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Response of terrestrial small mammals to varying amounts and patterns of green-tree retention in Pacific Northwest forests

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Abstract

To sustain native species in managed forests, landowners need silvicultural strategies that retain habitat elements often eliminated during traditional harvests such as clearcut logging. One alternative is green-tree or variable retention. We investigated the response of terrestrial small mammals to experimental harvests that retained large live trees in varying amounts (approximately 100, 75, 40, and 15% of original basal area) and patterns (aggregated versus dispersed) in mature coniferous forests of western Oregon and Washington. Treatments were applied in 36, 13-ha experimental units. We used pitfall traps to sample small mammals for 4 weeks each autumn during 2 years before and 2 years after treatments. We captured 21,351 individuals of 32 species. We analyzed effects of treatments on relative abundance of 12 species. As level of retention declined, we expected species associated with closed-canopy forests to decrease (*Sorex trowbridgii*, *Neurotrichus gibbsii*, *Peromyscus keeni*, *Myodes* [*Clethrionomys*] *californicus*, and *M. gapperi*); species associated with early successional habitats to increase (*S. vagrans*, *P. maniculatus*, *Microtus longicaudus*, and *Microtus oregoni*); and habitat generalists to show little response (*S. monticolus*, *S. pacificus*, and *S. sonomae*). As expected, *M. californicus* declined after harvest, and *P. maniculatus* and *M. longicaudus* increased. *Sorex sonomae* showed an unpredicted decrease. Other species did not show consistent changes. Responses of *S. monticolus*, *S. sonomae*, and *M. gapperi* varied among study areas. For *M. gapperi*, this variation was not explained by differences in habitat structure among areas. For all species, capture rates were similar in dispersed- and aggregated-retention units. Similarity in species composition between harvested sites and controls decreased with decreasing retention. Future sampling of these treatments is needed to assess long-term responses. Based on our initial results, green-tree retention strategies need to be sensitive to regional variation in environmental characteristics and small mammal community composition.
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1. Introduction

Forest managers worldwide seek to sustain native species while extracting timber. In many temperate and boreal regions, managers have adopted green-tree retention (Franklin et al., 1997) as an alternative to clearcut logging. Retention of large live trees in small aggregates or dispersed across a harvest unit may help sustain larger populations of forest species than would occur after clearcut harvesting. Green-tree retention may enable breeding populations of closed-canopy species to persist during the period between harvest and subsequent canopy closure. If so, green-tree retention would greatly increase connectivity of local populations for species with low dispersal ability (Matveinen-Huju et al., 2006). Compared to even-aged management, green-tree retention also may increase structural complexity and functional diversity of regenerating forests (Franklin et al., 2002). In time, these forests may support larger populations of mature-forest species and a more diverse fauna, thereby enhancing the ability of "working forests" to sustain native species (Carey et al., 1999; Lindenmayer et al., 2006). Studies from many forest ecosystems are testing these hypotheses (Sullivan et al., 2001; Vanha-Majamaa and Jalonen, 2001; Koivula, 2002; Hyvärinen et al., 2005; Vergara and Schlatter, 2006).

Because of these potential ecological benefits, green-tree retention is now required in harvest units on U.S. federal lands

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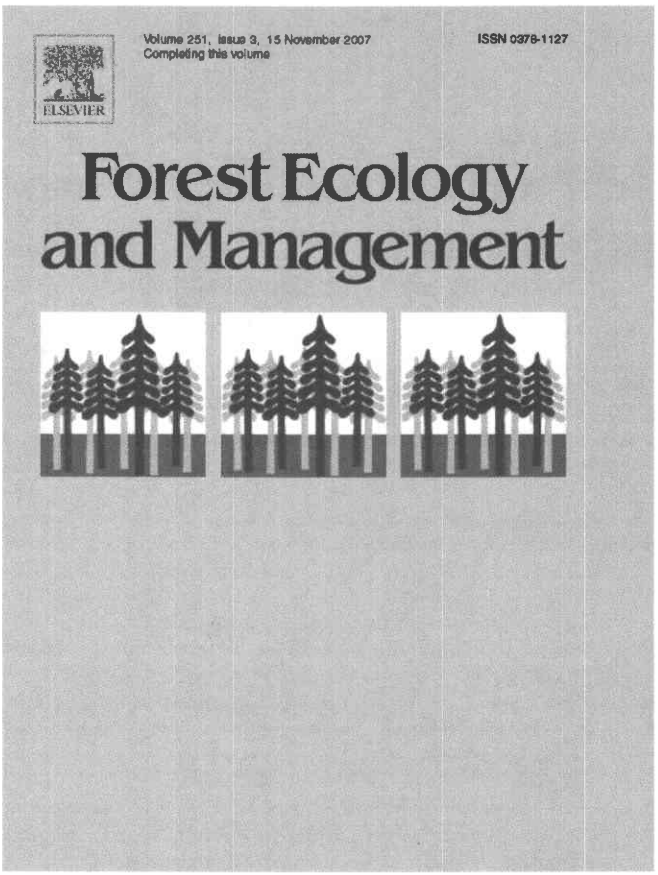

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within the range of the Northern Spotted Owl (western Oregon and Washington, and northern California; USDA and USDI, 1994a). In the Pacific Northwest, researchers and forest managers collaborated to design the Demonstration of Ecosystem Management Options (DEMO) experiment to examine effects of retention amount (proportion of original basal area; 15–100%) and spatial distribution (aggregated or dispersed) on persistence and recovery of forest organisms (Aubry et al., 1999; Franklin et al., 1999). In this paper, we examine effects of DEMO treatments on insectivores and small rodents.

In Pacific Northwest forests, numerous studies have addressed habitat associations of small mammals (e.g., Aubry et al., 1991; Carey and Johnson, 1995) and their comparative abundances in clearcuts versus mature forests (Gashwiler, 1970; Hooven and Black, 1976; Sullivan, 1980; Morrison and Anthony, 1989; Cole et al., 1998). The western Cascades and coastal ranges support a group of species most abundant in closed-canopy forests, a group most abundant in recent clearcuts and riparian areas, and generalists that can be equally abundant across successional stages (Lehmkuhl et al., 1999). As in other forest systems, small mammals of this region respond strongly to changes in the abundance of logs; litter cover and depth; density and composition of herbaceous vegetation and shrubs; and abundance of fruits, seeds, and fungal fruiting bodies (e.g., Carey and Johnson, 1995; Carey et al., 1999).

Previous studies in this region addressed responses of small mammals to partial disturbances such as thinning or shelterwood harvests (Waters and Zabel, 1998; Wilson and Carey, 2000; Suzuki and Hayes, 2003). However, few studies have explicitly examined responses across a range of harvest intensities or to different spatial patterns of overstory removal. Moreover, responses to green-tree retention may differ from responses to other partial-harvest methods, which emphasize silvicultural objectives (tree growth and regeneration). Green-tree retention emphasizes ecological objectives; i.e., managers retain large live trees to maintain forest species and habitat structure. Our study addresses these gaps in knowledge. To our knowledge, this is the first study of green-tree retention to examine effects of both retention amount and pattern on small mammals across multiple forest types and structural conditions.

We predicted that small mammal species associated with closed-canopy forests, early successional species, and habitat generalists would show different responses to retention amount and pattern in the first 2 years after harvest (Lehmkuhl et al., 1999). We anticipated that small mammals would show variable responses among our study areas due to variation in post-harvest habitat conditions. To clarify potential causes of these responses, we quantified treatment effects on key habitat elements. We addressed the following hypotheses:

Hypothesis 1. Closed-canopy species (Trowbridge's shrew, *Sorex trowbridgii*; shrew-mole, *Neurotrichus gibbsii*; Keen's mouse, *Peromyscus keeni*; western red-backed vole, *Myodes* [*Clethrionomys*] *californicus*; southern red-backed vole, *M. gapperi*) would decrease along the retention gradient (from 100 to 15% retention).

Hypothesis 2. Early successional species (vagrant shrew, *S. vagrans*; deer mouse, *P. maniculatus*; long-tailed vole, *Microtus longicaudus*; creeping vole, *Microtus oregoni*) would respond positively to lower levels of retention.

Hypothesis 3. Habitat generalists (montane shrew, *S. monticolus*; Pacific shrew, *S. pacificus*; fog shrew, *S. sonomae*) would show weak or no response to harvest.

Hypothesis 4. The magnitude of response by each species would vary among locations. This variation would be caused by among-location differences in post-harvest habitat conditions.

Hypothesis 5. Pattern of retention (aggregated versus dispersed) would not affect responses.

Hypothesis 6. Small mammal community composition would differ between intact forests (controls) and harvest treatments. Differences would be greatest at the lowest level of retention.

2. Methods

2.1. Experimental design and treatment implementation

The DEMO experiment is a randomized complete-block design with six treatments randomly assigned to six 13-ha experimental units at each of six locations (blocks; Fig. 1). Blocks are located in the southern Oregon Cascades (Watson Falls [WF] and Dog Prairie [DP]); in the southern Washington Cascades (Butte [BU], Little White Salmon [LW], and Paradise Hills [PH]); and in western Washington at the edge of the Coast Range (Capitol Forest [CF]). Before harvest, all blocks supported mature forests (age 65–170 years) dominated by Douglas-fir (*Pseudotsuga menziesii*). Elevations range from 210 to 275 m at CF to 1710 m at DP, with little snow accumulation at CF and snowpack lasting until May or early June at BU and PH. Study sites and vegetation responses to treatment are described by Aubry et al. (1999), Halpern et al. (1999, 2005), Halpern and McKenzie (2001), and Maguire et al. (2006, 2007).

Treatments include four levels of basal-area retention and two retention patterns. These treatments are (1) control (100% retention); (2) 75% aggregated (75%A), with three, 1-ha circular gaps; (3) 40% dispersed (40%D); (4) 40% aggregated (40%A), with five, 1-ha circular aggregates; (5) 15% dispersed (15%D); (6) 15% aggregated (15%A), with two, 1-ha aggregates (Fig. 1). In aggregated-retention treatments, all trees were retained within aggregates; trees >18-cm DBH were removed from harvest areas. In 40%D and 15%D, dominant and co-dominant trees were retained evenly across harvest units. Harvests were completed in autumn 1997 (BU and PH), spring 1998 (CF), or autumn 1998 (WF, DP, and LW). Logs were yarded with helicopters (DP, BU, and LW), suspension cables (CF), or ground-based equipment (WF, PH, and small sections of CF; Halpern and McKenzie, 2001). At four of six blocks, boles were yarded with tree canopies attached to reduce slash accumulation. At WF, some slash was piled on skid paths and burned.

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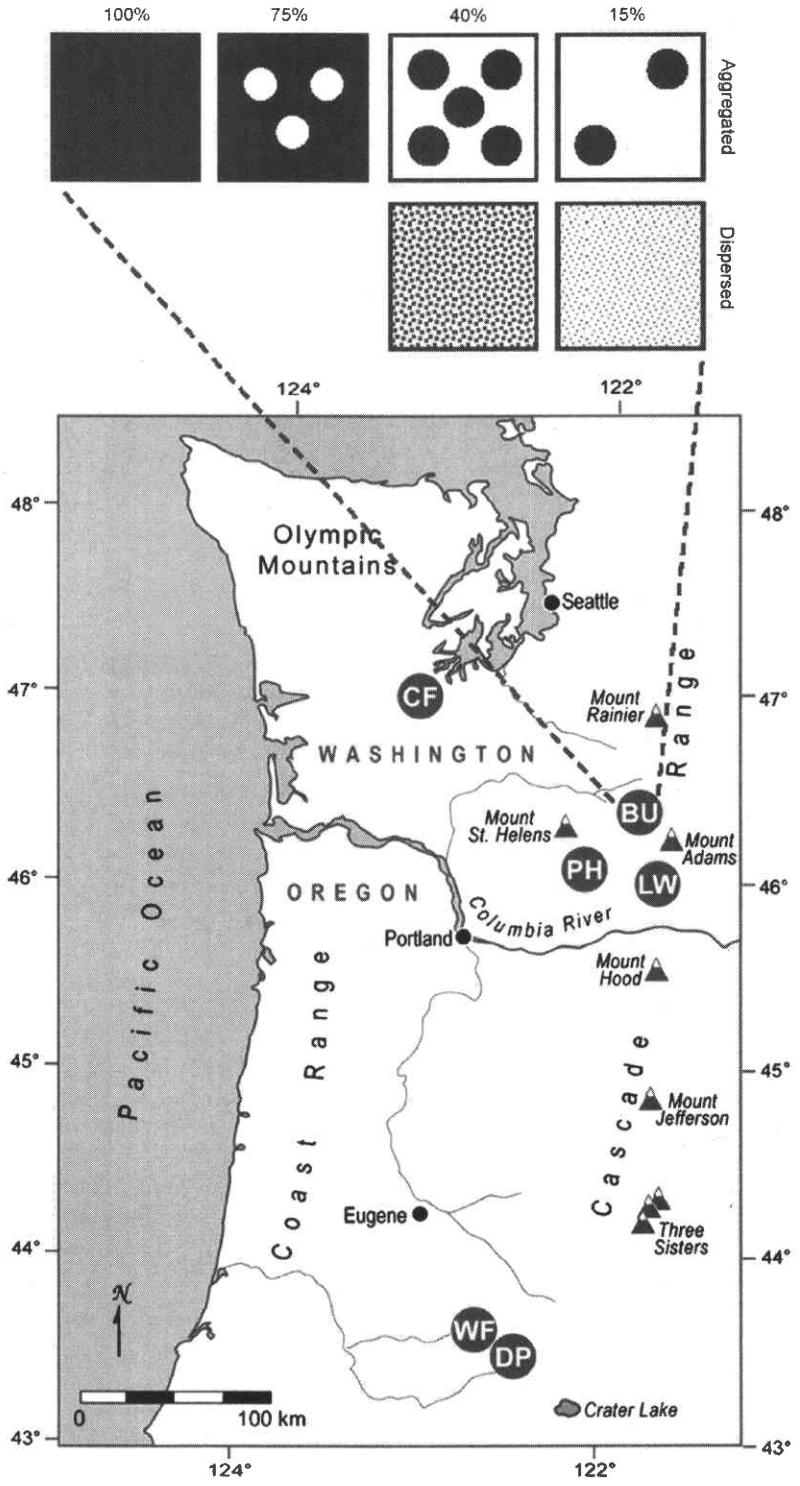

Fig. 1. Location of the six DEMO study blocks and a diagram of the six experimental treatments. In the latter, dark gray areas represent uncut forest (100 and 75% aggregated) or 1-ha forest aggregates (40 and 15% aggregated). Stippled areas represent dispersed retention (40 and 15% dispersed). Block codes from north to south are CF = Capitol Forest, BU = Butte, PH = Paradise Hills, LW = Little White Salmon, WF = Watson Falls, and DP = Dog Prairie. Figure is modified from Halpern et al. (2005), Copyright (2005), with permission from the Ecological Society of America. Schematic is reprinted from Halpern and McKenzie (2001), Copyright (2001), with permission from Elsevier.

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2.2. Field and laboratory methods

To sample small mammals, we used an 8 × 8 or 7 × 9 permanent, ~8-ha grid in each 13-ha experimental unit. Grid points were 40-m apart. Each grid was surrounded by a similarly treated buffer at least 40-m wide. At each point we installed a single pitfall trap (two No. 10 cans taped together to form a cylinder with diameter ~16 cm and depth ~35 cm) close to logs or other structures when possible (Corn and Bury, 1990). Traps were open continuously for ca. 28 days during autumn of each sampling year (late September to early November). We operated pitfalls as kill traps, filling them partially with water that remained at near-freezing temperatures during autumn sampling. Animals were collected weekly. Treatment units in each block were trapped nearly synchronously: all grids in a block were opened within a 5-day period each year. We sampled small mammals in each experimental unit before treatment ("Pre 2" and "Pre 1": 1995 and 1996) and after treatment ("Post 1" and "Post 2": 1998 and 1999 at BU, PH, and CF; 1999 and 2000 at WF, DP, and LW). University of Washington and Oregon State University Institutional Animal Care and Use committees approved our methods.

During dissections, we recorded species, sex, body measurements (total and tail length, mass) and reproductive data. We used dental or skull characters to identify shrews and voles. We used a tail-length threshold of 96 mm to separate adult *P. keeni* from *P. maniculatus* (Allard et al., 1987). In addition, we identified juveniles (<16 g) with undamaged tails ≤85 mm as *P. maniculatus*. Examination of tail-length histograms for blocks where only *P. keeni* was abundant indicated that most juvenile *P. keeni* were likely to have tails >85 mm by October.

Habitat variables were sampled during concurrent studies of ground conditions, understory vegetation, and forest structure (Halpern and McKenzie, 2001; Halpern et al., 2005; Maguire et al., 2007). These variables were measured at a subset of plots in the sampling grid (32–37 points per experimental unit) before and after harvest.

2.3. Data analysis

2.3.1. Habitat elements

To examine changes in habitat elements important to small mammals, we calculated average values in each experimental unit for five variables: volume ($m^3\ ha^{-1}$) of coarse woody debris (CWD); cover of slash (fine material < 10 cm in diameter originating from harvest; SLASH); cover of exposed mineral soil, including bare skid tracks (SOIL); cover of herbs and low shrubs (species with potential height <1 m; HERB); cover of tall shrubs (species with potential height >1 m; TALL SHRUB). Because residual basal area (BA) deviated somewhat from targeted levels, we used pre- and post-treatment measurements of trees (DBH ≥5 cm) to calculate the percentage of BA retained (%BA). To test for effects of %BA and pattern of retention on habitat variables, we used randomized-block ANCOVA. Pre-treatment values were included as covariates. For SLASH and SOIL, which were largely absent in uncut areas, we analyzed only 40 and 15% treatments. Cover variables were square-root transformed; CWD values were ln-transformed. We used package 'nlme' (Pinheiro and Bates, 2000) in S-PLUS 6.2 (Insightful Corp., 2003) for all linear-model analyses.

2.3.2. Relative abundance of small mammals

To maximize the relevance of this study to forest management, we used grids large enough to encompass within-stand habitat variability, and used pitfall traps because they effectively capture insectivores and small rodents. Because we could not livetrap insectivores in 36 large trap grids simultaneously, we used removal trapping. We used a wide trap spacing so that we did not deplete target populations enough to affect year-to-year population trajectories.

A drawback of this approach is that it did not conform closely to the removal model (which needs rapid depletion of populations to perform effectively; White et al., 1982:118), limiting our ability to account for heterogeneity in detectability (Anderson, 2001). However, we expected that overall detection probabilities for 4 weeks of trapping would converge to similar values among treatments, and that simultaneous trapping of units in each block would account for effects of weather on detectability (Skalski and Robson, 1992:145). For three species (*S. trowbridgii*, *P. keeni*, and *M. gapperi*), the removal model appeared sufficiently valid for us to use it to examine whether our assumptions about detectability were strongly violated. Using program MARK (Huggins and Yip, 1997; White and Burnham, 1999) we fit removal models incorporating effects of treatment, block, time, and weather on detectability. Our analyses indicated that detectability did not vary strongly among treatments for these three species, which were representative of the diverse natural histories of the small mammal assemblage we sampled. This supported our use of relative abundance (captures per 100 trap nights [TN]) to compare treatment effects on populations (Skalski and Robson, 1992). We analyzed relative abundance for five species captured in both states (*S. trowbridgii*, *S. vagrans*, *N. gibbsii*, *P. maniculatus*, and *M. oregoni*), three species captured only in Oregon (*S. pacificus*, *S. sonomae*, and *M. californicus*), and four species captured only in Washington (*S. monticolus*, *P. keeni*, *M. gapperi*, and *M. longicaudus*).

To determine small mammal responses to amount of retention (Hypotheses 1–3), we examined the relationship between capture rates and retention amount (%BA). We used a mixed-effects ANCOVA model appropriate for the randomized-block, repeated-measures design. Response variables were the two post-treatment abundance indices for each site, transformed as ln(captures per 100 TN + 0.1) to improve normality and additivity (Skalski and Robson, 1992). We used pre-treatment relative abundance as a covariate. We report significance of the treatment effect (regression coefficient $\beta_{\%BA}$, the change in transformed capture rates per percentage change in %BA) and the %BA × Time interaction. If %BA × Time was significant, we estimated $\beta_{\%BA}$ separately

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for each time; if it was not significant, we estimated the coefficient after refitting the model without the interaction term. Appendix A provides more details about these methods.

To examine whether effects of retention varied among blocks (Hypothesis 4), we used likelihood-ratio tests to compare models with and without a random effect modeling among-block variation in $\beta_{\%BA}$. When this among-block variation was present, we estimated block-specific regression coefficients ($\beta'_{\%BA}$). If among-block variation in the effect of %BA was explained by among-block differences in post-harvest habitat conditions, the %BA × block random effect would be unnecessary if we included relevant habitat variables. To examine this scenario, we added CWD and HERB (which was highly correlated with other vegetation variables) to models with and without this random effect, and compared these models again.

To examine effects of retention pattern on capture rates (Hypothesis 5), we conducted a second analysis limited to the two nominal retention amounts (40 and 15%) at which both dispersed and aggregated retention treatments were applied. We used the mixed-effects ANCOVA approach described above to compare dispersed with aggregated retention and to test for a Pattern × Time interaction. We estimated the contrast coefficient for the difference in ln-transformed capture rates, $\bar{x}_{\text{Dispersed}} - \bar{x}_{\text{Aggregated}}$.

Table 1
Total captures of small mammals by study block[a] during four sampling periods between 1995 and 2000

Species	Oregon		Washington				Total
	WF	DP	BU	LW	PH	CF	
Insectivora							
Sorex bendirii	1	2	7	7	7	66	90
Sorex cinereus/rohweri[b]			4	2	17	1	24
Sorex monticolus			443	102	265	283	1093
Sorex pacificus	66	57					123
Sorex palustris	0	1	1	0	1	0	3
Sorex sonomae	122	51					173
Sorex trowbridgii	764	805	1068	1159	651	2338	6785
Sorex vagrans	688	562	95	33	115	133	1626
Sorex species	3	3	22	28	12	45	113
Neurotrichus gibbsii	84	24	189	21	63	180	561
Scapanus orarius	3	3	2	9	7	21	45
Scapanus townsendii						2	2
Rodentia							
Tamias amoenus			5	0	0		5
Tamias siskiyou	10	18					28
Tamias townsendii	0	0	27	11	12	18	68
Tamias species	0	0	4	1	2	0	7
Tamiasciurus douglasii	0	0	4	4	0	3	11
Spermophilus lateralis	1	0					1
Glaucomys sabrinus	4	2	17	2	13	26	64
Thomomys mazama	45	35					80
Thomomys talpoides			1	12	10	0	23
Peromyscus keeni			870	325	214	472	1881
Peromyscus maniculatus	539	832	192	292	49	747	2651
Peromyscus species	0	0	88	91	22	151	352
Myodes californicus	744	469					1213
Myodes gapperi			1227	163	1138	279	2807
Arborimus albipes	1	0					1
Arborimus longicaudus	0	1					1
Phenacomys intermedius	6	0	12	0	42	0	60
Microtus longicaudus	0	0	36	5	7	51	99
Microtus oregoni	180	57	82	112	54	538	1023
Microtus richardsoni	2	5	3	0	2	0	12
Microtus townsendii	0	1	0	0	0	2	3
Microtus species	0	0	1	0	0	0	1
Zapus trinotatus	2	2	16	3	3	231	257
Carnivora							
Mustela erminea	7	6	14	12	8	18	65
Total	3272	2936	4430	2394	2714	5605	21351

Total trap effort was 256,896 trap nights; no value is listed for blocks outside the distributional range of each species.
[a] WF (Watson Falls), DP (Dog Prairie), BU (Butte), LW (Little White Salmon), PH (Paradise Hills), CF (Capitol Forest).
[b] Some shrews identified as *S. cinereus* may be the recently described *S. rohweri* (Rausch et al., 2007).

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2.3.3. Community measures

We used two approaches to examine treatment effects on community composition (Hypothesis 6). First, we used Renkonen's index (Renkonen, 1938 in Krebs, 1999) to compare the percentage similarity of species composition of captures between each harvest unit and the control (100%) in each block. We calculated similarity for pre-treatment samples (Pre 1 and Pre 2 combined) and for each post-treatment year (Post 1 and Post 2). We analyzed similarity with the same model used for species abundance, with pre-treatment similarity included as a covariate. We then used principal components analysis (PCA) to identify species responsible for changes in community composition. We conducted separate PCA analyses for each block because of large among-block variation in composition. For each harvest unit, we calculated the percentage that each species contributed to average post-treatment captures. We then performed PCA of these percentages with program R 2.01 (R Development Core Team, 2004). Because we performed PCA to clarify results of the similarity analysis, which used an index affected little by uncommon species, PCA included only species contributing $\geq 10\%$ of average post-treatment captures in each block.

3. Results

During 4 years of sampling, we caught 32 species of small mammals (Table 1), with comparable numbers of insectivores (10,638 captures) and rodents (10,648 captures). Eight species made up 89% of captures, each with over 1000 individuals (*S. monticolus*, *S. trowbridgii*, *S. vagrans*, *P. keeni*, *P. maniculatus*, *M. californicus*, *M. gapperi*, and *M. oregoni*). Total captures varied greatly among blocks, with more than twice as many captures at CF than at PH. Yearly variation was also high. In Washington, total captures were two to three times higher in 1998 than in other years even at control sites located several hundred meters from other treatments.

3.1. Habitat elements

Treatments strongly affected habitat attributes (Fig. 2). Cover of herbs and tall shrubs decreased while disturbed soil and slash increased as retention decreased. These changes occurred at varying rates across blocks (comparison of models with and without random effect of %BA × block: $\chi^2_2 > 17$, $P < 0.01$ for each variable). In contrast, volume of CWD varied minimally among treatments at all blocks. HERB, TALL

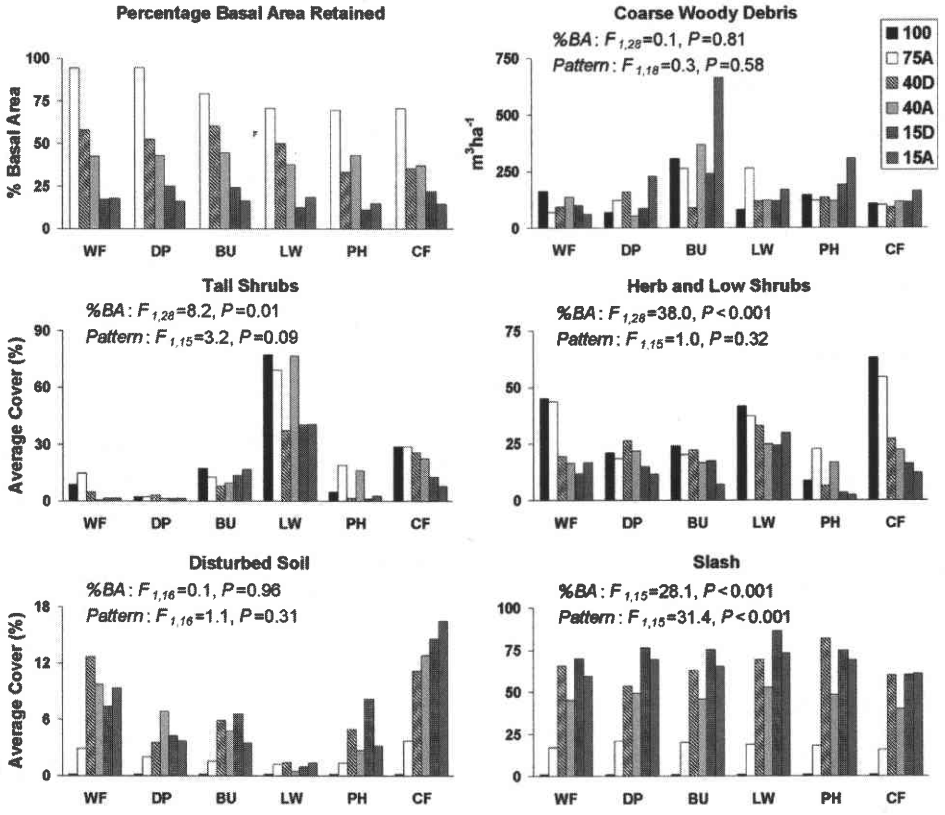

Fig. 2. Post-treatment values for percentage of basal area retained (%BA) and habitat variables. Significance levels for each habitat variable are for separate randomized-block ANCOVAs examining effects of %BA and retention pattern. All treatments were included in analyses of the effects of %BA on volume of coarse woody debris, cover of tall shrubs, and cover of herbs and low shrubs. Only 40 and 15% retention treatments were included in analyses of disturbed soil and slash, and in analyses of effects of pattern for all variables. Treatment codes are: 100% = control, 75A = 75% retention, 40D = 40% retention dispersed, 40A = 40% retention aggregated, 15D = 15% retention dispersed, and 15A = 15% retention aggregated.

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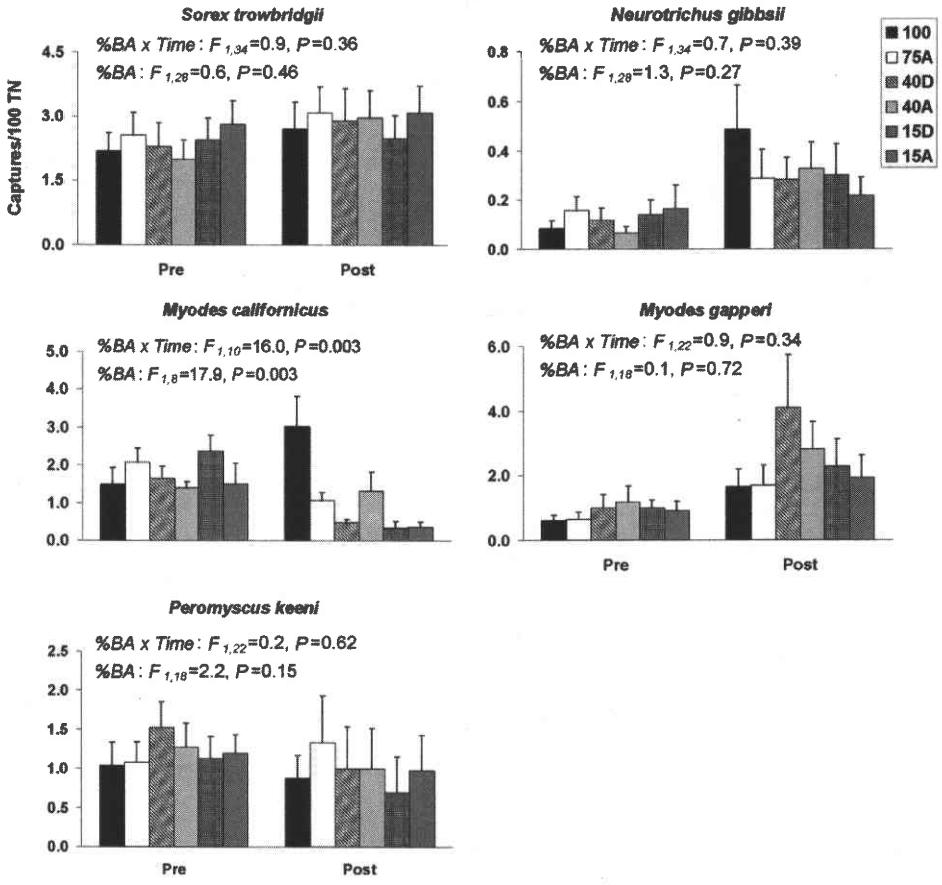

Fig. 3. Average captures per 100 trap nights before and after treatment for small mammals expected to decrease in abundance with decreasing retention amount. Error bars (+1 S.E.) include among-block and among-year variation. Significance levels are for randomized-block ANCOVA examining effect of %BA on captures 1 and 2 years after treatment. The %BA × Time interaction tests whether this effect was similar in both years. See Fig. 2 for additional information.

SHRUB, SOIL, and CWD did not differ between dispersed and aggregated treatments. Cover of slash was consistently high (>40%) at 40 and 15% retention, and greater in dispersed than in aggregated treatments.

3.2. Relative abundance of small mammals

Of the species expected to respond negatively to treatments (Hypothesis 1), only *M. californicus* decreased as retention amount decreased (Fig. 3). This response was strongest 2 years after harvest. Transformed capture rates of *M. californicus* increased by 0.011 in Post 1 and 0.024 in Post 2 for each 1% increase in retention amount (S.E. = 0.005 for both coefficients). These estimates corresponded to back-transformed approximate decreases in relative abundance of 43% (Post 1) and 67% (Post 2) for a 50% decrease in retention amount. Other closed-canopy species showed inconsistent or neutral responses (*S. trowbridgii*, $\beta_{\%BA} = 0.002$, S.E. = 0.002; *N. gibbsii*, $\beta_{\%BA} = 0.002$, S.E. = 0.002; *P. keeni*, $\beta_{\%BA} = 0.006$, S.E. = 0.004; *M. gapperi*, $\beta_{\%BA} = 0.001$, S.E. = 0.004).

Our expectation that early successional species would respond positively to lower levels of retention (Hypothesis 2) was partially confirmed (Fig. 4). Capture rates of *P. maniculatus* and *M. longicaudus* increased as retention decreased (*P. maniculatus*, $\beta_{\%BA} = -0.015$, S.E. = 0.002, back-transformed estimate of ~110% increase in relative abundance with a 50% decrease in retention; *M. longicaudus*, $\beta_{\%BA} = -0.006$, S.E. = 0.002). *Microtus oregoni* showed a weaker increase than expected ($\beta_{\%BA} = -0.005$, S.E. = 0.003). We did not detect a response by *S. vagrans* ($\beta_{\%BA} = -0.002$, S.E. = 0.002).

As predicted (Hypothesis 3), we did not detect a clear response to treatments by *S. pacificus*, a habitat generalist (Fig. 5; $\beta_{\%BA} = 0.007$, S.E. = 0.005). *Sorex monticolus* also responded minimally in Post 1 but showed evidence of increased abundance with increasing retention in Post 2 (Post 1, $\beta_{\%BA} = 0.000$, S.E. = 0.003; Post 2, $\beta_{\%BA} = 0.007$, S.E. = 0.003). Captures of *S. sonomae* decreased in harvested units ($\beta_{\%BA} = 0.011$, S.E. = 0.003).

Consistent with Hypothesis 4, three species (*S. monticolus*, *S. sonomae*, and *M. gapperi*) showed variable responses among blocks. For *S. monticolus* and *S. sonomae*, this was explained by among-block variation in habitat variables (likelihood ratio tests comparing models with and without %BA × block random effect after adding CWD and HERB: *S. monticolus*,

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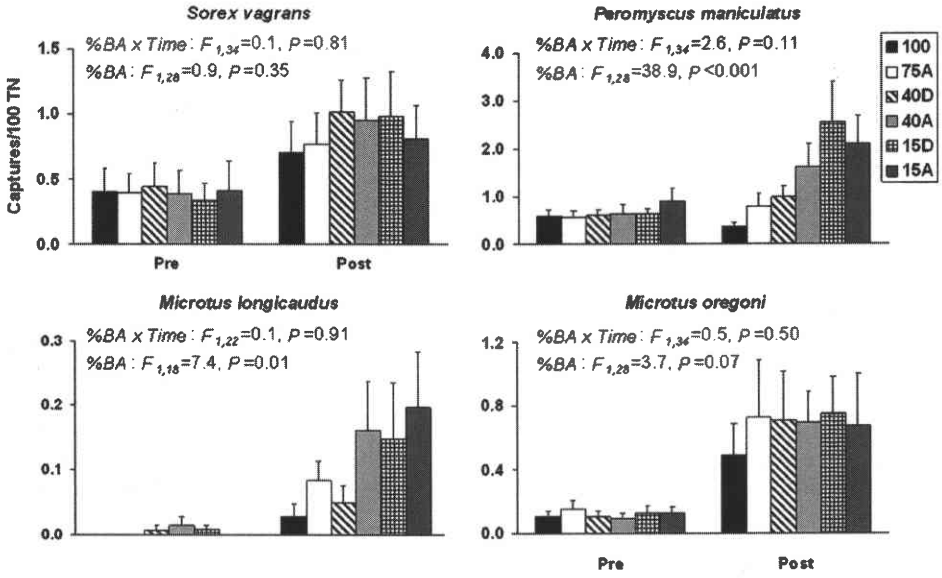

Fig. 4. Average capture rates before and after treatment for small mammals expected to increase in abundance with decreasing retention amount. See Fig. 3 for additional information.

$\chi^2_2 = 4.1$, $P = 0.13$; *S. sonomae*, $\chi^2_2 = 4.8$, $P = 0.09$). However, among-block variation in the response of *M. gapperi* was not explained by habitat variation ($\chi^2_2 = 8.2$, $P = 0.02$). *Myodes gapperi* responded negatively to low retention in two blocks where it was uncommon: low-elevation CF ($\beta'_{\%BA} = 0.008$) and drier LW ($\beta'_{\%BA} = 0.008$). However, at two higher elevations Washington blocks where it was most abundant, *M. gapperi* showed little response (BU, $\beta'_{\%BA} = -0.004$) or responded positively to harvest (PH, $\beta'_{\%BA} = -0.013$). For other species, we did not find evidence of similar variation among blocks ($P > 0.10$).

We examined demographic characteristics of shrews and rodents, including sex ratios and size-class (age) distributions, numbers of adult females, percentage of adult females showing evidence of reproduction during the breeding season prior to each sample, and average productivity of females that were pregnant or had visible uterine scars. We saw no strong differences in these demographic characteristics among treatments.

We did not detect responses to pattern of retention (dispersed versus aggregated), consistent with our expectation (Hypothesis 5; Table 2). *Post hoc* comparisons of models with and

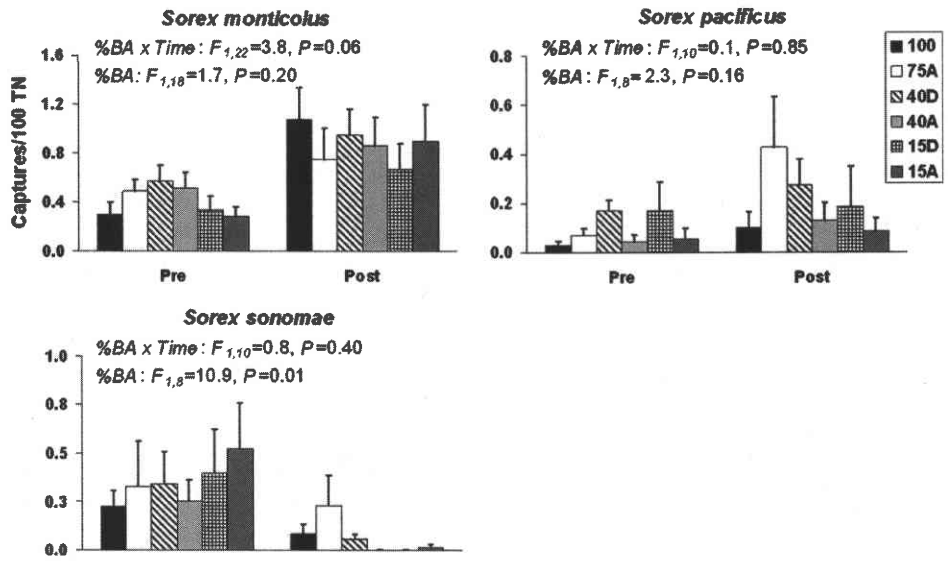

Fig. 5. Average capture rates before and after treatment for shrews expected to show minimal changes in abundance with changes in retention amount. See Fig. 3 for additional information.

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Table 2
Effects of retention pattern (dispersed [D] vs. aggregated [A]) on capture rates (ln[captures per 100 trap nights + 0.1]) in 40 and 15% retention treatments

Species	Pattern × Time		Pattern		$D - A$ (S.E.)
	F	P	F	P	
Sorex monticolus[a]	0.1	0.78	0.1	0.45	−0.10 (0.13)
Sorex pacificus[b]	0.1	0.94	5.1	0.11	−1.31 (0.54)
Sorex sonomae[b]	0.2	0.65	0.4	0.58	0.09 (0.15)
Sorex trowbridgii[c]	0.6	0.46	0.4	0.52	−0.13 (0.19)
Sorex vagrans[c]	0.3	0.60	1.0	0.34	0.16 (0.16)
Neurotrichus gibbsii[c]	0.1	0.94	0.1	0.85	0.03 (0.16)
Peromyscus keeni[a]	0.6	0.46	2.7	0.13	−0.41 (0.25)
Peromyscus maniculatus[c]	0.1	0.73	0.1	0.78	−0.05 (0.17)
Myodes californicus[b]	0.2	0.70	3.2	0.17	−0.83 (0.47)
Myodes gapperi[a]	0.3	0.58	0.1	0.81	0.05 (0.20)
Microtus longicaudus[a]	0.4	0.53	2.6	0.14	−0.28 (0.17)
Microtus oregoni[c]	0.1	0.78	<0.1	0.84	0.00 (0.23)

For each species, a randomized-block, repeated-measures ANCOVA mixed-effects model was used to analyze captures from the two post-treatment samples; in(average pre-treatment capture rate + 0.1) and the observed percentage basal area retained were included as covariates. $D - A$ is the estimated contrast of average values, dispersed – aggregated.

[a] $F_{1,14}$ for Pattern × Time; $F_{1,9}$ for Pattern; $n = 4$.

[b] $F_{1,6}$ for Pattern × Time; $F_{1,3}$ for Pattern; $n = 2$.

[c] $F_{1,22}$ for Pattern × Time; $F_{1,15}$ for Pattern; $n = 6$.

without an interaction between %BA and retention pattern indicated that pattern had little effect at either 15 or 40% retention.

3.3. Community similarity and composition

As predicted (Hypothesis 6), similarity in species composition between harvested and control treatments decreased as harvest intensity increased (Fig. 6; %BA × Time: $F_{1,28} = 2.1$, $P = 0.15$; %BA: $F_{1,22} = 13.3$, $P = 0.001$; $\beta_{\%BA} = 0.18$). This relationship did not vary strongly among blocks ($\chi^2_2 = 1.9$, $P = 0.38$), although differences in similarity were greatest in Oregon blocks and CF and smallest in two higher elevation Washington blocks (average similarity between control and 15% retention treatments in Post 2 = 49% for WF, DP, and CF; 72% for BU and PH). As with abundance, pattern of retention had little effect on similarity of harvested sites with controls (Pattern × Time, $F_{1,22} = 0.1$, $P = 0.89$; Pattern, $F_{1,15} = 0.4$, $P = 0.53$).

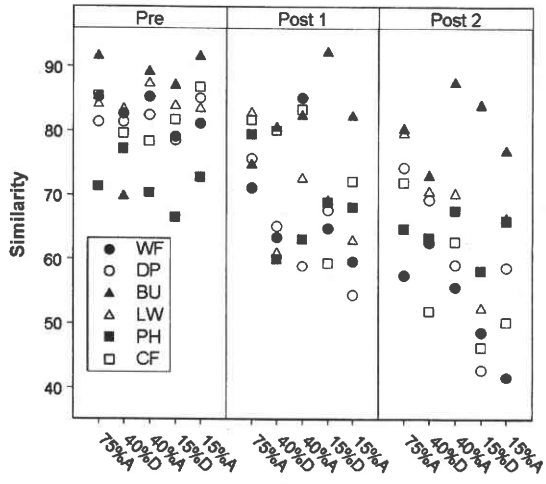

Fig. 6. Similarity of retention treatments with control units in composition of small mammals before (Pre; calculated for combined captures in the two pre-treatment years) and for 2 years after harvest (Post 1 and Post 2). See Figs. 1 and 2 for block and treatment codes.

On average, the first principal component (PCA1) explained 71% of the variance among experimental units in species composition. At WF, DP, LW, and CF, variation in species composition was linked to the retention gradient (Fig. 7). For Oregon blocks (WF, DP), separation of treatments along PCA1 reflected changes in relative abundances of *P. maniculatus* and *M. californicus*. At LW and CF, the percentage contribution of *P. maniculatus* separated treatments. However, at BU and PH, where *P. maniculatus* was uncommon even after harvest, PCA1 did not correspond to the retention gradient. Relative contributions of three closed-canopy species, *S. trowbridgii*, *P. keeni*, and *M. gapperi*, were weakly linked to retention at some blocks, but had no clear relation to retention at BU or PH. We saw no obvious interpretation of PCA2.

4. Discussion

Based on previously described habitat associations and responses to forest harvest, we hypothesized that small mammals would show varied but predictable responses to the gradient in overstory retention. However, many of our predictions were partly inaccurate. We hypothesized that species associated with closed-canopy forests would decline with decreasing retention, yet only the response of *M. californicus* was consistent with this prediction. Similarly, only two of four early successional species (*P. maniculatus* and *M. longicaudus*) showed strong positive responses to overstory removal. Others showed either a small increase (*M. oregoni*) or no change (*S. vagrans*). Decreased similarity in community

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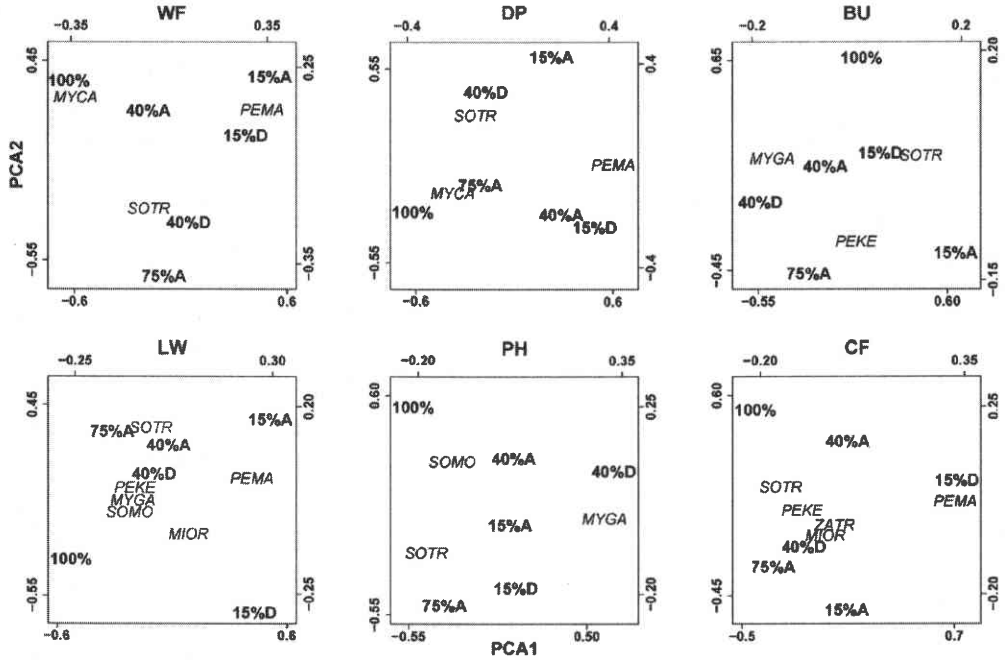

Fig. 7. Principal components analysis of post-treatment community composition by study block. For each experimental unit, species abundance was computed as average percentage contribution to total captures. For each block, species contributing <10% of captures were omitted from the analysis. Species close to the origin are omitted for clarity (*S. monticolus* [SOMO] for BU and CF; *S. vagrans* [SOVA] for WF, DP, and PH; *N. gibbsii* [NEGI] for BU; *P. keeni* [PEKE] for PH; *P. maniculatus* [PEMA] for BU; *M. gapperi* [MYGA] for CF; *M. oregoni* [MIOR] for WF). Other abbreviations are *S. trowbridgii* (SOTR), *Z. trinotatus* (ZATR), and *M. californicus* (MYCA). Site scores are on lower and left axes; species scores are on upper and right axes. See Figs. 1 and 2 for block and treatment codes.

composition between controls and harvest sites was driven by changes in abundances of *M. californicus* and *P. maniculatus*. Community composition of harvested sites was similar to controls at two Washington blocks (PH and BU) where *P. maniculatus* remained uncommon after treatments and *M. gapperi* showed little response. Consistent with our expectation, pattern of retention had little effect on any species.

4.1. Persistence after harvest by closed-canopy species

Several factors may explain the unpredicted responses of species associated with closed-canopy forests. First, population declines may not occur within the first 2 years after harvest. Short-term increases by forest species after logging have been reported in other studies (reviewed by Kirkland, 1990), probably due to influx of resources such as canopy lichens, seeds, invertebrates, and woody debris to the forest floor (Lovejoy, 1975; Von Trebra et al., 1998). In addition, for three blocks in Washington, the first post-treatment sample occurred in a year of high relative abundance among all treatments, obscuring any detectable negative effects of treatments.

Second, our results may reflect greater than expected flexibility in habitat occupancy by *S. trowbridgii*, *N. gibbsii*, *P. keeni*, and *M. gapperi* in our region. These species can occupy a range of forest age classes (Aubry et al., 1991), and are generally present in lower numbers in early successional sites (West, 1991; Songer et al., 1997). Species that respond negatively to clearcutting often persist or increase in abundance after moderate-intensity or small-scale disturbances (Gitzen and West, 2002; MacCracken, 2005). Thinning treatments that retained ~40–70% of basal area (BA) in younger *P. menziesii* forests did not reduce abundance of *S. trowbridgii* or *N. gibbsii* in the Oregon Coast Range (Suzuki and Hayes, 2003) nor of *S. trowbridgii*, *N. gibbsii*, *P. keeni*, or *M. gapperi* in Washington (Wilson and Carey, 2000). Elsewhere, *M. gapperi* did not decline after harvests that removed 30–60% of BA (Monthey and Soutiere, 1985; Steventon et al., 1998; Von Trebra et al., 1998; Sullivan and Sullivan, 2001; Klenner and Sullivan, 2003; Fuller et al., 2004), although responses to pre-commercial thinning have been variable (Etcheverry et al., 2005; Homyack et al., 2005; Sullivan et al., 2005).

Below a critical threshold, retention treatments may be no more effective than clearcuts in sustaining forest species immediately after harvest. We predicted that species sensitive to clearcut logging would show similarly strong responses to 15% retention, the minimum level in this experiment. Instead, for most forest species, we detected no consistent difference between 15 and 100% retention. For species such as *M. gapperi*, even 5–15% retention may offer benefits. For example, in *P. menziesii* / *Pinus contorta* forests of British Columbia, *M. gapperi* persisted in moderate numbers in aggregated-retention treatments supporting only ~6% of the BA of uncut stands (Sullivan and Sullivan, 2001; Sullivan et al., 2001). In contrast, it was nearly absent from clearcuts and from harvest units with ~2% retention. Similarly, in boreal hardwood forests of Alberta, *M. gapperi* maintained abundance in treatments

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with 10% retention, but was nearly absent from those with 1–2% retention (Moses and Boutin, 2001).

Third, in the current experiment, conditions on the forest floor may not have been altered enough to reduce habitat quality for some forest species, at least in the short term. Post-harvest site preparation and slash disposal were minimal in most blocks. Although cover of ground vegetation was reduced, it was not eliminated. For example, average cover of herbs and low shrubs in the harvested area of 15%A was 34% of cover in controls. Moreover, understory species present before harvest dominated the post-harvest plant community (Halpern et al., 2005). Volume of coarse woody debris was not reduced, and many large, partially decayed logs remained intact in harvested areas of some units. Slash was not treated at five of six blocks, resulting in high cover and depth of fine woody debris that may have compensated for reductions in vegetation cover (Halpern and McKenzie, 2001). On the other hand, truffles, an important food for *Myodes* and other forest species, were nearly absent in 15%A (Luoma et al., 2004). Nevertheless, post-harvest conditions were relatively benign compared to those resulting from broadcast burning or other intensive slash treatments (Gashwiler, 1970; Dyrness, 1973). These site-preparation methods can amplify effects of clearcutting on *M. gapperi* and *Peromyscus* (Martell, 1984; Sullivan and Boateng, 1996; Sullivan et al., 1999).

4.2. Regional variation

Our results suggest that effects of green-tree retention on small mammal communities may vary regionally due to numerous factors. These factors include differences in composition of small mammal communities and strong climatic gradients associated with latitude and elevation—factors that may be confounded. For example, summer microclimate is harsher in southern Oregon than in western Washington. Species assemblages differ because of the Columbia River barrier, and species present in each area may differ in their sensitivities to timber harvest. In this study, common small rodents in western Washington forests (*M. gapperi* and *P. keeni*) showed weak and variable responses to treatments during the first 2 years after harvest. However, the most common small rodent of closed-canopy forests in our Oregon study areas, *M. californicus*, nearly disappeared from 15%-retention treatments. It is an obligate fungivore strongly associated with logs and moist conditions of mature forests (Ure and Maser, 1982). It is absent or rare in young managed forests and recently harvested sites (Rosenberg et al., 1994; Mills, 1995; Tallmon and Mills, 2004), including shelterwoods (Waters and Zabel, 1998). *Sorex sonomae* declined after harvest in Oregon, but this response was strong in only one block. Our results and those of Martin and McComb (2002) support the hypothesis that *S. sonomae* is most abundant in closed-canopy forests, but there are insufficient studies of this species to confirm this association. Another Oregon vole that appears to require high amounts of retention, *Arborimus longicaudus* (Huff et al., 1992), was captured too infrequently in the current study to assess responses to treatments (Manning and Maguire, 1999). Regardless of the mechanism (differences in environment or species' habitat requirements), our results, combined with those of previous studies, indicate that higher retention is needed in western Oregon than in western Washington to sustain forest small mammals.

In addition to latitudinal variation and differences in composition due to major biogeographic barriers, green-tree retention strategies may need to vary with elevation gradients and other factors. Winter snowpack and cooler conditions of higher elevation forests in Washington (BU, PH) might ameliorate effects of canopy removal compared to lower elevation (CF) or warmer, drier forests (LW). Multiple factors may contribute to species' responses. For example, *P. keeni* and *P. maniculatus* were most abundant at opposite ends of the retention gradient at CF and LW. However, *P. maniculatus* did not increase after logging at BU and PH. At these blocks, insensitivity of *P. keeni* to harvest might be explained by physical environment, habitat conditions, or lack of competition with *P. maniculatus* in harvested areas (Songer et al., 1997; Gitzen, 2006).

Others have observed regional variation in effects of forest disturbances on small mammals (Converse et al., 2006). For example, although *M. gapperi* is considered a mature-forest species in western North America, across its range it has shown mixed responses to logging (Kirkland, 1990; Hayward et al., 1999). In cool, moist forests, it may be less sensitive to canopy removal (Smith and Nichols, 2004). *Peromyscus keeni* shows similar differences between drier, warmer areas of western Washington (Carey and Johnson, 1995; Songer et al., 1997) versus cooler, moister sites in southeastern Alaska (Smith and Nichols, 2004). In addition, its potential competitor, *P. maniculatus*, is absent in southeastern Alaska. Within and across regions, scientists and managers should expect widespread species to show variable responses to silvicultural treatments, except for species strongly dependent on early successional or mature-forest habitats. In regional studies, replication of treatments within study areas would improve our understanding of this variation. Meta-analyses that contrast hypotheses about sources of variation may also help to explain these diverse responses (Gliwicz and Glowacka, 2000).

4.3. Sampling issues

Our treatment units and sampling grids were large compared to scales of movement of our target species. Therefore, we assumed that immigration into treatment units during each trapping period was low, and that the relative difference between actual and effective area trapped was small. Our trapping was unlikely to have altered population responses to treatments. Trap density was low and sampling occurred at the end of the breeding season. Our high captures reflect the large area sampled (total area of all trap grids was $\sim$2.8 km^2), high insectivore densities in some blocks, and unusually high capture rates in Washington blocks in 1998.

Although our sampling methods limited our ability to examine assumptions about detectability, supplemental analyses supported our inferences about population responses.

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Subsets of the data, such as number of animals caught during the first week of trapping each year, showed the same trends as data presented. Populations of closed-canopy species were demographically similar in harvested and unharvested units, based on comparisons of size-class (age) distributions, numbers of adult females and their reproductive states, and sex ratios.

5. Conclusions

Compared to patterns observed after clearcut logging, we saw less dramatic shifts in composition and abundance of small mammals. In part, this may reflect the short time frame of sampling, but also the beneficial effects of retained habitat structures, even at retention levels as low as 15%. In addition, species such as *S. trowbridgii* and *M. gapperi* may respond more strongly to methods of site preparation than to level of overstory retention.

As with forest treatments such as fuels management (Converse et al., 2006), appropriate strategies for green-tree retention will vary with regional changes in environmental conditions and the assemblage of forest species. In federal forests within the range of the Northern Spotted Owl, live trees must be retained over at least 15% of each harvest unit, with most trees retained in small aggregates (0.2–1.0 ha; USDA and USDI, 1994b; Tuchmann et al., 1996). At mid- to higher elevations in the Washington Cascades, 15–40% retention may be sufficient to benefit small rodents and insectivores. However, in the southern Oregon Cascades, managers may need to retain higher amounts of trees to achieve similar benefits.

Both aggregated and dispersed retention could play important but temporally distinct roles for forest species—aggregates as refugia immediately after harvest and dispersed trees as spatially continuous sources of structure when the regenerating stand reaches canopy closure. Clearly, a full assessment of green-tree retention effects will require periodic, long-term sampling. With long-term monitoring, DEMO and similar experiments will meet an important research need for forest management (DeStefano, 2002).

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Appendix A. Analysis of effects of retention amount on relative abundance

Several factors led us to use %BA to model treatment effects, rather than a categorical treatment variable. First, residual %BA often deviated from targeted amounts. Second, estimating only one coefficient for %BA increased power to detect responses (Maguire et al., 2007). Supplemental analyses indicated that this log-linear model fit data adequately. Third, this model allowed us to examine among-block variation in responses (Hypothesis 4). Results were similar regardless of whether we used %BA or absolute BA to model treatments.

We modeled small mammal relative abundance as:

$$\begin{aligned}
&\log(y_{ijk} + 0.1) \\
&\quad = \mathrm{Time}_k + \beta_{\mathrm{pre}} \times \log(\mathrm{Pre}_{ij} + 0.1) \\
&\qquad + (\beta_{\%\mathrm{BA}} + X_k \times \Delta\beta_{\%\mathrm{BA}}) \times \%\mathrm{BA}_{ij} + \mathrm{block}_i + \mathrm{unit}_{ij} \\
&\qquad + e_{ijk}\ \mathrm{block}_i \sim N(0, \sigma^2_{\mathrm{block}}) \\
&\mathrm{unit}_{ij} \sim N(0, \sigma^2_{\mathrm{unit\ in\ block}}) \quad e_{ijk} \sim N(0, \sigma^2)
\end{aligned}$$

where the response variable y_{ijk} = captures per 100TN in block i, experimental unit j, and time k (Post 1 or Post 2). Fixed effects included: Time_k = effect of time k across all units; Pre_{ij} = average pre-treatment capture rates in block i, unit j; β_{pre} = regression effect of average pre-treatment captures; $\%\mathrm{BA}_{ij}$ = percentage of basal area retained in block i, unit j; $\beta_{\%\mathrm{BA}}$ = change in ln-transformed capture rate per 1% increase in %BA; X_k = indicator variable, 0 if k = Post 1 or 1 if k = Post 2; $\Delta\beta_{\%\mathrm{BA}}$ = adjustment to $\beta_{\%\mathrm{BA}}$ in Post 2 (i.e., the %BA × Time interaction to allow the effect of %BA to vary between Post 1 and Post 2). Random effects included block (block_i), experimental unit in block (unit_{ij}), and residual error (e_{ijk}). We examined normality plots of random effects and residuals to ensure that parametric models were appropriate.

To examine whether there was high among-block variation in responses (Hypothesis 4), we expanded the above model, adding a random effect of %BA × block:

$$\begin{aligned}
&\log(y_{ijk} + 0.1) \\
&\quad = \mathrm{Time}_k + \beta_{\mathrm{pre}} \times \log(\mathrm{Pre}_{ij} + 0.1) \\
&\qquad + [(\beta_{\%\mathrm{BA}} + b_{\%\mathrm{BA,block}\,i}) + X_k \times \Delta\beta_{\%\mathrm{BA}}] \times \%\mathrm{BA}_{ij} \\
&\qquad + \mathrm{block}_i + \mathrm{unit}_{ij} + e_{ijk} \\
&b_{\%\mathrm{BA,block}\,i} \sim N(0, \sigma^2_{\%\mathrm{BA}\times\mathrm{block}})
\end{aligned}$$

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where $b_{\%BA,block\ i}$ is a random, block-specific adjustment to the across-block average fixed effect of $\beta_{\%BA}$. We compared models with and without this random effect, testing the null hypotheses that $\sigma^2_{\%BA\times block} = 0$ (Pinheiro and Bates, 2000:87). When we detected variable responses among blocks, we extracted block-specific regression coefficients ($\beta'_{\%BA} = \beta_{\%BA} + b_{\%BA,\ block\ i}$), added habitat covariates to the models, and re-tested whether $\sigma^2_{\%BA\times block}$ was different from 0.

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