory conditions dominated by bare ground, rock cover, and forb cover to understories with dense (primarily woody) vegetation, mainly in the 1.75–2.25 m height range (VegDen3 habitat variable; Fig. 1A). Relationships among treatments and habitat variables indicated that shelterwood and single-tree

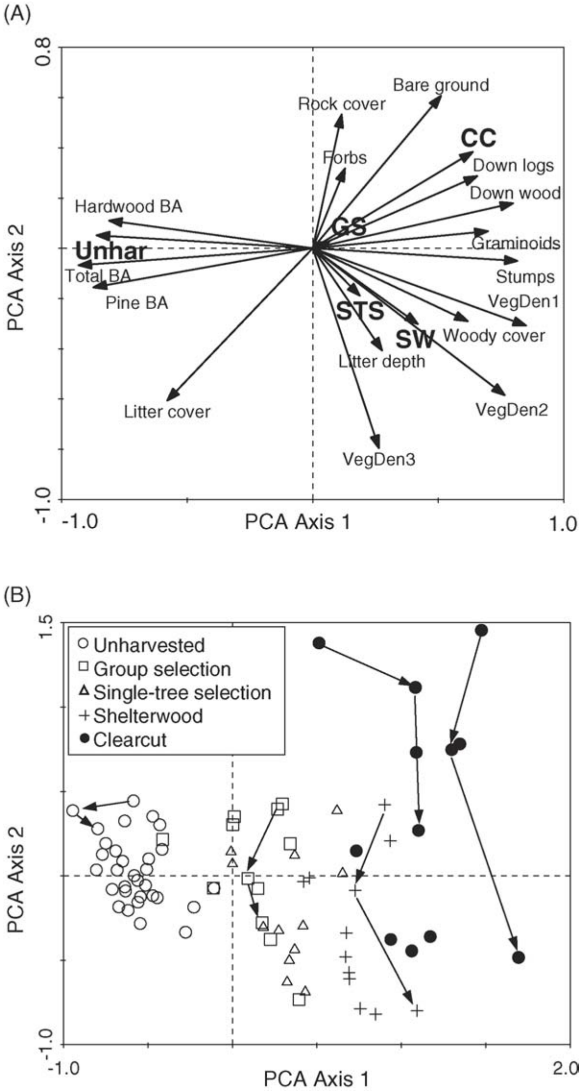

Fig. 1. Relationship among clearcut (CC), shelterwood (SW), single-tree selection (STS), group selection (GS) and unharvested control stands (Unhar) and 16 small-mammal habitat variables (A), and positions of individual stands on PCA axes 1 and 2 during the study (B). PCA axis 1 corresponded with a gradient in BA (higher BAs to the left), whereas PCA axis 2 corresponded roughly with a gradient from open understories dominated by bare ground and forbs (top of diagrams) to dense shrubby understory vegetation (bottom of diagrams). Treatments were included in the ordination as passive (supplementary) variables. See text for descriptions of all habitat variables. Arrows on diagram B illustrate examples of progressive changes in habitat of individual stands in 1995, 1997, and 1999 after regeneration treatments were imposed in 1993.

selection stands were more associated with dense woody understory vegetation than other treatments during the 3 post-harvest sample years. Clearcuts were more associated with herbaceous understory vegetation, bare ground, down logs, and coarse woody debris than other treatments. Unharvested control stands were associated with high BA, little herbaceous and woody understory vegetation, and sparse down wood and logs.

Individual stands changed position in ordination space during the study. Each sample year after harvest, harvested stands followed a general trend of moving toward increased understory vegetation density, while unharvested stands remained relatively constant in sample space (Fig. 1B). Shrubs and small saplings were sparse in the understory of clearcuts 1.5 years after harvest (1995). However, understory shrub density in clearcuts was similar to (or greater than) other treatments by 1999. Although single-tree selection stands and shelterwoods were more associated with dense shrub cover than other treatments 1.5 years after harvest, by 5.5 years after harvest, shrub densities were similar among clearcuts, shelterwoods, and single-tree selection stands.

3.4. Responses of small mammals to habitat components

Canonical correspondence analysis of habitat variables and small-mammal capture rates resulted in a CCA with axis 1 explaining 57.8% of the variation among capture rates for different taxa; axis 2 explained an additional 14.6% of the variation (72.4% total variation explained by axes 1 and 2). All axes were significant (permutation test; $P = 0.002$). Axis 1 represented a BA gradient and axis 2 corresponded roughly with an understory vegetation gradient from open, herbaceous conditions to dense woody conditions (Fig. 2A). The two habitat variables exerting greatest influence (as indicated by the lengths of the arrows in Fig. 2A) on capture rates of different small-mammal taxa were graminoid cover and pine BA. Cotton rats, fulvous harvest mice, and pine voles were associated with abundant grasses in the understory and relatively low BA (Fig. 2B). Eastern woodrats, golden mice, and *Peromyscus* spp. were associated with intermediate BA levels and moderate-high understory woody

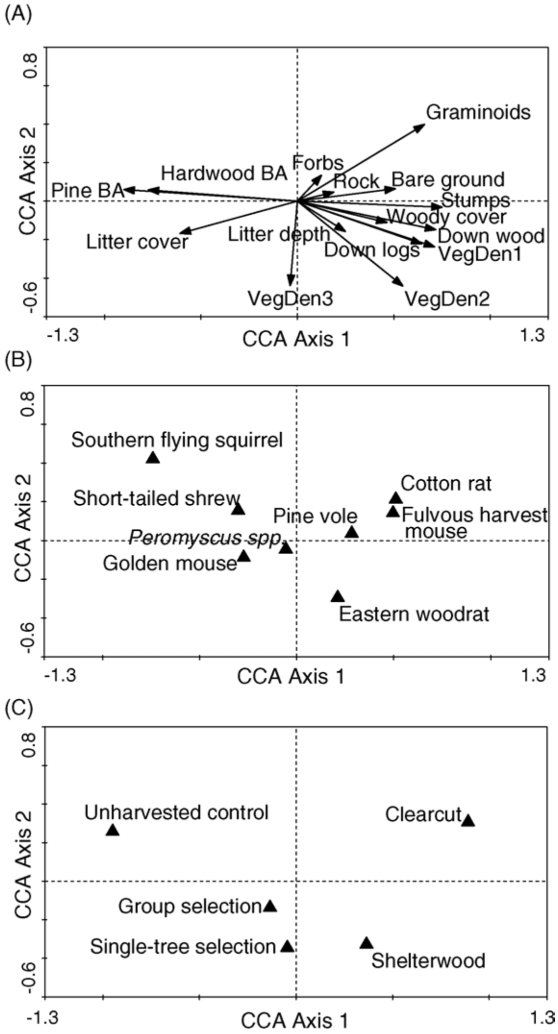

Fig. 2. Relationships among 15 habitat variables (A), position of seven species and one genera (B), and location of five forest treatments (C) on CCA axes 1 and 2. Treatment variables were entered in the analysis as passive (supplementary) variables. CCA axis 1 corresponded with a gradient in BA (higher BAs to the right), whereas CCA axis 2 roughly corresponded with a gradient from open understories dominated by bare ground and forbs (top of diagrams) to dense shrubby understory vegetation (bottom of diagrams). See text for complete descriptions of all habitat variables.

vegetation. Short-tailed shrews appeared to be associated with intermediate to high BAs and less-dense understory vegetation. Among all taxa, southern flying squirrels (*Glaucomys volans*) were associated with the highest BAs.

4. Discussion

4.1. Small-mammal responses to treatments

Total numbers and capture rates of small mammals increased substantially in treated stands after timber harvest. Total capture rates of small mammals generally increased in proportion to the amount of timber removed, with clearcuts consistently having the highest capture rates. Most small-mammal taxa responded positively to harvest treatments regardless of method and most taxa in this study appeared to be either disturbance-adapted or tolerant to disturbance at intermediate to high levels. Further, some taxa appeared to be more closely associated with certain levels of harvest-induced disturbance. Many species of small mammals exploit resource-rich early-succession/disturbed habitats because many small mammals of temperate forests have evolved in environments characterized by periodic disturbances (Kirkland, 1990). In the Southeast, forests have been greatly influenced by natural and anthropogenic disturbances for several thousand years (Sharitz et al., 1992). Land cleared by Native Americans for agriculture and settlement, frequent fires (both naturally ignited and anthropogenic), hurricanes, tornadoes, and ice storms created a mosaic of grasslands and forests varying in age and structure throughout the region (Sharitz et al., 1992; Lorimer, 2001).

Fulvous harvest mice appear to be strongly associated with stands having low BA and abundant grasses in the understory; their capture rates were consistently highest in clearcuts. In the Ouachita Mountains, Masters et al. (1998) found fulvous harvest mice abundant in stands that had undergone thinning, midstory removal, and burning; this species was absent in mature, unmanaged control stands. They also found that fulvous harvest mouse presence was related to low pine BA and abundant herbaceous vegetation in the understory.

Numbers of hispid cotton rats and pine voles increased after harvest in treated stands, and neither species was captured in unharvested controls. Habitat associations for cotton rats were similar to those of fulvous harvest mice; cotton rats were associated with grassy understories and relatively low BA. Mengak and Tipton (1978) frequently collected cotton rats and harvest mice (*R. humulis*) together in early-successional habitats. Pine voles were associated with grassy understories and low-moderate BA. Masters et al. (1998) did not capture pine voles or cotton rats in unmanaged control stands but both were present in thinned and burned stands. Thus, herbaceous understory conditions that initially result from more-intensive disturbances such as clearcut or shelterwood harvesting appear to be important to fulvous harvest mice, pine voles, and cotton rats. Furthermore, these favorable understory conditions may be maintained by frequent burning after initial overstory reduction (Masters et al., 1998). Oak and pine grasslands maintained by frequent fire, with open overstories and primarily herbaceous understories, were once abundant throughout the Southeast and the Interior highlands (the Ozark and Ouachita Mountain physiographic region), but are now limited to a few recently restored areas (Masters et al., 1995; Lorimer, 2001). These three species likely evolved to utilize these and other habitats having abundant grasses and other herbaceous vegetation.

No taxon was associated solely with unharvested control stands. Prior to treatment, all stands had high overstory BAs and low densities of understory shrubs and herbs (Thill et al., 1994). These second-growth stands also were characterized by low small-mammal abundance and diversity (Tappe et al., 1994). Only flying squirrels appeared to be associated primarily with unharvested stands. However, the southern flying squirrel is an arboreal species; our trapping method targeted terrestrial small mammals and was not suitable for accurately quantifying the abundance of this species. Capture rates were too low to make conclusions about the effects of treatments or habitat associations for chipmunks and least shrews, but it is unlikely either species was associated primarily with unharvested control stands given the sparse amounts of understory vegetation and down wood in these stands. Least shrews are most often found in brushy areas and grasslands (Sealander and Heidt, 1990). Chipmunks are associated with brushy woodlands and areas with abundant logs, rock piles, or wood piles (Sealander and Heidt, 1990); they were abundant in at least one of our single-tree selection stands during summer (personal observation).

Because we could not differentiate *Peromyscus* spp., we cannot make definitive statements about individual species in this group. Our samples may have contained all four sympatric species. Thus, this group's location in ordination space represents a weighted average (weighted by the most abundant species) for the group as a whole. However, all species of *Peromyscus* that occur in the Ouachita Mountains are either habitat generalists or are associated with brushy or grass-dominated habitats. In southwestern Arkansas, the Texas mouse is closely associated with rock outcroppings in open pine–hardwood forest (Montgomery, 1974), whereas in southern Missouri, they are associated with cedar glades that have abundant grass and shrub cover (Brown, 1964). Stancampiano and Schnell (2004) found a positive association between Texas mice and annual (herbaceous) cover in southwestern Oklahoma. The cotton mouse is associated with swamps, upland forests, old fields, and areas with abundant woody vegetation, but it tends to be more associated with mesic habitats (Gentry et al., 1968; Wolfe and Linzey, 1977; Mengak and Guynn, 2003). The deer mouse is known to have broad ecological tolerances across its wide range (Hamilton and Whitaker, 1979), and they have been reported to respond positively to reductions in the forest overstory (e.g., Kirkland, 1990). In Arkansas, deer mice primarily inhabit open areas, including fields, hay meadows, and cropland and they are typically absent in dense forests (Sealander and Heidt, 1990). The habitats of white-footed mice are diverse and include brushy fields and woodlots and areas with vertically well-stratified ground cover (Barry and Franq, 1980; Lackey et al., 1985; Yahner, 1986). Thus, it is unlikely any species of *Peromyscus* in this study were associated primarily with unharvested control stands.

We found *Peromyscus* spp. and golden mice associated with intermediate levels of BA. Masters et al. (1998) found a significant positive correlation between herbaceous understory vegetation and golden mice, but other studies suggest it is associated with coniferous or mixed overstories and dense undergrowths of shrubs, brush, and vines (Goodpaster and Hoffmeister, 1954; Linzey, 1968; Dueser and Shugart, 1979). Our results suggest that golden mice in the Ouachita Mountains are associated with moderate BA and moderate to dense levels of woody vegetation in the understory, similar to results found by Montgomery (1984) in the Ouachita Mountains. In industrial forests of the Ouachita Mountains, this species was the most frequently captured small mammal in edge habitats between streamside management zones and industrial pine plantations (Miller et al., 2004).

4.2. Effects of treatments on small-mammal habitat

Although pine BA and graminoid cover exerted the greatest influence on capture rates of individual taxa in our CCA, the importance of coarse woody debris and down logs to small mammals is well documented in other studies. Several studies have indicated small mammals selectively use logs for travel (e.g., Barnum et al., 1992; McMillan and Kaufman, 1995; McCay, 2000), and abundance of some species can be correlated with abundance of coarse woody debris (e.g., Goodwin and Hungerford, 1979; Loeb, 1999). Shrub cover also is important to small mammals and may play a role in niche partitioning (Montgomery, 1984; Carey and Johnson, 1995; Bellows et al., 2001). Stumps serve as important day refuges to some small-mammal species (McCay, 2000).

Amounts of coarse woody debris, stumps, and shrub cover were directly affected by timber harvest. Increased stumps and woody debris resulted from tree harvest, logging slash, and midstory trees that were felled and left on site. Increased shrub and sapling density resulted from reduced shading and sprouting from stumps. Although woody debris, stumps, and down logs were abundant in most treated stands, amounts were positively associated with the disturbance level. Clearcuts generally had the most stumps, down wood, and logs and these habitat components were lowest in unharvested control stands. We expect woody debris to decline in all harvest treatments over time as the woody material created during logging decomposes. However, the long-term effects of regeneration treatments on production and decay rates of down woody material in the Southeast are unknown.

Increased food supply typically results in increased vertebrate density. For example, Boutin (1990) reviewed 62 studies of terrestrial vertebrates and found that supplementary feeding commonly resulted in density increases. Although we did not include the effects of mast production on small mammals in this study, soft mast production increased substantially in harvested stands and overall hard mast production was generally greater in harvested stands than unharvested stands (Perry et al., 1999; Perry and Thill, 2003). Thus, given the substantial increases in down wood, down logs, stumps, woody and herbaceous understory vegetation, and food resulting from timber harvest, it is not surprising that small-mammal capture rates increased substantially after harvest.

It should be noted that our study took place during the first 5.5 years after harvest. Small-mammal abundance and community structure are likely to change as these stands mature or receive additional treatments. Because understory conditions in even-aged stands are ephemeral, canopies eventually will close as these stands mature, likely resulting in short-term reductions in understory vegetation and small-mammal abundance. Langley and Shure (1980) found a complete shift in understory vegetation composition and structure, and low small-mammal densities in even-aged pine plantations after canopy closure. Additional disturbance and reduced BA associated with the removal of all or most of the seed trees (typically at about 10 years after harvest) in shelterwood stands, or prescribed fire may prolong the length of time these stands provide early-successional small-mammal habitat. Likewise, thinning and/or burning to promote pine regeneration or growth may also perpetuate favorable understory conditions.

Because single-tree selection stands in this study were undergoing initial conversion to an uneven-aged structure, we expect shading caused by midstory development to eventually reduce understory vegetation. However, effects of future overstory removals (roughly every 10 years in the Southeast) on understory conditions and small-mammal abundance are unknown. We expect group selection stands, which have new openings created on a periodic basis (typically every 10 years in the Southeast), will continue to provide small patches of early-seral habitat and more spatially heterogeneous conditions than other treatments.

5. Conclusions

In mature second-growth pine–hardwood forests, reduced BA and disturbance from timber harvest increased most of the habitat parameters that are positively associated with abundance of small mammals during the first 5 years after harvest. Increases in understory herbaceous and woody vegetation, down wood and logs, and soft mast were accompanied by increases in overall numbers of small mammals. Even less-intense regeneration methods such as group selection resulted in significant increases in small-mammal abundance. Although all terrestrial small-mammal species in this study responded either favorably or appeared to be unaffected by regeneration treatments, multivariate analysis indicated some species are more associated with certain levels of BA (and the associated understory conditions resulting from the regeneration method). Because a mix of regeneration treatments mimics a wider range of naturally occurring types of disturbance than any single regeneration method, a variety of regeneration methods, varying in size and intensity throughout the landscape, would increase the likelihood that adequate habitats are maintained for a variety of small mammals and other wildlife species.

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