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Forest Ecology and Management 205 (2005) 1–14

Forest Ecology and Management

www.elsevier.com/locate/foreco

Long-term responses of ecosystem components to stand thinning in young lodgepole pine forest

II. Diversity and population dynamics of forest floor small mammals

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Received 30 March 2004; received in revised form 5 October 2004; accepted 5 October 2004

Abstract

A variety of silvicultural practices may be used to diversify second-growth forests that have regenerated from clearcut harvesting. These young stands are structurally simple and amenable to practices such as variable-density and conventional thinnings to accelerate ecosystem development. This study was designed to test the hypotheses that (i) abundance and diversity of forest floor small mammals, and (ii) population dynamics (reproduction, recruitment, and survival) of the southern red-backed vole (*Clethrionomys gapperi*) would be maintained at levels recorded in old-growth forest, by large-scale thinning to various densities in young lodgepole pine (*Pinus contorta*) forest. Replicate study areas were located near Penticton, Kamloops, and Prince George in south-central British Columbia, Canada. Each study area had three stands thinned to densities of ~500 (low), ~1000 (medium), and ~2000 (high) stems/ha, with an unthinned young pine and old-growth pine stand for comparison. Forest floor small mammal communities were sampled intensively in 2000, 2001, and 2002 at 12–14-years after the pre-commercial thinning treatment.

Mean total abundance of small mammals was similar among stands with the highest overall numbers recorded in 2002. Mean species richness and diversity of small mammals were similar among stands. Mean abundance of *C. gapperi* was similar among stands and increased significantly with time. This pattern of abundance of *C. gapperi* will likely be consistent except perhaps in years of high numbers when productivity of this species may be highest in old-growth forest. Reproduction, recruitment, and early juvenile survival of *C. gapperi* was similar among stands; Jolly–Seber summer survival was higher in the thinned than unthinned stands with no difference in winter survival among stands. Our results supported hypotheses (i) and (ii) that abundance and diversity of forest floor small mammals and the demographic attributes

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doi:10.1016/j.foreco.2004.10.001

of *C. gapperi* populations would be maintained in young managed lodgepole pine stands (thinned or unthinned) at levels recorded in old-growth forest.

Keywords: Abundance; *Clethrionomys gapperi*; Forest-floor small mammals; Lodgepole pine; Population dynamics; Pre-commercial thinning; Species diversity

1. Introduction

Second-growth forests, that develop after disturbances such as clearcut harvesting or wildfire in western North America, are often structurally simple with a single canopy layer, limited abundance and diversity of understory vegetation, few tree species, and variable quantities of snags and coarse woody debris (Perry, 1994; Hayes et al., 1997). The Pacific Northwest has vast areas of both Douglas-fir (*Pseudotsuga menziesii*) and lodgepole pine (*Pinus contorta*) forests which are classic examples of young stands with these attributes. Such stands are amenable to various silvicultural practices that could diversify within-stand structural heterogeneity (McComb et al., 1993; Hayes et al., 1997). Variable-density thinning (Carey and Johnson, 1995; Carey et al., 1999) and conventional pre-commercial thinning over a wide range of densities (Sullivan et al., 2001) are being investigated for their development of biocomplexity and old growth structural features over relatively short time intervals (McComb et al., 1993; Carey and Wilson, 2001).

In many of these studies, abundance and diversity of forest floor small mammal communities serve as ecological indicators of significant change in forest structure and function. Forest floor small mammals are widespread across temperate forest ecosystems and have a variety of functions, including prey for many predators (Martin, 1994; Carey and Johnson, 1995), distribution of beneficial mycorrhizal fungi (Maser et al., 1978; Ure and Maser, 1982), and consumers of plants and plant products (Buckner, 1966; Sullivan et al., 1990). The southern red-backed vole (*Clethrionomys gapperi*), in particular, is an important indicator species of "old forest conditions" (Raphael, 1988; Nordyke and Buskirk, 1991). This microtine commonly inhabits late successional coniferous and deciduous forests across temperate North America (Merritt, 1981), and hence is a good candidate species for evaluation of the development of "old forest" structural attributes in young stands.

To date, results from variable-density thinning of older ($\geq$60 years) stands of Douglas-fir indicated higher abundance of deer mice (*Peromyscus maniculatus*), Oregon voles (*Microtus oregoni*), and vagrant shrews (*Sorex vagrans*) in these stands compared to controls at 3 years post-treatment (Carey and Wilson, 2001). Similar forests subjected to commercial thinnings had 1.5 times the individual small mammals and 1.7 times the mammal biomass of forests managed with legacies of snags and coarse woody debris with no thinnings (Wilson and Carey, 2000). Total number of small mammals captured was greater in previously thinned than unthinned stands in 52–100-year-old Douglas-fir forests of western Oregon (Suzuki and Hayes, 2003). In pre-commercially thinned stands of 17–27-year-old lodgepole pine, abundance and species diversity of small mammals were positively influenced by stand thinning at 10 years post-treatment (Sullivan et al., 2001). A comparative investigation of variable-density and conventional pre-commercial thinning in 13-year-old lodgepole pine stands indicated similarity in mean abundance, species richness, and species diversity of small mammals between stands at 5 years post-treatment (Sullivan et al., 2002). Deer mice were most abundant in variable-density stands and heather voles (*Phenacomys intermedius*) in conventionally thinned stands, with no differences between stands for the other species.

Abundance may be a misleading indication of habitat quality (Van Horne, 1983) and the associated demographic attributes of reproduction, recruitment, and survival of small mammal populations also need to be evaluated. Such an approach requires intensive sampling of small mammals on replicate sites over at least 3 years to provide a rigorous analysis of the habitat quality derived from various thinning regimes. Thus, this study was designed to test the hypotheses that: (i) abundance and diversity of forest floor small mammals, and (ii) population dynamics (reproduction, recruitment, and survival) of the red-backed vole would be maintained at levels recorded in old-growth forest, by large-scale thinning to various densities over the 12–14-year period after treatment in young lodgepole pine forest. This paper is one of several periodic papers reporting on long-term responses of small mammal communities to these treatments.

2. Methods

2.1. Study areas and experimental design

A description of the study areas and experimental design is given in Ransome et al. (2004).

2.2. Small mammal populations

Populations of forest floor small mammals were live-trapped at 4-week intervals from May to October 2000, 2001, and 2002. One trapping grid (1 ha) with 49 (7 × 7) trap stations at 14.3 m intervals and one Longworth live-trap at each station was located on each site (Ritchie and Sullivan, 1989). Traps were supplied with whole oats and carrot, and cotton as bedding. Traps were set on the afternoon of day 1, checked on the morning and afternoon of day 2 and morning of day 3, and then locked open between trapping periods.

Forest floor small mammal species sampled by this procedure included the deer mouse, northwestern chipmunk (*Tamias amoenus*), meadow vole (*Microtus pennsylvanicus*), long-tailed vole (*M. longicaudus*), southern red-backed vole, heather vole, montane shrew (*Sorex monticolus*), common shrew (*S. cinereus*), wandering shrew (*S. vagrans*) and short-tailed weasel (*Mustela erminea*).

All small mammals (except shrews and weasels) captured were ear-tagged with individually numbered tags, sexed, reproductive condition noted, weighed on Pesola spring balances, and released at point of capture. Palpation of male testes and mammaries of females was used to measure reproductive state (Krebs et al., 1969). Unfortunately, there was a high mortality rate for shrews in the traps overnight, but this was unavoidable in practice. Shrews that died in traps were collected and identified according to Nagorsen (1996).

The western jumping mouse (*Zapus princeps*), meadow jumping mouse (*Z. hudsonius*), and northern bog-lemming (*Synaptomys borealis*) all occurred within the range of our study areas but are relatively uncommon and tend to prefer earlier successional or moister habitats (Whitaker, 1972; Banfield, 1974), and hence were not captured. The pygmy shrew (*Sorex hoyi*) and water shrew (*S. palustris*) may also have been present in our sampling areas but were not captured. The pygmy shrew is relatively uncommon, ranging in density from 0.5 to 1.2 animals/ha (Nagorsen, 1996). The water shrew is strongly associated with wet habitats at densities similar to the pygmy shrew (Nagorsen, 1996). The northern pocket gopher (*Thomomys talpoides*) occurred in our study areas at Penticton and Kamloops, but rarely appeared above ground and was not captured. The primarily arboreal red squirrel (*Tamiasciurus hudsonicus*), northern flying squirrel (*Glaucomys sabrinus*), and bushy-tailed woodrat (*Neotoma cinerea*) were not considered part of the forest floor small mammal community. The responses of these arboreal species, as another part of the overall study on ecosystem components, are reported in Ransome et al. (2004).

2.3. Demographic analysis

Trappability and population density per hectare were measured to determine the effects of stand treatments on abundance of the three major species. Jolly trappability was calculated as per the estimate reported by Krebs and Boonstra (1984). Abundance estimates of *C. gapperi*, *P. maniculatus*, and *T. amoenus* were derived from the Jolly–Seber (J–S) stochastic model (Seber, 1982). The minimum number of animals known to be alive (MNA) (Krebs, 1966) was used as the population estimate for the first and last sampling periods of the study when the J–S estimate was not calculated. The reliability of the J–S model declines when population sizes are very low and no marked animals are captured (Krebs et al., 1986). In these cases, the total number of individuals captured was used to estimate populations of *M. pennsylvanicus*, *M. longicaudus*, *P. intermedius*, *S. monticolus*, *S. cinereus*, *S. vagrans*, and *Mustela erminea*. We evaluated reproduction, recruitment, and survival as additional demographic parameters for the three major species. Reproductive performance was based on the number of successful pregnancies calculated for each population in 2000, 2001, and 2002. A pregnancy was considered successful if a female was lactating during the period following the estimated time of birth of a litter. Each record of a lactating female was considered an independent litter based on a 3-week nursing period within our 4-week trapping intervals. Early juvenile survival is an index relating recruitment of young into the trappable population to the number of lactating females (Krebs, 1966). A modified version of this index is number of juvenile animals at week t divided by the number of lactating females caught in week $t-3$. Animals captured for a first time in a stand were called recruits. Mean J–S 28-day survival rates were calculated for each population during summer (May–September) and winter (October–April) periods each year.

We used age at sexual maturity to determine age classes of animals. Body mass was used as an index of age. The percentage of sexually mature animals was used to determine the mass limitations for juveniles, subadults, and adults assuming that juveniles were seldom, if ever, sexually mature; that <50% of the subadults in the upper mass class were mature; and that at least 50% of the adults were sexually mature in the lowest mass class. Animals were classified as juvenile (includes juvenile and subadult classes pooled) or adult by body mass: red-backed voles and deer mice, juvenile = 1–18 g, adult $\geq$ 19 g; chipmunks, juvenile = 1–44 g, adult $\geq$ 45 g.

2.4. Diversity measurements

Species richness was the total number of species sampled for the small mammal community in each stand (Krebs, 1999). Species diversity was based on the Shannon–Wiener index which is well represented in the ecological literature (Magurran, 1988; Burton et al., 1992). This measurement was calculated using the estimated abundance of each species for a given sampling period and then averaged over the number of sampling periods for each year.

2.5. Statistical analysis

A repeated measures analysis of variance (RM-ANOVA) was used to determine the effect of thinning treatments on mean abundance of each species, total abundance, mean species richness, and mean species diversity of the small mammal communities. It was also used to evaluate mean number of successful pregnancies, mean number of recruits, a mean index of early juvenile survival, and mean summer and winter survival among treatments. Before performing any analyses, data not conforming to properties of normality and equal variance were subjected to various transformations to best approximate the assumptions required by any ANOVA (Zar, 1999). Mauchly's W-test statistic was used to test for sphericity (independence of data among repeated measures) (Littel, 1989; Kuehl, 1994). For data found to be correlated among years, the Huynh–Feldt (H–F) correction (Huynh and Feldt, 1976) was used to adjust the degrees of freedom of the within-subjects F-ratio. Proportional data were arcsine-transformed prior to the RM-ANOVA analysis (Zar, 1999). Duncan's multiple range test (DMRT) was used to compare mean values based on RM-ANOVA results. Mean abundance of *C. gapperi* was also compared among stands and years with 95% confidence intervals (CI). In all analyses, the level of significance was at least $P = 0.05$.

3. Results

3.1. Abundance and diversity

C. gapperi was the most abundant species with a total of 1116 individuals captured (47.9% of a total of 2328 small mammals). The next two most abundant species were *P. maniculatus* (335 individuals) and *T. amoenus* (337 individuals). Numbers of individuals for the less common microtines: 72 *M. pennsylvanicus*, four *M. longicaudus*, and three *P. intermedius*. Total numbers of individuals of the three insectivore species were 260 for *S. monticolus*, 131 for *S. cinereus*, and 50 for *S. vagrans*. Twenty individual *M. erminea* were captured over the 3-year study.

Susceptibility to capture was measured by Jolly trappability estimates with mean values ranging from 35.5% to 91.8% for *C. gapperi*, 37.8% to 100.0% for *P. maniculatus*, and 55.1% to 73.7% for *T. amoenus*. Based on this variable susceptibility to capture, Jolly–Seber population estimates were calculated for the three major species (Jolly and Dickson, 1983). The total number of individuals captured represented the population estimates for the other species.

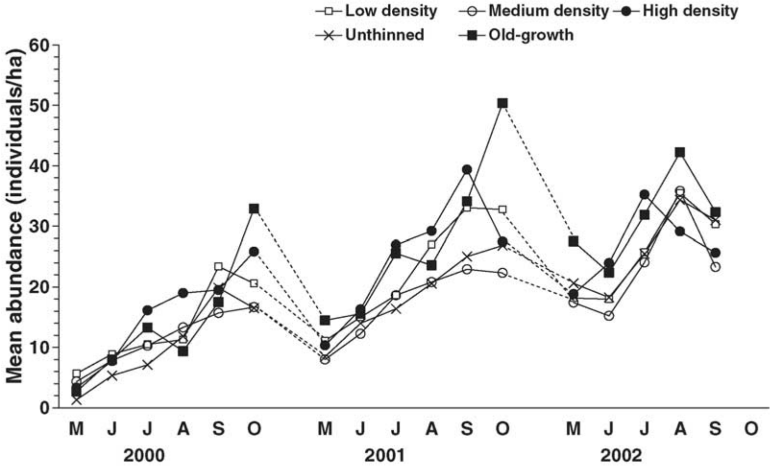

Fig. 1. Mean ($n = 3$ replicate stands) total abundance of small mammals per hectare for the five treatments 2000–2002.

Mean total abundance of the 10 species of small mammals was similar among stands with the highest overall numbers recorded in 2002 (Fig. 1; Table 1). Mean species richness and species diversity were similar among stands (Table 1).

Mean abundance of *C. gapperi* was statistically similar among stands, but increased significantly with time (Fig. 2; Table 2). It may be biologically important that abundance of *C. gapperi* appeared higher in the old-growth stands than other stands in both October 2000 and 2001, owing to recruitment of young animals (Fig. 2). However, mean abundance of this microtine was similar (overlapping 95% CI) between old-growth and at least one of the thinned pine stands in eight of nine cases (Fig. 3). Mean abundance of *C. gapperi* was higher (non-overlapping 95% CI) in the old-growth than the unthinned pine stands in four of nine cases (Fig. 3).

Mean abundance of *P. maniculatus* was significantly different among stands, with the highest numbers occurring in the low-density, high-density,

Table 1
Mean ($n = 3$ replicate stands) ± S.E. total abundance/ha and species richness and species diversity for the five treatments during 2000–2002 and results of RM-ANOVA

Parameter and year	Low density	Medium density	High density	Unthinned	Old growth	Treatment		Time		Treatment × time	
						$F_{4,8}$	P	$F_{2,20}$	P	$F_{8,20}$	P
Total abundance											
2000	13.4 ± 2.2	11.4 ± 0.9	15.3 ± 4.9	10.3 ± 3.7	14.0 ± 3.9	2.54	0.12	8.61*	**<0.01**	0.10*	1.00
2001	22.9 ± 0.7	17.5 ± 1.1	24.9 ± 2.5	18.6 ± 0.3	27.3 ± 0.8						
2002	25.5 ± 3.5	23.2 ± 4.5	26.6 ± 2.3	25.9 ± 4.0	31.3 ± 3.2						
Species richness											
2000	2.83 ± 0.00	3.89 ± 0.72	3.00 ± 0.50	2.50 ± 0.60	2.28 ± 0.46	1.86	0.21	2.36	0.12	0.44	0.88
2001	4.05 ± 0.28	3.72 ± 0.05	3.44 ± 0.47	2.95 ± 0.37	2.78 ± 0.43						
2002	4.27 ± 0.35	3.67 ± 0.47	3.33 ± 0.47	3.67 ± 0.13	2.87 ± 0.37						
Species diversity											
2000	1.01 ± 0.06	1.46 ± 0.26	0.96 ± 0.02	0.93 ± 0.31	0.84 ± 0.27	2.27	0.15	0.97	0.40	0.33	0.95
2001	1.56 ± 0.09	1.36 ± 0.10	1.33 ± 0.21	1.02 ± 0.16	0.93 ± 0.22						
2002	1.55 ± 0.13	1.34 ± 0.32	1.19 ± 0.23	1.19 ± 0.25	0.91 ± 0.33						

F-values identified by * were calculated using an H–F correction factor, which decreased the stated degrees of freedom due to correlation of data among repeated measures (years).

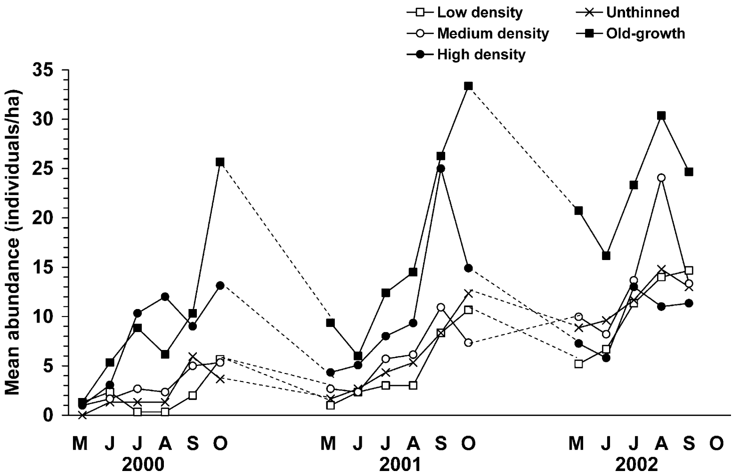

Fig. 2. Mean ($n = 3$ replicate stands) total abundance of *Clethrionomys gapperi* per hectare for the five treatments 2000–2002.

and unthinned stands (Fig. 4; Table 2). Populations of *T. amoenus* were similar among stands and over time (Table 2). The less common species, *M. pennsylvanicus*, *S. monticolus*, *S. cinereus*, *S. vagrans*, and *Mustela erminea* all had similar mean abundances among stands.

3.2. Population dynamics of the major species

The mean number of successful pregnancies was similar among stands for each of the three major species (Table 3). This measure of reproductive performance increased significantly through time for *C. gapperi* but not for *P. maniculatus* or *T. amoenus* (Table 3).

Mean recruitment of new animals was similar among stands for each of the three major species (Table 4). Recruitment of *C. gapperi* increased significantly through time in all stands, but this pattern was not evident for either *P. maniculatus* or *T. amoenus* (Table 4).

An index of early juvenile survival was similar among stands for *C. gapperi* and *T. amoenus*, but was

Table 2

Mean ($n = 3$ replicate stands) ± S.E. abundance/ha of small mammal species for the five treatments during 2000–2002 and results of RM-ANOVA

Species and year	Low density	Medium density	High density	Unthinned	Old growth	Treatment		Time		Treatment × time	
						$F_{4,8}$	P	$F_{2,20}$	P	$F_{8,20}$	P
Clethrionomys gapperi											
2000	2.0 ± 1.9	3.0 ± 1.4	8.1 ± 6.3	2.3 ± 1.2	9.6 ± 4.1	3.45	0.06	12.28	<**0.01**	0.64	0.74
2001	4.7 ± 3.4	5.9 ± 3.4	11.1 ± 5.8	5.8 ± 4.4	17.0 ± 5.4						
2002	10.4 ± 5.2	13.8 ± 6.2	9.7 ± 6.2	11.6 ± 7.2	23.1 ± 6.2						
Peromyscus maniculatus											
2000	2.4 ± 1.1 A	0.9 ± 0.1 BC	1.4 ± 0.8 AB	2.8 ± 1.4 AB	0.3 ± 0.3 C	4.35	**0.04**	1.74	0.20	0.22	0.98
2001	8.0 ± 0.8 A	1.3 ± 0.9 BC	5.1 ± 2.5 AB	5.6 ± 3.5 AB	0.9 ± 0.5 C						
2002	4.8 ± 1.3 A	1.7 ± 1.0 BC	7.1 ± 4.0 AB	4.3 ± 2.5 AB	2.2 ± 2.2 C						
Tamias amoenus											
2000	7.4 ± 3.0	5.0 ± 1.5	4.0 ± 1.6	4.3 ± 3.2	3.2 ± 1.9	1.21	0.38	0.87	0.43	0.46	0.87
2001	7.0 ± 3.2	7.6 ± 2.5	6.1 ± 2.7	5.3 ± 3.6	7.7 ± 4.7						
2002	6.7 ± 3.3	4.3 ± 2.4	7.1 ± 4.1	7.3 ± 5.9	4.9 ± 3.1						

Columns of mean values with different letters are significantly different by DMRT.

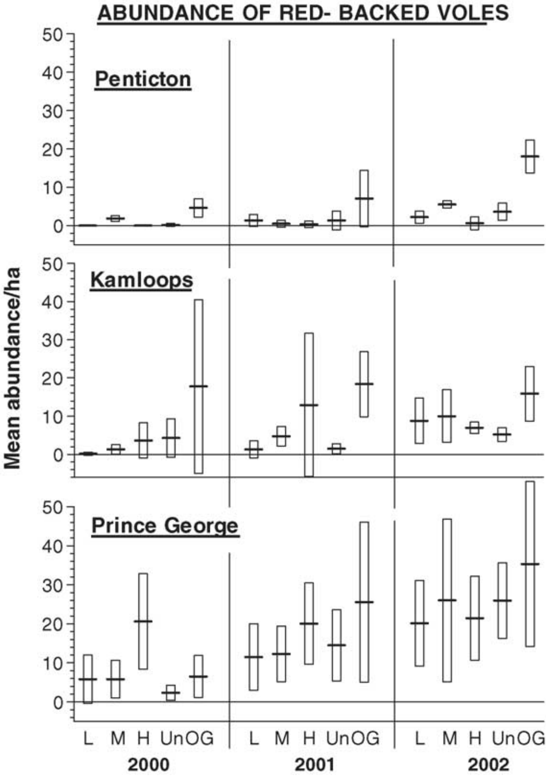

Fig. 3. Mean abundance per hectare and 95% confidence intervals for *Clethrionomys gapperi* for the five treatment stands at each study area in 2000, 2001, and 2002. L = low density, M = medium density, H = high density, Un = unthinned, and OG = old-growth.

significantly different among stands for *P. maniculatus* (Table 5). This measure of mean juvenile survival was higher in the high-density than either of the medium-density or old-growth stands. Juvenile survival of *P. maniculatus* in these latter stands was similar to that in the low-density and unthinned stands (Table 5).

Mean estimates of J–S summer survival of *C. gapperi* were significantly different among stands, with higher survival of red-backed voles in the low- and high-density stands than in the unthinned stands (Table 6). Winter survival of *C. gapperi* was similar among stands as were summer and winter survival estimates for *P. maniculatus* (Table 6). Mean estimates of J–S summer survival for *T. amoenus* were significantly different among stands, being highest in the high-density stands (Table 6).

4. Discussion

4.1. Abundance and diversity

Our study is the first investigation of a relatively long-term response of forest-floor small mammal communities at 12–14 years after pre-commercial thinning of young lodgepole pine forest. A total of 10 species comprised these communities (Table 7). The similarity in total abundance, species richness, and diversity among stands was surprising considering the higher numbers and diversity of small mammals in the heavily thinned and old-growth stands than other

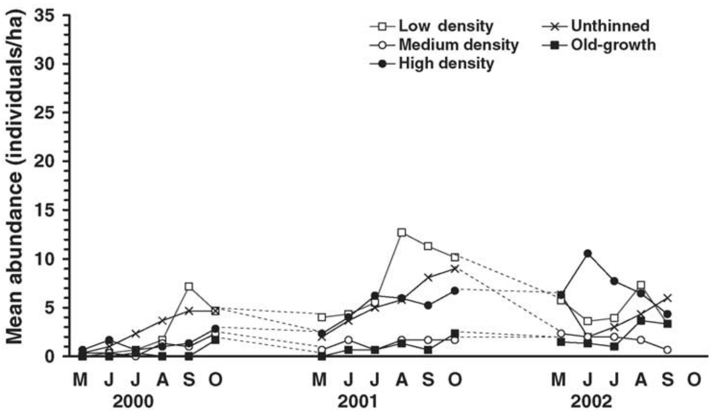

Fig. 4. Mean (*n* = 3 replicate stands) total abundance of *Peromyscus maniculatus* per hectare for the five treatments 2000–2002.

Table 3
Mean ($n = 3$ replicate stands) ± S.E. number of successful pregnancies for the three major species for the five treatments during 2000–2002 and results of RM-ANOVA

Species and year	Low density	Medium density	High density	Unthinned	Old growth	Treatment		Time		Treatment × time	
						$F_{4,8}$	P	$F_{2,20}$	P	$F_{8,20}$	P
Clethrionomys gapperi											
2000	1.7 ± 1.7	2.7 ± 0.9	2.7 ± 1.8	2.3 ± 0.7	4.7 ± 2.3	2.48	0.13	7.73	**<0.01**	0.12	1.00
2001	3.3 ± 2.8	4.0 ± 2.1	5.7 ± 4.7	4.3 ± 2.3	8.7 ± 3.7						
2002	6.7 ± 3.0	11.7 ± 2.0	8.3 ± 4.3	8.0 ± 3.6	16.7 ± 2.7						
Peromyscus maniculatus											
2000	0.0	0.0	0.7 ± 0.3	2.0 ± 1.5	0.0	1.50	0.29	2.57	0.10	0.30	0.96
2001	3.3 ± 0.3	0.7 ± 0.7	1.3 ± 0.3	4.7 ± 2.9	1.0 ± 1.0						
2002	2.0 ± 0.6	2.0 ± 1.2	4.3 ± 2.4	3.3 ± 2.8	2.3 ± 2.3						
Tamias amoenus											
2000	2.0 ± 0.6	2.3 ± 0.3	1.7 ± 0.7	1.3 ± 0.9	0.7 ± 0.3	2.03	0.18	0.17	0.85	0.27	0.97
2001	2.3 ± 0.7	2.3 ± 0.3	2.0 ± 1.0	1.0 ± 0.6	2.3 ± 1.2						
2002	2.0 ± 1.0	1.7 ± 0.9	2.3 ± 0.9	1.3 ± 0.7	1.7 ± 0.9						

stands at 10 years, but not at 2–3 years, post-thinning as reported by Sullivan et al. (2001). In other studies, total abundance of individuals of eight targeted species was higher in conventionally thinned stands than in stands with variable-density thinnings at 4–5 years post-treatment (Carey and Wilson, 2001). A retrospective analysis reported 1.5 times the individual mammals in forests managed with conventional thinning than in those with legacy retention (Wilson and Carey, 2000). Similarly, Suzuki and Hayes (2003) recorded greater numbers of small mammals in thinned than unthinned stands in a retrospective study.

Although not formally significant ($P = 0.06$), mean abundance of *C. gapperi* did appear highest in the old-growth stands in 2002. There was little difference among young pine stands in 2002 (range of 9.7–13.8 red-backed voles/ha), a year of higher abundance, compared to the 23.1 animals/ha in the old-growth stands (Table 2). Thus, as concluded by Sullivan et al. (2001), numbers of *C. gapperi* in thinned stands were

Table 4
Mean ($n = 3$ replicate stands) ± S.E. recruitment/ha for the three major species for the five treatments during 2000–2002 and results of RM-ANOVA

Species and year	Low density	Medium density	High density	Unthinned	Old growth	Treatment		Time		Treatment × time	
						$F_{4,8}$	P	$F_{2,20}$	P	$F_{8,20}$	P
Clethrionomys gapperi											
2000	10.7 ± 10.2	13.3 ± 7.3	14.7 ± 9.7	8.7 ± 3.8	26.0 ± 6.6	2.93	0.09	10.75	**<0.01**	0.75	0.65
2001	19.0 ± 13.5	17.0 ± 9.1	24.3 ± 16.7	23.7 ± 16.2	40.7 ± 16.7						
2002	31.7 ± 14.1	39.3 ± 16.8	25.3 ± 14.0	29.0 ± 16.4	48.7 ± 21.2						
Peromyscus maniculatus											
2000	8.3 ± 3.8	4.7 ± 1.2	3.7 ± 2.7	7.0 ± 3.5	2.0 ± 2.0	2.66	0.11	0.36	0.70	0.25	0.97
2001	14.0 ± 1.5	4.0 ± 2.6	10.0 ± 5.0	14.7 ± 9.0	4.0 ± 2.0						
2002	8.3 ± 2.7	2.7 ± 1.3	11.3 ± 5.2	10.7 ± 5.8	6.3 ± 6.3						
Tamias amoenus											
2000	14.7 ± 6.6	9.3 ± 2.7	8.3 ± 3.7	9.3 ± 6.6	7.3 ± 3.7	1.56	0.27	1.55	0.24	0.40	0.91
2001	7.7 ± 3.3	10.0 ± 2.9	5.3 ± 2.6	5.7 ± 3.8	6.3 ± 3.8						
2002	7.7 ± 2.9	3.7 ± 1.2	7.3 ± 4.9	6.7 ± 4.8	3.0 ± 1.0						

Table 5
Mean ($n = 3$ replicate stands) ± S.E. index of early juvenile survival (number of juvenile recruits per successful pregnancy) for the three major species for the five treatments during 2000–2002 and results of RM-ANOVA

Species and year	Low density	Medium density	High density	Unthinned	Old growth	Treatment		Time		Treatment × time	
						$F_{4,8}$	P	$F_{2,20}$	P	$F_{8,20}$	P
Clethrionomys gapperi											
2000	1.6 ± 1.6	4.4 ± 2.2	3.3 ± 1.7	1.7 ± 0.8	5.0 ± 1.3	0.55	0.71	1.04	0.37	1.15	0.37
2001	3.7 ± 2.0	2.6 ± 1.9	3.0 ± 1.6	3.5 ± 1.1	3.6 ± 0.4						
2002	2.9 ± 0.6	2.0 ± 0.9	1.4 ± 0.7	2.5 ± 1.2	2.2 ± 1.3						
Peromyscus maniculatus											
2000	0.0 AB	0.0 B	3.0 ± 2.5 A	3.3 ± 2.4 AB	0.0 B	3.74	**0.05**	0.51	0.61	0.48	0.86
2001	3.4 ± 0.6 AB	0.2 ± 0.2 B	5.8 ± 3.5 A	1.4 ± 0.7 AB	0.2 ± 0.2 B						
2002	3.4 ± 1.7 AB	0.7 ± 0.7 B	1.6 ± 0.3 A	2.7 ± 2.2 AB	0.5 ± 0.5 B						
Tamias amoenus											
2000	0.9 ± 0.5	1.0 ± 0.6	1.4 ± 1.3	0.8 ± 0.4	0.7 ± 0.7	0.86	0.53	2.05	0.16	0.12	1.00
2001	0.7 ± 0.2	0.8 ± 0.6	0.5 ± 0.3	0.2 ± 0.2	0.4 ± 0.3						
2002	0.1 ± 0.1	0.0	0.2 ± 0.2	0.3 ± 0.3	0.0						

Columns of mean values with different letters are significantly different by DMRT.

comparable to those in old-growth stands during low to moderate years of abundance. This pattern was evident by the overlapping 95% CIs around mean abundances between old-growth and at least one or more of the thinned stands at both Kamloops and Prince George in all years, and at Penticton in 2000 and 2001 (Fig. 3). Microhabitat development for *C. gapperi* in thinned stands at 12–14 years post-treatment may be sufficient to support high numbers of animals, at least in the sub-boreal spruce forests at Prince George. The number of western red-backed voles (*C. californicus*) captured decreased within 2 years of thinning Douglas-fir stands, but was similar in older stands thinned 7–24 years previously and in unthinned stands in western Oregon (Suzuki and Hayes, 2003). This latter result was different from those recorded for *C. gapperi* in Douglas-fir stands in western Washington where the abundance of this microtine was similar in thinned and unthinned legacy stands (Wilson and Carey, 2000), and showed no response to variable-density thinning (Carey and Wilson, 2001).

C. gapperi is a good indicator of old-growth or late successional forest conditions, particularly spruce-fir (*Abies* spp.) forests in western North America (Merritt, 1981; Raphael, 1988; Nordyke and Buskirk, 1991; Hayward and Hayward, 1995). The distribution of this microtine extends across Canada (south of the tundra) and northern regions of the United States with southern extensions into the Rocky and Appalachian mountain chains (Merritt, 1981). Its dependence on mesic habitats in coniferous, deciduous, and mixed forests with an abundance of stumps, rotting logs, and exposed roots that help to provide a moist microclimate is likely related to its high water requirements (McManus, 1974; Getz, 1968). Development of understory shrubs and young conifers also appear to be important habitat elements for this species (Carey and Johnson, 1995; Moses and Boutin, 2001), and may help to ameliorate microclimatic conditions (Miller and Getz, 1973). Thus, relatively dry interior forests such as those at Penticton, in the Interior Douglas-fir ecological zone, do not appear to support high populations of *C. gapperi*. A synthesis of mean and maximum levels of abundance of *C. gapperi* in uncut mature/old-growth forest in several ecological zones across BC, using our sampling methodology, tended to support this pattern (Table 8).

Our thinned stands had higher volumes of herbaceous vegetation than the unthinned or old-growth stands, but overall species richness and diversity were similar among stands (Lindgren et al., unpublished). Structural diversity of vegetation appeared highest in the heavily thinned stands (Lindgren et al., unpublished). Thus, it is not surprising that *P. maniculatus*, *M. pennsylvanicus*,

Table 6

Mean ($n = 3$ replicate stands) ± S.E. estimates of Jolly–Seber 28-day survival for the three major species during summer and winter periods 2000–2002 for the five treatments

Species and year	Low density	Medium density	High density	Unthinned	Old growth	Treatment		Time		Treatment × time	
						$F_{4,8}$	P	$F_{2,20}$	P	$F_{8,20}$	P
Clethrionomys gapperi											
Summer											
2000	0.75 ± 0.13 A	0.42 ± 0.11 AB	0.63 ± 0.05 A	0.51 ± 0.11 B	0.44 ± 0.12 AB	4.27	**0.05**	1.45	0.26	0.56	0.80
2001	0.80 ± 0.20 A	0.73 ± 0.14 AB	0.80 ± 0.20 A	0.55 ± 0.10 B	0.74 ± 0.04 AB						
2002	0.39 ± 0.11 A	0.65 ± 0.04 AB	0.68 ± 0.04 A	0.66 ± 0.04 B	0.68 ± 0.03 AB						
Winter											
2000–2001	0.85 ± 0.15	0.86 ± 0.04	0.92 ± 0.06	0.87 ± 0.07	0.84 ± 0.03	0.09	0.98	0.88[a]	0.37	0.33[a]	0.85
2001–2002	0.79 ± 0.03	0.83 ± 0.05	0.77 ± 0.02	0.79 ± 0.04	0.91 ± 0.04						
Peromyscus maniculatus											
Summer											
2000	0.72 ± 0.15	0.74 ± 0.26	0.71 ± 0.29	0.67 ± 0.00	0.85 ± 0.16	2.24	0.23	0.45	0.65	0.10	1.00
2001	0.78 ± 0.06	0.55 ± 0.04	0.77 ± 0.05	0.65 ± 0.02	0.73 ± 0.28						
2002	0.59 ± 0.08	0.73 ± 0.18	0.71 ± 0.12	0.48 ± 0.15	0.83 ± 0.18						
Winter											
2000–2001	0.83 ± 0.06	0.84 ± 0.06	0.89 ± 0.08	0.82 ± 0.08	0.89 ± 0.12	0.86	0.54	0.47[a]	0.51	0.29[a]	0.88
2001–2002	0.89 ± 0.01	0.96 ± 0.02	0.91 ± 0.02	0.87 ± 0.03	0.92 ± 0.02						
Tamias amoenus											
Summer											
2000	0.76 ± 0.10 B	0.77 ± 0.01 B	0.85 ± 0.11 A	0.65 ± 0.11 B	0.60 ± 0.17 B	5.47	**0.05**	0.96	0.41	0.38	0.91
2001	0.83 ± 0.08 B	0.73 ± 0.05 B	0.96 ± 0.04 A	0.78 ± 0.03 B	0.82 ± 0.05 B						
2002	0.74 ± 0.11 B	0.73 ± 0.13 B	0.94 ± 0.05 A	0.96 ± 0.04 B	0.86 ± 0.15 B						

Columns of mean values with different letters are significantly different by DMRT.

[a] Because there are only two repeated measures for winter survival, the degrees of freedom for the within subjects F-ratio are $F_{1,10}$ and $F_{4,10}$ for time and treatment × time, respectively.

Table 7

Summary of responses in abundance per hectare and diversity parameters (overall mean values, $n = 17$ trapping periods) for small mammals in the five treatments 2000–2002

Parameter and species	Low density	Medium density	High density	Unthinned	Old growth
Mean abundance					
Clethrionomys gapperi	5.42	7.20	9.62	6.25	16.17
Peromyscus maniculatus	5.09	1.29	4.36	4.23	1.09
Tamias amoenus	7.02	5.74	5.67	5.52	5.32
Microtus pennsylvanicus	0.41	0.61	0.41	0.21	0.10
Microtus longicaudus	0.04	0.04	0.00	0.00	0.00
Phenacomys intermedius	0.02	0.02	0.00	0.02	0.00
Sorex monticolus	1.17	0.96	1.14	0.98	0.84
Sorex cinereus	0.73	0.53	0.70	0.47	0.13
Sorex vagrans	0.35	0.55	0.06	0.02	0.00
Mustela erminea	0.08	0.06	0.04	0.12	0.10
Total	20.33	17.00	22.00	17.82	23.75
Species richness	3.69	3.77	3.26	3.00	2.63
Species diversity	1.36	1.39	1.15	1.04	0.89

Table 8
Summary of mean and maximum abundances per hectare of southern red-backed voles in uncut mature/old-growth forests across a range of latitudes and ecological zones in the interior of British Columbia, Canada

Ecological zone	Major tree species	Latitude	Maximum abundance	Range of mean annual abundance	Reference
ESSF	Spruce–subalpine fir	54°2′N, 127°24′W	84.5	2.2–23.3	Sullivan et al. (1999)
ESSF	Spruce–subalpine fir	50°50′N, 119°50′W	80.0	26.9–33.2	Klenner and Sullivan (2003)
SBS	Douglas-fir–pine	52°29′N, 121°39′W	55.0	2.4–47.0	Von Trebra et al. (1998)
SBS	Pine–spruce	53°52′N, 123°32′W	53.9	6.5–35.3	This study
MS	Pine–spruce–subalpine fir	50°28′N, 120°32′W	60.0	15.8–18.4	This study
MS	Pine–Douglas-fir	49°40′N, 119°53′W	28.0	10.2–18.8	Sullivan et al. (2000)
MS	Pine–Douglas-fir	49°40′N, 119°53′W	30.0	10.8–20.2	Sullivan and Sullivan (2001)
IDF	Pine–spruce	49°34′N, 119°27′W	23.4	4.6–18.0	This study

ESSF (Engelmann spruce–subalpine fir); SBS (sub-boreal spruce); MS (montane spruce); IDF (interior Douglas-fir). Spruce (*Picea engelmannii* × *Picea glauca*); subalpine fir (*Abies lasiocarpa*); Douglas-fir (*Pseudotsuga menziesii*), pine (*Pinus contorta*). For definitions of ecological zones, see Meidinger and Pojar (1991).

and *S. vagrans* were common in the thinned stands with herbaceous understories. This pattern fits that reported for Douglas-fir stands in Washington (Wilson and Carey, 2000; Carey and Wilson, 2001). *Microtus* spp. and *S. vagrans* prefer early successional stages after forest disturbance as well as open coniferous forests with understory vegetation (Banfield, 1974; Newman, 1976; Hawes, 1977; Reich, 1981). *P. maniculatus* is typically reported in a wide variety of early successional habitats (Baker, 1968; Carey and Johnson, 1995; Sullivan et al., 1999). *T. amoenus* was a generalist with respect to our stands which fits the reports by Sutton (1992) and Hayes et al. (1995), but not Sullivan and Klenner (2000). The comparable numbers across stands of the two other species of *Sorex* also fit the pattern reported by Carey and Wilson (2001) and Sullivan et al. (2001), but Wilson and Carey (2000) found greater numbers of montane shrews in thinned than legacy stands. Thus, with respect to hypothesis (i), abundance and diversity of forest floor small mammals were maintained in young managed lodgepole pine stands (thinned or unthinned) at levels recorded in old-growth forest.

4.2. Population dynamics

Our intensive live-trapping regime with multiple samples throughout the summer months allowed reasonably precise measurements of reproductive performance, recruitment, and survival for the three major species. These demographic attributes may be more reliable than abundance to determine the quality of habitats for small mammals (Maguire, 1973; Van Horne, 1983). Of particular interest are the demographic responses of *C. gapperi*, since this species is much more of a specialist than either *P. maniculatus* or *T. amoenus*.

Reproductive performance, based on successful pregnancies for females and proportion of animals breeding for males, indicated a similarity across treatment stands for the three major species. This pattern was reflected in recruitment of new animals for each of the species as well. An index of juvenile survival was also similar among stands for *C. gapperi* and *T. amoenus*, but not *P. maniculatus*. The significant difference in mean Jolly–Seber summer survival (and similar mean winter survival) for *C. gapperi* suggested that the thinned stands did provide suitable habitat conditions for this microtine to persist throughout the year.

Thus, with respect to hypothesis (ii), reproduction, recruitment, and survival of *C. gapperi* were maintained in young managed lodgepole pine stands (thinned or unthinned) at levels recorded in old-growth forest. As expected, generalist species such as *P. maniculatus* and *T. amoenus* did not fit this prediction

4.3. Late-seral forest conditions

The ability of *C. gapperi* to successfully breed and produce young in the thinned stands suggests that these habitats are developing some attributes that approximate conditions in old-growth forest. Our heavily thinned stands have started to develop old-growth characteristics such as large-diameter trees, large crowns, diverse coniferous stand structure, and diverse vegetative understories (Sullivan et al., 2001; Lindgren et al., unpublished). Although *C. gapperi* seemed to do as well in the unthinned as thinned stands of pine, the latter stands clearly have greater structural diversity, and hence ability to support a wide range of wildlife species. They also will produce a diverse array of future wood products in a relatively shorter period of time than the unthinned stands (Jozsa and Middleton, 1994; Barbour et al., 1997; Lippke and Fretwell, 1997). Our results are contrary to those of Wilson and Carey (2000) and Carey and Wilson (2001) who concluded that conventional thinning, as compared to variable-density thinning, may produce undesirable and unintended consequences for plant and small-mammal communities. A range of stand densities of conventional pre-commercial thinning, as documented in our study, induced spatial heterogeneity at a stand-level scale and seemed to accelerate development of late-seral forest conditions. Pre-commercial variable-density thinning of lodgepole pine resulted in no differences in mean abundance, species richness, or diversity of forest-floor small mammals at 5 years post-treatment (Sullivan et al., 2002).

5. Management implications

Our results supported hypotheses (i) and (ii) that abundance and diversity of forest-floor small mammals and the demographic attributes of *C. gapperi* populations would be maintained in young managed stands (thinned or unthinned) at levels recorded in old-growth forest. The late successional forest species such as *C. gapperi* dominated the small-mammal communities with the early successional generalist species such as *P. maniculatus* and *T. amoenus* being less prevalent in our treatment stands than recorded in an earlier study (Sullivan et al., 2001). This change in relative species composition likely balanced abundance and diversity attributes in these small mammal communities across the stand types. Our overall study represents a 15-year vision of the results of pre-commercial thinning of young lodgepole pine stands to a range of densities and compares these relatively long-term responses to those in unthinned and old-growth stands. The three study areas, in three different ecological zones, acted as regional replicates thereby extending our inferences on responses of forest-floor small mammals to lodgepole pine stands across the interior of British Columbia.

The results of our study suggest that abundance and diversity of forest-floor small mammals will be similar among thinned and unthinned stands of young lodgepole pine and old-growth forests at 12–14-years after thinning. Inherent in this community similarity will be comparable productivity of *C. gapperi* populations, at least in terms of reproduction, recruitment, and survival among stands. Abundance of *C. gapperi* should also be reasonably similar among stands except in years of high numbers. This latter difference will likely decline with time as the heavily thinned stands approach structural and compositional similarity to old-growth forest. Thus, appropriate thinning regimes that provide a variety of stand structures, either within (variable-density thinning) or between stand treatments (conventional thinning) should help manage for plant and animal diversity across forest landscapes. Old-growth attributes may be produced in perhaps decades in intensively managed young stands rather than waiting centuries with the alternative of no management intervention.

Acknowledgements

We thank Weyerhaeuser Company Limited, Canadian Forest Products Limited (Grande Prairie, Alberta), L & M Lumber Ltd., and the Sustainable Forest Management Network, University of Alberta for financial support, and H. Sullivan for assistance with fieldwork.

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