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Influence of variable retention harvests on forest ecosystems: Plant and mammal responses up to 8 years post-harvest

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Abstract

Green-tree retention systems are an important management component of variable retention harvests in temperate zone coniferous forests. Residual live trees (''legacy trees'') provide mature forest habitat, increase structural diversity, and provide continuity in the regenerating stand. This study was designed to test the hypotheses that, at up to 8 years after harvest, abundance and species diversity of communities of (i) understory plants and (ii) forest-floor small mammals, and (iii) relative habitat use by mule deer (*Odocoileus hemionus*), will decline with decreasing levels of tree retention. Communities of plants and forest floor small mammals were sampled in replicated clearcut, single seed-tree, group seed-tree, patch cut, and uncut forest sites in mixed Douglas-fir (*Pseudotsuga menziesii*)—lodgepole pine (*Pinus contorta*) forest in southern British Columbia, Canada from 2000 to 2003 (5–8 years post-harvest). Habitat use by mule deer was measured during summer and winter periods each year from 1999 to 2003 in these same sites.

Mean total abundance (crown volume index) of herbs, shrubs, mosses, and lichens was similar among sites. Mean species richness of herbs, shrubs, and total plants was similar among sites, but total species diversity and structural diversity were significantly lower in the patch cut and uncut forest sites than in the other harvesting treatments. Thus, hypothesis (i) was not supported. Mean total abundance, species richness, and species diversity of small mammals were similar among sites, contrary to hypothesis (ii). However, the southern red-backed vole (*Clethrionomys gapperi*) declined in abundance as conditions became intolerable for this microtine to persist at numbers > 1/ha in the clearcut and seed-tree sites. The early successional and mycophagist northwestern chipmunk (*Tamias amoenus*) occurred at 2.3–4.4 times higher abundance on the seed-tree sites than the other sites. Relative habitat use by mule deer was highest in the seed-tree sites during summer periods and highest in the group seed-tree, patch cut and uncut sites in winter periods. The responses to our treatments were species specific, and hence a range of different harvesting systems should be used to maintain plant and mammal diversity across forest landscapes.

Keywords: Abundance; *Clethrionomys gapperi*; Forest floor small mammals; Green-tree retention; Species diversity; *Tamias amoenus*; Understory vegetation; Variable retention

1. Introduction

Concern for conservation of mature and old-growth forests has dominated much of temperate zone forest management over the last two decades, at least in the Pacific Northwest (PNW) of North America. One of the central tenets of this premise is to maintain plant and mammal diversity within commercial forest landscapes. To meet this challenge, an array of variable retention harvests or ''green-tree retention systems'' has been implemented to counter the historical and standard practice of clearcutting. A gradient of tree retention includes several silvicultural systems from seed-tree, shelterwood, patch, and selection cutting (Smith, 1986; Larsen, 1995; Franklin et al., 1997). Variable retention harvests include long-term reserves, for at least one rotation, of individual trees or groups of trees within the traditional silvicultural system.

These alternative harvesting systems are designed to create silvicultural approaches that are more aligned with natural processes by retaining large live trees, snags, and downed logs after harvest (Franklin et al., 1997, 2002). Residual live trees (''legacy trees'') provide attributes of mature forest habitat, increase structural diversity, and provide continuity in the regenerating stand (McComb et al., 1993; Hayes et al., 1997; Franklin et al., 2000). As discussed by Sullivan et al. (2001a),

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the seed-tree silvicultural system leaves a variable number of wind-firm seed trees standing singly, or in groups, to provide seed to naturally regenerate a harvested area (Smith, 1986). Patch cutting is a variation on clearcutting and may harvest trees either individually or in groups, leaving openings of various sizes (≤1 ha) dispersed over a given area of forest.

There is much interest in expanding these traditional systems to new variable retention situations in a variety of forest ecosystems. Thus, periodic measurements of the responses of forest ecosystem components, from the time of harvest, through to recovery of late-successional forest functions are essential. Up until the initiation of our study in 1996 (Sullivan et al., 2001a) and the Demonstration of Ecosystem Management Options (DEMO) study (Aubry et al., 1999; Halpern et al., 1999; Halpern and Raphael, 1999) launched in the late 1990s in the PNW, large-scale harvest studies in mature and old-growth forests have been lacking, other than several retrospective studies (see Sullivan et al., 2000).

Monitoring forest understory communities of vascular plants provides a measure of habitat change in response to harvesting practices, which may have profound influences on forest-floor small mammal communities. Changes in ecosystem structure and function within temperate coniferous forests may be evaluated by the abundance and diversity of this mammalian group (Maser et al., 1978; Aubry et al., 1991; Carey and Johnson, 1995). Much research has been done to document plant (Halpern, 1989; Halpern and Spies, 1995; Roberts and Zhu, 2002) and small mammal responses to clearcut harvesting in coniferous forests (Gashwiler, 1970; Martell and Radvanyi, 1977; Scott et al., 1982; Sullivan et al., 1999). Kirkland's (1990) review of 21 published studies concluded that relative abundance of small mammals tends to increase after clearcutting of temperate North American forests. Similarly, as discussed by Halpern et al. (2005), many understory plant species seem to be resilient to changes in microclimate and associated disturbances associated with clearcut harvesting. Other plant species, particularly late-successional ones, may be adversely affected and disappear from harvested sites (Schoonmaker and McKee, 1988; Halpern and Spies, 1995).

There have been far fewer studies reporting on understory plant responses to partial harvesting and retention treatments (Lieffers et al., 1996; Fries et al., 1997). In terms of immediate (1–3 years after harvesting) effects, abundance and species richness of vascular plants declined in all treatments, particularly those with the least retention of residual trees (Beese and Bryant, 1999; Jalonen and Vanha-Majamaa, 2001; Halpern et al., 2005). Conversely, up to 4 years post-harvest, mean abundance and diversity of understory vegetation was similar across a gradient of Douglas-fir (*Pseudotsuga menziesii*) tree retention from uncut to clearcut sites (Sullivan et al., 2001a).

Lehmkuhl et al. (1999) postulated that, across a gradient of tree retention, abundance of small mammal species would increase, decrease, or remain constant based on their association with early or late successional forests and their status as habitat specialists or generalists. This pattern was evident in the first 4 years after harvest in our study area in the southern interior of British Columbia (BC) (Sullivan and Sullivan, 2001). Small (≤0.02 ha) patch cuts in coniferous forests had no effect on closed-canopy small mammal species such as the southern red-backed vole (*Clethrionomys gapperi*) (Medin and Booth, 1989; Hayward et al., 1999; Gitzen and West, 2002). This microtine seemed to persist in the immediate 1–3 years after cutting of various forests harvested by selection, patch, and shelterwood methods (Martell, 1983; Steventon et al., 1998; Von Trebra et al., 1998; Klenner and Sullivan, 2003; Fuller et al., 2004). To our knowledge, no studies have provided a relatively long-term (1–8 years post-harvest) investigation of the responses of forest-floor small mammal communities to a gradient of tree retention.

Large herbivorous mammals such as mule deer (*Odocoileus hemionus*) may also be affected by variable retention harvests. Habitat use by this species is particularly important during winter periods when this ungulate seems to require late-successional closed canopy forests to provide snow interception and forage from herbs, shrubs and litterfall of arboreal lichens and Douglas-fir (Dawson et al., 1990; Nyberg, 1990; Armleder et al., 1994). To date, investigation of relative habitat use by mule deer during summer and winter seasons in those sites harvested by various retention schemes has received little attention. This is an ongoing issue with respect to winter range conditions for mule deer and other ungulates and timber management in the southern interior of BC and elsewhere in the PNW.

This is the third component of a forest ecosystems study with large-scale (operational) treatments that, across a gradient of green-tree retention, is investigating responses of plants and mammals up to 8 years post-harvest. We reported earlier on the responses of stand structure attributes and small mammal communities to experimentally manipulated levels of basal area and density of residual trees over the first 4 years after harvesting (Sullivan et al., 2001a; Sullivan and Sullivan, 2001).

This study was designed to test the hypotheses that, at up to 8 years after harvest, (i) abundance and species diversity of communities of understory plants, (ii) abundance and species diversity of forest-floor small mammals, and (iii) relative habitat use by mule deer, will decline with decreasing levels of tree retention. In all hypotheses, response variables should be greater in sites with green-tree retention than in clearcut sites.

2. Materials and methods

2.1. Study area

This study was located in mixed Douglas-fir—lodgepole pine (*Pinus contorta*) mature and old-growth forests in the Bald Range 25 km west of Summerland in south-central British Columbia, Canada (49°40′N; 119°53′W). This area is within the upper Interior Douglas-fir (IDF_{dk}) and Montane Spruce (MS_{dm}) biogeoclimatic zones (Meidinger and Pojar, 1991). Topography is rolling hills at 1300–1520 m elevation. These ecological zones have a cool, continental climate with cold winters and moderately short, warm summers. The average temperature is below 0 °C for 2–5 months, and above 10 °C for 2–5 months, with mean annual precipitation ranging from 30 to 90 cm. Much of the IDF zone has open to closed mature forests of Douglas-fir, with even-aged post-fire lodgepole pine stands at higher elevations. In the Montane Spruce landscape, there are extensive, young and maturing seral stages of lodgepole pine, which have regenerated after wildfire and clearcut harvesting. Hybrid interior spruce (*Picea glauca* × *P. engelmannii*) and subalpine fir (*Abies lasiocarpa*) are the dominant shade-tolerant climax trees. Douglas-fir is an important seral species in zonal ecosystems and is a climax species on warm south-facing slopes in the driest ecosystems. Trembling aspen (*Populus tremuloides*) and black cottonwood (*P. trichocarpa*) are common seral species (Meidinger and Pojar, 1991).

There were five treatments of variable retention harvests: clearcut, single seed-tree, group seed-tree, patch cut, and uncut forest. In all cases, these systems had long-term reserves of residual trees. Prior to harvesting in 1996, all stands were composed of a mixture of lodgepole pine with variable amounts of Douglas-fir, spruce, and subalpine fir. Mean ages of lodgepole pine ranged from 82 to 120 years and for Douglas-fir ranged from 120 to 228 years. Mean tree heights ranged from 10.5 to 19.5 m for lodgepole pine and from 16.7 to 27.5 m for Douglas-fir. In all cases, Douglas-fir was left as residual trees on harvested units, with most lodgepole pine and spruce removed as crop trees. Area of sites ranged from 4.6 to 12.8 ha for clearcuts, 3.6 to 6.8 ha for single seed-tree, 3.6 to 10.9 ha for group seed-tree, 0.5 to 0.7 ha openings for the patch cut, and 10 to 100+ ha for the mature and old-growth stands which represented uncut forest.

The clearcut and seed-tree sites were harvested in February, March and July 1996. These units were site prepared in August 1996 using a mechanical rake to distribute and pile coarse woody debris in preparation for planting of lodgepole pine, Douglas-fir, and interior spruce seedlings in the spring of 1997. The patch cut units were chosen from the 31 openings (mean patch cut area was 0.7 ha with a total of 21.5 ha) over a 65-ha area, which was harvested in June and July 1996. Since approximately one-third of the area was partially cut, three replicate openings were chosen which had 30–40% logged area (with retention of some understory conifers and larger Douglas-fir trees) and 60–70% uncut forest. These patch cut units had no site preparation and were planted with seedlings in fall of 1997. Three units of uncut forest were selected for comparison with harvested units.

2.2. Experimental design

This study had a completely randomized design with three replicates of each experimental unit. The 15 units (5 treatments × 3 replicates) were selected on the basis of operational scale, reasonable proximity, and availability of variable retention harvest sites which were the size of typical forestry operations. All units were spatially segregated to enhance statistical independence (Hurlbert, 1984).

2.3. Understory vegetation

Three 25-m transects, consisting of five 5-m × 5-m plots, were located randomly in each of the 15 experimental units to sample understory vegetation, following the method of Stickney (1980). For each of the patch cut sites, one transect was located in the patch-cut opening and two transects were located in the adjacent uncut forest to sample accurately the one-third cut and two-thirds uncut pattern of this harvesting treatment. Each plot contained three sizes of nested subplots: a 5-m × 5-m subplot for sampling trees, a 3-m × 3-m subplot for sampling shrubs; and a 1-m × 1-m subplot for sampling herbaceous species, mosses and lichens. These layers were subdivided into height classes: 0–0.25, 0.25–0.50, 0.50–1.0, 1.0–2.0, 2.0–3.0, and 3.0–5.0 m. A visual estimate of percentage ground cover was made for each species/height class combination within the appropriate nested subplot. These data were then used to calculate crown volume index (m^3/0.01 ha) for each species. The product of percent cover and representative height gave the volume of a cylindroid which represented the space occupied by the plant in the community. Crown volume index values were then averaged by species for each plot size, and converted to 0.01-ha base to produce the values given for each species and layer (mosses-lichens, herbs, shrubs, and trees). Sampling was conducted annually in July and August 2000–2003 by the same person. Grasses, mosses, and lichens were not identified to species. Plant species were identified in accordance with Hitchcock and Cronquist (1973) and Parish et al. (1996). Calculations of species richness, species diversity and structural diversity were done with these datasets.

2.4. Coniferous stand structure

Basal area (m^2/ha), density (stems/ha), dbh (diameter at breast height, 1.3 m above the soil surface) and tree height of the overstory residual trees (primarily Douglas-fir) were measured in three 20 m × 20 m plots per site, or as a complete census of residual trees in the clearcut, single seed-tree, and group seed-tree sites, as reported by Sullivan et al. (2001a). As a measure of understory coniferous stand structure, the numbers of coniferous trees (planted and naturally regenerated), in layers in 0–1, 1–2, and 2–3 m height classes, were counted in twenty 0.44 m^2 circular plots located randomly within the 36 units of the 7 × 7 checkerboard live-trapping grid (see below) at each site.

2.5. Small mammal communities

Forest floor small mammal populations were sampled at 4-week intervals from May to October in 2000–2002, and from May to June 2003. One trapping grid (1 ha) was located on each site and had 49 (7 × 7) trap stations at 14.3-m intervals with one Longworth live-trap at each station. 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 (*Peromyscus maniculatus*), northwestern chipmunk (*Tamias amoenus*), meadow vole (*Microtus pennsylvanicus*), long-tailed vole (*Microtus longicaudus*), southern red-backed vole, heather vole (*Phenacomys intermedius*), western jumping mouse (*Zapus princeps*), montane shrew (*Sorex monticolus*), common shrew (*S. cinereus*), and short-tailed weasel (*Mustela erminea*). All small mammals (except shrews and weasels) captured were ear-tagged and immediately released at the point of capture (Krebs et al., 1969). There was a high mortality rate for shrews because of the overnight trapping technique. Shrews that died in traps were collected and identified according to Nagorsen (1996).

The northern bog-lemming (*Synaptomys borealis*) also occurred within the range of our study area, but is rare (Banfield, 1974), and was not captured. The pygmy shrew (*S. 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 and the water shrew is strongly associated with wet habitats (Nagorsen, 1996). The northern pocket gopher (*Thomomys talpoides*) also occurred in our study area but rarely appeared above ground and was not captured. The primarily arboreal red squirrel (*Tamiasciurus hudsonicus*) and northern flying squirrel (*Glaucomys sabrinus*), as well as the bushy-tailed woodrat (*Neotoma cinerea*) were not considered part of the forest floor small mammal community.

Trappability (susceptibility to capture) and population density per ha were measured to determine the effects of the harvest treatments on abundance and diversity. Jolly trappability was calculated as per the estimate reported by Krebs and Boonstra (1984). Abundance estimates of *P. maniculatus*, *T. amoenus*, *C. gapperi*, *M. longicaudus*, *M. pennsylvanicus*, and *P. intermedius* were derived from the Jolly–Seber 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 weeks of the study when the Jolly–Seber estimate cannot be calculated. The reliability of the Jolly–Seber model declines when population sizes are very low and no marked animals are captured (Krebs et al., 1986). For these situations, the total number of individuals captured was used to estimate populations of *Z. princeps*, *S. monticolus*, *S. cinereus*, and *M. erminea*. Abundance of small mammals was calculated using the estimated abundance of each species for a given sampling period, and also averaged over the number of sampling periods for each year.

2.6. Relative habitat use by deer

Sampling of fecal pellet-groups was used to measure relative habitat use by mule deer for summer (May–September) and winter (October–April) periods 1999–2003. We counted all new pellet-groups (minimum of 20 pellets per group) on cleared permanent 5-m^2 ($r = 1.26$ m) circular plots (Loft and Kie, 1988; Edge and Marcum, 1989). A total of 100 plots were located systematically, every 100 m in a grid pattern, throughout each site. Plots were permanently marked with a flagged aluminum ''pig-tail'' stake in the plot center. Counts of pellet-groups used a rope of 1.26-m radius attached to the center stake and rotated around the plot. Plots were cleared of all pellet-groups at the initial sampling time in early May 1999, and during each subsequent sample. To measure summer habitat use by deer, pellet-group counts were done in early October. Similarly, relative habitat use in winter was measured by counting pellet-groups in early May. This same procedure was followed for five summer and five winter periods. All sample plots at the 15 sites were assessed by the same observers throughout the 5 years. Pellet-group degradation was not likely an issue as only new pellets deposited during a given summer or winter period were counted. Pellet-groups located on the edge of a sample plot had to have 50% or more of the group within the plot in order to be counted. The consistency of sampling personnel and the relatively small edge to area ratio of our plots likely minimized potential inclusion bias. Density of pellet-groups was estimated per 5 m^2 plot and then converted to a per ha value.

2.7. Diversity measures

Diversity of plant and forest floor small mammal communities was measured by species richness, species diversity, and structural diversity. Species richness was the total number of species sampled for the plant (herbs, shrubs, and trees) and small mammal communities in each stand (Krebs, 1999). Species diversity was based on the Shannon–Wiener index, which is well represented in the ecological literature (Burton et al., 1992; Magurran, 2004). Diversity of the small mammal community was also evaluated by log-series alpha which provides a robust parametric measure (Magurran, 2004).

For the plant communities, species diversity of herbs, shrubs, and trees was calculated separately, using the crown volume index for each plant species averaged across the three transects in a given site. Species diversity was calculated separately for herbs, shrubs, and total trees (each year 2000–2003), and understory coniferous trees (2003). Diversity of small mammals was calculated using the estimated abundance of each species for a given sampling period and averaged over the number of sampling periods for each year.

Structural diversity was based on the same indices as for species richness and diversity with the height classes of the herb, shrub, and tree layers acting as ''species'' (Sullivan et al., 2001b). This measure of foliage height diversity (MacArthur and MacArthur, 1961) used the Shannon–Wiener index with plant species represented by height classes and the amount (crown volume index) of vegetation in each class.

2.8. Statistical analysis

A repeated measures analysis of variance (RM-ANOVA) (SPSS Institute Inc., 1997) was conducted to determine the effects of treatment and time (5–8 years post-harvest) on mean crown volume index of mosses, lichens, herbs, shrubs, and trees, mean species richness and diversity, and mean total structural diversity of the herb, shrub, and tree layers. The RM-ANOVA model was also used to test for significant differences in mean abundance of each species, total abundance, mean species richness, and mean species diversity of the small mammal communities across the five treatment sites; as well as mean number of fecal pellet-groups of mule deer during summer and winter periods. 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 correction was used to adjust the degrees of freedom of the within-subjects F-ratio. A one-way ANOVA was used to determine the effect of harvest treatments on mean basal area (BA) and density of overstory trees (Sullivan et al., 2001a), understory coniferous stand structure, and total species diversity of vascular plants for the year 2003 (8 years post-harvest).

Overall mean ($n = 15$; 3 replicates × 5 years) values and 95% confidence intervals (CIs) were calculated for the number of deer pellet-groups on treatment sites during summer and winter periods. Duncan's multiple range test (DMRT) was used to compare mean values, whenever a significant difference was found, based on ANOVA results. In all analyses, the level of significance was at least $P = 0.05$.

3. Results

3.1. Coniferous stand structure

Variable retention harvests had a significant effect on BA ($F_{4,10} = 41.08$; $P < 0.01$) and density ($F_{4,10} = 18.33$; $P < 0.01$) of overstory coniferous trees (Table 1). Mean BAs were similar and ranged from 0.1 to 2.5 m^2/ha in clearcut, single seed-tree, and group seed-tree sites, with significantly (DMRT; $P = 0.05$) higher levels on patch cut (23.4 m^2/ha) and uncut forest (39.0 m^2/ha) sites (see Sullivan et al., 2001a). This same pattern was observed for density with numbers ranging from 0.7 to 16.3 stems/ha on the clearcut to group seed-tree sites and up to 769.4 and 2050.0 stems/ha in the patch cut and uncut forest sites, respectively (Table 1). Mean diameters of residual trees ranged from 15.8 to 70.0 cm (Sullivan et al., 2001a).

Mean abundance of coniferous regeneration was highest in the clearcut sites for both total conifers ($F_{4,10} = 3.62$; $P = 0.05$) and the 0–1 m height class ($F_{4,10} = 3.55$; $P = 0.05$) (Table 1). Although not statistically significant, the seed-tree sites had 6–7 times, and 2 times, the number of total coniferous seedlings than the patch cut and uncut forest, respectively. Lodgepole pine was the dominant understory conifer in all harvested sites, followed closely by Douglas-fir in the patch cut sites (Table 1). Mean species diversity of coniferous regeneration was significantly ($F_{4,10} = 4.14$; $P = 0.03$) higher in the seed-tree and patch cut sites than the uncut forest. The group seed-tree sites seemed to have the most even composition of coniferous species in addition to lodgepole pine (Table 1).

3.2. Understory vegetation

Mean total crown volume index of herbs was similar ($F_{4,10} = 0.89$; $P = 0.50$) among sites, but decreased significantly ($F_{3,30} = 11.81$; $P < 0.01$) through time (Table 2). Prominent herb species on these sites included wild strawberry (*Fragaria virginiana*), fireweed (*Epilobium angustifolium*), grasses, white-flowered hawkweed (*Hieracium albiflorum*), heart-leaved arnica (*Arnica cordifolia*), Arctic lupine (*Lupinus arcticus*), racemose pussytoes (*Antennaria racemosa*), and one-sided wintergreen (*Orthilia secunda*) (Table 3).

The following herbs were generally considered to be forest species. Red columbine (*Aquilegia formosa*) was present in small quantities in the seed-tree sites during all three sample periods. *A. cordifolia* was absent from all sites but the patch cut in 1996, and was present in all retention sites during 2000 and 2003. However, it was also present in the clearcut sites. Rattlesnake plantain (*Goodyera oblongifolia*) persisted in the patch cut sites. Mountain sweet-cicely (*Osmorhiza chilensis*) persisted in the seed-tree sites but not the clearcut sites (Table 3). Bracted lousewort (*Pedicularis bracteosa*) was

Table 1
Mean ($n = 3$ replicate sites) ± SE basal area and stand density of overstory conifers (primarily Douglas-fir) (from Sullivan et al., 2001a), and abundance (per sample unit), composition, and species diversity of understory coniferous regeneration and results of analyses

Parameter	Treatment					Analysis	
	Clearcut	Single seed-tree	Group seed-tree	Patch cut	Uncut forest	$F_{4,10}$	P
Overstory conifers							
Basal area (m^2/ha)	$0.1^a \pm 0.1$	$0.7^a \pm 0.1$	$2.5^a \pm 1.0$	$23.4^b \pm 1.9$	$39.0^c \pm 5.7$	41.08	<0.01
Density (stems/ha)	$0.7^a \pm 0.7$	$9.0^a \pm 3.4$	$16.3^a \pm 4.2$	$769.4^b \pm 179.8$	$2050.0^b \pm 429.8$	18.33	<0.01
Understory conifers							
0–1 m height class	$139.3^b \pm 57.5$	$36.3^a \pm 3.3$	$52.3^{ab} \pm 10.7$	$5.0^a \pm 2.1$	$24.3^a \pm 19.5$	3.55	0.05
1–2 m height class	$3.3^a \pm 0.7$	$8.7^b \pm 2.7$	$4.0^a \pm 0.6$	$2.7^a \pm 1.2$	0.0^a	5.13	0.02
Total conifers	$142.6^b \pm 56.9$	$45.0^a \pm 5.8$	$56.3^{ab} \pm 11.0$	$7.7^a \pm 3.3$	$24.3^a \pm 19.5$	3.62	0.05
Lodgepole pine (%)	92.5	70.5	57.6	55.6	0.0	–	–
Douglas-fir (%)	1.6	4.1	13.0	44.4	0.0	–	–
Interior spruce (%)	0.4	2.9	10.7	0.0	0.0	–	–
Subalpine fir (%)	5.5	22.5	18.7	0.0	100.0	–	–
Species diversity	$0.44^{ab} \pm 0.1$	$1.02^b \pm 0.2$	$1.27^b \pm 0.5$	$0.97^b \pm 0.03$	0.00^a	4.14	0.03

Mean values followed by different letters are significantly different by DMRT.

Table 2
Mean ($n = 3$ replicate sites) ± SE crown volume index (m^3/0.01 ha) for vegetation in the five treatments during 2000–2003 (5–8 years post-harvest) and results of RM-ANOVA

Vegetation attribute and year	Treatment					Overall analysis					
	Clearcut	Single seed-tree	Group seed-tree	Patch cut	Uncut forest	Treatment		Time		Treatment × time	
						$F_{4,10}$	P	$F_{3,30}$	P	$F_{12,30}$	P
Herbs						0.89	0.50	11.81*	<0.01	0.79*	0.65
2000	10.8 ± 2.3	10.3 ± 1.9	14.7 ± 1.0	8.3 ± 1.0	8.8 ± 5.2						
2001	10.8 ± 3.6	11.4 ± 2.4	16.2 ± 3.0	5.5 ± 0.3	9.6 ± 5.2						
2002	10.7 ± 4.3	11.0 ± 4.2	11.4 ± 2.1	4.5 ± 0.1	7.5 ± 3.7						
2003	7.6 ± 3.1	8.2 ± 2.5	7.5 ± 2.3	2.8 ± 0.2	5.6 ± 2.8						
Shrubs						1.58	0.25	11.78	<0.01	2.78	0.01
2000	4.6 ± 1.1a	3.2 ± 0.6a	1.5 ± 0.2a	8.4 ± 5.0a	3.8 ± 2.2a						
2001	6.9 ± 1.6a	5.5 ± 1.3a	2.3 ± 0.3a	12.2 ± 7.4a	4.3 ± 2.4a						
2002	10.1 ± 3.0a	4.5 ± 0.7a	2.3 ± 0.4a	9.2 ± 5.0a	3.9 ± 2.3a						
2003	8.7 ± 2.2a	3.8 ± 0.1a	2.0 ± 0.3a	9.1 ± 5.1a	3.4 ± 1.8a						
Trees	B	B	B	A	A	22.60	<0.01	1.25	0.31	1.57	0.15
2000	2.8 ± 0.5	13.2 ± 5.8	31.8 ± 19.9	126.6 ± 14.2	132.8 ± 9.6						
2001	4.4 ± 0.7	11.7 ± 5.9	20.3 ± 16.2	140.2 ± 13.7	185.3 ± 30.3						
2002	6.3 ± 2.1	10.5 ± 5.3	19.5 ± 8.3	121.1 ± 9.9	164.1 ± 37.0						
2003	8.0 ± 1.5	9.8 ± 2.2	7.5 ± 3.9	121.5 ± 9.5	161.7 ± 35.4						

Columns of mean values with different letters are significantly different by Duncan's multiple range test (adjusted for multiple contrasts). F-values identified by * were calculated using the H-F correction factor, which decreased the stated degrees of freedom due to correlation of data among repeated measures (years).

absent from all sites in 1996, but was present in the group seed-tree and patch cut sites in 2000 and 2003. Similarly, sickletop lousewort (*P. racemosa*) appeared in the group seed-tree sites in 2000 and 2003. Showy aster (*Aster conspicuus*), fairyslipper (*Calypso bulbosa*), queen's cup (*Clintonia uniflora*), and western meadowrue (*Thalictrum occidentale*) were absent from all harvested sites in 1996, but were present in retention sites in 2000 or 2003 (Table 3).

Mean total crown volume index of shrubs was similar ($F_{4,10} = 1.58$; $P = 0.25$) among sites (Table 2). Shrub volume generally increased significantly ($F_{3,30} = 11.78$; $P < 0.01$) over time. Prominent shrubs included kinnikinnick (*Arctostaphylos uva-ursi*), twinflower (*Linnaea borealis*), Utah honeysuckle (*Lonicera utahensis*), falsebox (*Pachistima myrsinites*), birch-leaved spirea (*Spiraea betulifolia*), and grouseberry (*Vacciniium scoparium*).

Black gooseberry (*Ribes lacustre*), a forest species, was limited to uncut forest and single seed-tree sites in 1996, but was present in all sites in 2000 and 2003. Red raspberry (*Rubus idaeus*), an early seral species, was absent from all sites in 1996, but was present in clearcut, group seed-tree, and patch cut sites during 2000 and 2003 (Table 3). Prickly rose (*Rosa acicularis*), a forest species, was absent from all harvested sites in 1996, but was present in retention sites in 2000 and 2003.

Mean total crown volume index of trees was significantly ($F_{4,10} = 22.60$; $P < 0.01$) different among sites, with the patch cut and uncut forest sites higher (DMRT; $P = 0.05$) in crown volume than that of the other sites (Table 2). Tree species included Douglas-fir, lodgepole pine, subalpine fir, and interior spruce.

Mean total crown volume index of mosses ($F_{4,10} = 1.19$; $P = 0.37$) and terrestrial lichens ($F_{4,10} = 1.59$; $P = 0.25$) were similar among sites. Mean volume of mosses in the uncut forest (1.9–4.3 m^3/0.01 ha) tended to be 4.0–6.0 times higher than the average of the other four sites.

3.3. Plant species and structural diversity

There was a total of 52 species of herbs, 27 species of shrubs, and 6 species of trees sampled during 2000–2003, at 5–8 years post-harvest. Mean species richness of herbs ($F_{4,10} = 0.74$; $P = 0.59$) and shrubs ($F_{4,10} = 1.00$; $P = 0.45$) was similar among sites. Mean richness of trees was significantly ($F_{4,10} = 4.84$; $P = 0.02$) different among sites with seed-tree and uncut sites having greater richness than patch cut sites (DMRT; $P = 0.05$). Total species richness of plants was similar among sites (Fig. 1A). Mean species diversity of herbs was similar among sites, but increased significantly ($F_{3,30} = 5.71$; $P < 0.01$) with time. Shrub species diversity was significantly ($F_{4,10} = 5.74$; $P = 0.01$) different (Table 4), being generally highest in the seed-tree sites, followed by the uncut forest, clearcut and patch cut sites (DMRT; $P = 0.05$). In addition, mean species diversity of trees was significantly ($F_{4,10} = 9.65$; $P < 0.01$) different among sites (Table 4), with diversity of trees similar in the uncut forest, clearcut and seed-tree sites, and all higher than the patch cut sites (DMRT; $P = 0.05$). In 2003, 8 years post-harvest, total species diversity was significantly ($F_{4,10} = 30.78$; $P < 0.01$) lower (DMRT; $P = 0.05$) in the patch cut and uncut forest sites than in the other harvesting treatments (Fig. 1B).

Mean total structural diversity (layers of vegetation and relative amounts of vegetation in those layers) was significantly ($F_{4,10} = 10.03$; $P < 0.01$) different among sites, with a lower diversity (DMRT; $P = 0.05$) in the uncut forest and patch cut

Table 3
Mean ($n = 3$ replicate sites) crown volume index (m^3/0.01 ha) for plant species in the herb and shrub layers on the five sites during the study 1996, 2000, and 2003

Species	1996					2000					2003				
	CC	SST	GST	PC	UF	CC	SST	GST	PC	UF	CC	SST	GST	PC	UF
Herbs															
Achillea millefolium	–	–	–	–	–	–	–	–	0.02	–	–	–	0.01	0.01	–
Anaphalis margaritacea	–	–	–	–	–	–	–	0.12	–	–	–	–	0.01	–	–
Antennaria microphylla	–	–	–	–	–	–	–	0.03	0.02	–	–	–	–	0.01	–
Antennaria neglecta	–	–	–	–	–	–	–	0.17	–	–	–	–	0.01	–	0.02
Antennaria racemosa	0.01	0.02	–	–	0.54	–	0.88	1.10	3.22	3.38	–	0.03	0.19	0.49	0.24
Aquilegia formosa	–	0.01	–	–	0.01	–	–	0.05	–	–	–	–	0.01	–	–
Arnica cordifolia	–	–	–	0.01	–	0.17	0.52	1.20	1.17	1.60	0.04	0.13	0.13	0.09	0.36
Aster ciliolatus	–	–	–	–	–	–	–	–	–	–	–	0.01	–	–	–
Aster conspicuus	–	–	–	–	–	–	–	–	–	–	–	0.03	–	–	–
Calypso bulbosa	–	–	–	–	–	–	–	–	0.02	0.15	–	–	–	–	0.01
Carex spp	–	–	–	–	–	0.03	–	0.03		0.10	0.12	0.28	0.73	0.25	0.04
Cerastium arvense	–	–	–	–	–	–	0.08	–	0.05	–	–	–	–	–	–
Cirsium vulgare	–	–	–	–	–	0.03	0.12	0.05	0.18	–	–	–	–	–	–
Clintonia uniflora	–	–	–	–	–	–	0.05	0.02	–	–	–	0.01	–	–	–
Cornus canadensis	0.07	0.01	–	–	–	1.22	0.30	–	–	–	0.43	0.13	–	–	–
Epilobium angustifolium	–	0.01	–	–	–	1.45	3.75	13.98	0.07	–	0.66	1.07	2.19	0.01	0.01
Epilobium ciliatum	–	–	–	–	–	0.18	0.30	0.22	0.02	0.05	0.01	0.02	0.02	0.03	–
Fragaria virginiana	0.02	0.06	0.01	0.12	0.02	0.22	0.85	0.05	0.77	0.13	0.08	0.37	0.05	0.08	0.02
Galium triflorum	–	–	–	–	0.01	–	–	–	–	–	–	–	–	–	–
Gentianella amarella	–	–	–	–	–	–	–	0.07	0.12	0.03	–	–	–	–	–
Goodyera oblongifolia	0.01	–	–	0.04	0.02	–	–	–	0.10	0.10	–	–	–	0.02	0.01
Grasses	0.61	0.43	0.52	2.17	2.88	25.10	16.52	22.18	11.53	17.27	5.33	3.84	3.24	1.27	3.89
Hieracium albiflorum	0.05	0.06	0.02	0.04	0.06	1.35	0.80	0.93	0.20	0.57	0.21	0.23	0.29	0.06	0.08
Hieracium aurantiacum	–	–	–	–	–	–	–	–	–	–	–	0.01	–	–	–
Hieracium gracile	–	–	–	–	–	–	–	0.03	–	–	–	–	–	–	–
Hieracium umbellatum	–	–	–	–	–	–	–	–	–	0.23	–	–	–	–	0.03
Lilium columbianum	–	–	–	–	0.01	–	0.12	0.03	–	0.10		0.04	0.02	–	0.03
Lupinus arcticus	0.32	0.65	0.11	0.51	0.38	2.55	3.25	2.97	7.28	3.30	0.62	1.96	0.31	0.46	0.74
Melampyrum lineare	–	–	0.01	–	–	–	–		–	–	–	–	–	–	–
Mitella nuda	–	–	–	–	–	–	–	0.02	–	–	–	–	–	–	–
Orthelia secunda	0.04	0.02	0.01	0.04	0.47	0.15	0.05	0.03	0.03	0.15	0.03	–	0.02	0.01	0.03
Osmorhiza chilensis	–	0.01	–	–	0.01	–	0.03	0.27	–	0.03	–	0.02	0.01	–	0.02
Pedicularis bracteosa	–	–	–	–	–	–	–	0.07	0.03	–	–	–	0.04	0.03	–
Pedicularis racemosa	–	–	–	–	–	–	–	0.05	–	–	–	–	0.11	–	–
Plantathera unalaschensis	–	–	–	–	–	–	–	0.03	–	0.07	–	–	–	–	–
Pyrola asarifolia	–	–	–	0.01	–	–	–	–	–	–	–	–	–	–	–
Smilacina racemosa	–	–	–	–	–	–	–	–	–	0.07	–	–	–	–	0.03
Sonchus arvense	–	–	–	–	–	–	–	0.03	–	–	–	–	–	–	–
Streptopus amplexifolius	–	–	–	–	0.01	–	–	–	–	–	–	–	–	–	–
Taraxacum officinale	–	–	–	–	–	–	–	0.02	–	–	–	–	0.01	0.01	–
Thalictrum occidenatle	–	–	–	–	–	–	–	0.03	–	–	–	–	0.04	–	–
Tragopogon dubius	–	–	–	–	–	–	–	0.07	–	–	–	–	–	–	–
Veratrum viride	–	–	–	–	0.02	–	–	–	–	–	–	–	–	–	–
Verbascum thapsus	–	–	–	–	–	–	–	0.03	–	–	–	–	–	–	–
Viola sp.	0.04	0.04	–	–	0.01	0.02	0.23	–	–	–	0.01	0.01	0.01	–	–
Zigadenus venenosus	–	–	–	–	–	–	–	0.05	–	–	–	–	0.01	–	–
Shrubs															
Alnus incana	0.01	0.02	–	–	–	1.00	0.07	–	–	–	1.36	–	–	–	–
Amelanchier alnifolia	–	–	–	0.13	–	0.07	0.13	–	1.12	–	0.02	0.03	–	0.17	–
Arctostaphylos uva-ursi	0.06	0.22	0.13	1.71	0.08	1.35	1.02	0.62	8.05	0.22	1.27	0.76	0.55	3.44	0.06
Betula glandulosa	–	–	–	–	0.54	–	–	–	–	–	–	–	–	–	–
Chimaphila umbellata	0.04	0.02	–	0.02	0.02	0.10	0.02	0.02	0.07	0.07	0.01	–	–	–	0.02
Juniperus communis	0.01	–	0.01	0.04	0.01	0.03	–	0.02	0.20	0.03	0.02	–	0.01	0.04	–
Ledum glandulosum	0.24	0.07	0.01	–	–	3.85	0.52	0.03	–	–	2.94	0.24	0.01	–	–
Linnaea borealis	0.11	0.14	0.04	0.12	0.15	0.82	0.98	0.60	0.35	0.52	0.32	0.31	0.21	0.09	0.22
Lonicera involucrata	0.01	0.07	–	–	–	0.08	0.52	–	–	–	0.04	0.21	–	0.01	–
Lonicera utahensis	0.23	0.21	0.09	0.44	0.39	1.60	1.70	1.25	0.82	1.03	0.79	0.78	0.44	0.22	0.29
Mahonia aquifolium	–	0.01	–	–	–	–	0.02	–	–	–	–	–	–	–	–
Menziesia ferruginea	–	–	–	–	–	–	–	–	–	–	–	–	0.01	–	–
Paxistima myrsinites	0.12	0.22	0.12	0.13	0.17	0.77	0.73	0.62	0.38	1.59	0.26	0.22	0.28	0.09	0.42
Ribes lacustre	–	0.01	–	–	0.01	0.10	0.55	0.57	0.45	0.03	0.03	0.17	0.22	0.06	0.02

Table 3 (*Continued*)

Species	1996					2000					2003				
	CC	SST	GST	PC	UF	CC	SST	GST	PC	UF	CC	SST	GST	PC	UF
Rubus parviflorus	–	–	–	–	0.02	–	–	–	–	–	–	–	–	–	–
Ribes viscosissimum	–	–	–	0.06	0.03	–	–	0.02	0.13	0.10	–	–	0.02	0.11	0.01
Rosa acicularis	–	–	–	–	–	–	–	0.02	0.22	–	–	–	0.02	0.08	–
Rubus idaeus	–	–	–	–	–	0.02	–	0.14	0.05	–	0.01	–	0.03	0.22	–
Salix spp	–	0.01	–	–	0.04		0.03	0.03	–	–	–	0.06	0.03	–	0.02
Sambucus racemosa	–	–	–	–	–	–	–	–	0.03	–	–	–	–	–	–
Shepherdia canadensis	–	–	–	3.64	–	–	–	–	12.45	–	–	–	–	–	–
Sorbus sitchensis	–	–	–	–	–	–	–	–	–	0.02	–	–	–	–	–
Spiraea betulifolia	0.10	0.16	0.07	0.22	0.14	1.67	1.15	0.28	0.62	0.38	0.56	0.35	0.15	0.21	0.16
Vaccinium membranaceum	–	–	–	–	0.46	–	–	–	–	0.73	–	–	–	–	0.91
Vaccinium scoparium	0.65	0.28	0.14	0.14	1.46	2.25	2.13	0.33	0.30	2.78	1.04	0.72	0.06	0.09	1.33
Viburnum edule	0.04	–	–	–	–	–	–	–	–	–	0.01	–	0.02	0.01	–

sites than at the seed-tree and clearcut sites (Table 4; Fig. 1C). The higher structural diversity in the low retention sites was related to the higher abundance and diversity of coniferous regeneration than in the patch cut and uncut forest sites.

3.4. Small mammal abundance and diversity

Of 10 species, *P. maniculatus* was the most abundant with a total of 1144 individuals captured (45.7% of a total of 2501 forest floor mammals) over the 4-year study. The next most abundant species, in terms of individuals, were *T. amoenus* (479), *C. gapperi* (260), *S. monticolus* (254), *M. pennsylvanicus* (160), and *M. longicaudus* (114). Numbers of individuals for the less common species were 50 for *P. intermedius*, 19 for *S. cinereus*, 5 for *Z. princeps* and 16 for *M. erminea*.

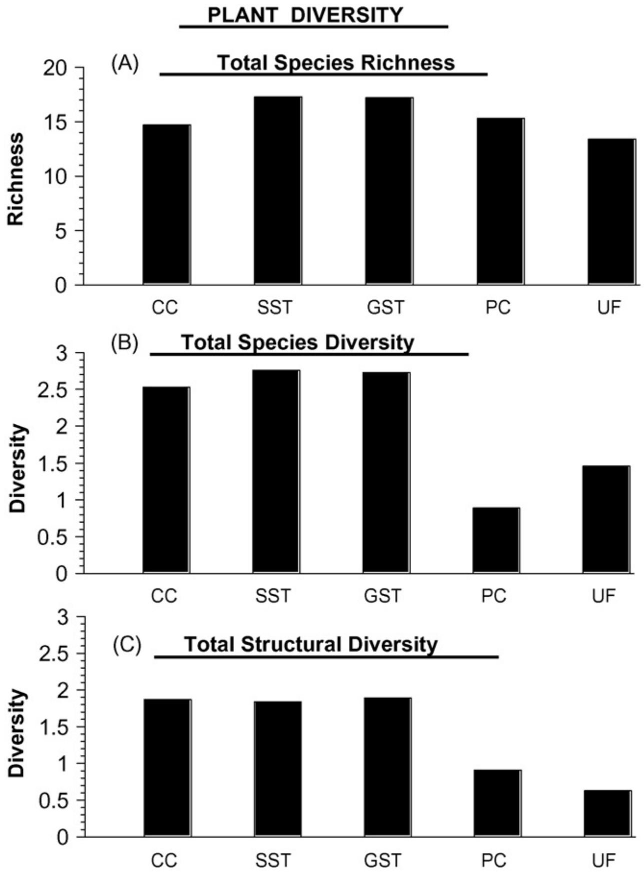

Fig. 1. Mean ($n = 3$) total plant species richness, species diversity, and structural diversity in clearcut, single seed-tree, group seed-tree, patch cut, and uncut forest sites in 2003, 8 years post-harvest.

Susceptibility to capture was measured by Jolly trappability estimates with mean values of 86.4% for *P. maniculatus*, 82.4% for *C. gapperi*, 69.8% for *T. amoenus*, 73.9% for *M. longicaudus*, and 65.5% for *M. pennsylvanicus*.

Mean total abundance of small mammals per ha was similar ($F_{4,10} = 2.21$; $P = 0.14$) among sites, although a significant ($F_{12,30} = 2.07$; $P = 0.05$) treatment × time interaction was also noted (Fig. 2; Table 5). This interaction was the result of significantly ($F_{4,10} = 6.14$; $P < 0.05$) higher numbers of small mammals (DMRT; P = 0.05) within clearcut and seed-tree sites during 2001 and similar abundance among all treatment sites during the other 3 years. Mean species richness was also similar ($F_{4,10} = 0.53$; $P = 0.71$) among treatment sites as was mean species diversity for both the Shannon–Wiener ($F_{4,10} = 0.22$; $P = 0.92$) and log-series ($F_{4,10} = 0.40$; $P = 0.80$) parameters (Table 5). The significant ($P < 0.01$) time factor for all parameters was likely related to the limited sampling regime (two trapping periods) in spring 2003.

Mean abundance of *P. maniculatus* was similar ($F_{4,10} = 2.05$; $P = 0.16$) among sites, but with higher numbers in 2000–2001 than in 2002–2003 (Table 6; Fig. 3). *T. amoenus* appeared to have higher mean numbers in the seed-tree sites than the other sites, but this difference only approached significance ($F_{4,10} = 3.00$; $P = 0.07$) (Fig. 4; Table 6). On average, there were 2.3 times as many *T. amoenus* on the seed-tree sites than the clearcut and patch cut sites; and 4.4 times as many on the seed-tree sites than in the uncut forest sites.

Of the four microtine species, mean abundance of *P. intermedius* was significantly ($F_{4,10} = 5.09$; $P = 0.02$) higher on clearcut and seed-tree sites than at other sites (Table 6). *M. longicaudus* populations were at similar low numbers across the variously harvested sites (Table 6). *M. pennsylvanicus* was similarly at relatively low (<10 voles/ha) abundance, but tended ($F_{4,10} = 3.12$; $P = 0.07$) to have higher (2.0–4.7 times) numbers in the clearcut and single seed-tree sites than the other sites (Table 6). There appeared to be a peak population of *Microtus* in 2002, at least on a relative basis among years

Table 4
Mean ($n = 3$ replicate sites) ± SE species diversity and total structural diversity for vegetation in the five treatments during 2000–2003 (5–8 years post-harvest) and results of RM-ANOVA

Vegetation attribute and year	Treatment					Overall analysis					
Treatment × time	Clearcut	Single seed-tree	Group seed-tree	Patch cut	Uncut forest	Treatment		Time			
						$F_{4,10}$	P	$F_{3,30}$	P	$F_{12,30}$	P
Herbs						1.50	0.27	5.71	<0.01	0.46	0.92
2000	0.9 ± 0.2	1.4 ± 0.4	1.4 ± 0.3	1.7 ± 0.0	1.0 ± 0.5						
2001	1.1 ± 0.2	1.5 ± 0.3	1.6 ± 0.2	1.8 ± 0.1	1.1 ± 0.2						
2002	1.2 ± 0.2	1.6 ± 0.2	1.8 ± 0.4	2.2 ± 0.1	1.2 ± 0.5						
2003	1.2 ± 0.3	1.6 ± 0.3	1.6 ± 0.3	2.0 ± 0.1	1.1 ± 0.6						
Shrubs	B	A	A	B	AB	5.74	0.01	2.06	0.13	0.41	0.95
2000	1.7 ± 0.2	2.2 ± 0.1	2.1 ± 0.2	1.4 ± 0.1	1.8 ± 0.1						
2001	1.6 ± 0.1	2.2 ± 0.1	2.1 ± 0.2	1.4 ± 0.1	1.8 ± 0.2						
2002	1.5 ± 0.1	2.2 ± 0.1	2.0 ± 0.2	1.4 ± 0.2	1.8 ± 0.2						
2003	1.6 ± 0.1	2.2 ± 0.2	2.0 ± 0.2	1.3 ± 0.2	1.7 ± 0.1						
Trees	A	A	A	B	A	9.65	<0.01	0.56	0.64	0.70	0.74
2000	0.9 ± 0.1	0.9 ± 0.0	0.9 ± 0.2	0.2 ± 0.1	1.2 ± 0.2						
2001	0.8 ± 0.0	1.1 ± 0.2	0.9 ± 0.3	0.2 ± 0.1	1.2 ± 0.2						
2002	0.9 ± 0.0	0.9 ± 0.2	0.9 ± 0.1	0.2 ± 0.1	1.0 ± 0.1						
2003	0.8 ± 0.0	0.9 ± 0.1	0.9 ± 0.2	0.2 ± 0.1	1.1 ± 0.2						
Structural diversity	A	A	A	B	B	10.03	<0.01	12.38	<0.01	5.67	<0.01
2000	1.6 ± 0.1a	1.4 ± 0.1a	1.4 ± 0.1a	1.0 ± 0.2ab	0.7 ± 0.2b						
2001	1.6 ± 0.1a	1.8 ± 0.1a	1.7 ± 0.1a	1.0 ± 0.2b	0.6 ± 0.2b						
2002	1.8 ± 0.2a	1.7 ± 0.1a	1.7 ± 0.0a	0.9 ± 0.2b	0.6 ± 0.2b						
2003	1.9 ± 0.1a	1.8 ± 0.0a	1.9 ± 0.1a	0.9 ± 0.2b	0.6 ± 0.2b						

Columns of mean values with different letters are significantly different by Duncan's multiple range test (adjusted for multiple contrasts).

(Table 6). Mean abundance of *C. gapperi* was significantly ($F_{4,10} = 26.76$; $P < 0.01$) different among sites, with highest (DMRT; $P = 0.05$) numbers in the uncut forest and lowest numbers in the single seed-tree sites (Table 6; Fig. 5).

Of the two insectivore species, mean abundance of *S. monticolus* was significantly ($F_{4,10} = 7.94$; $P < 0.01$) different among harvested sites, with highest (DMRT; $P = 0.05$) numbers of montane shrews in the clearcut and seed-tree sites than other sites (Table 6). Abundance of shrews declined significantly ($F_{4,10} = 7.94$; $P < 0.01$) with time. Populations of *S. cinereus* were low (<1 shrew/ha) on all sites (Table 6).

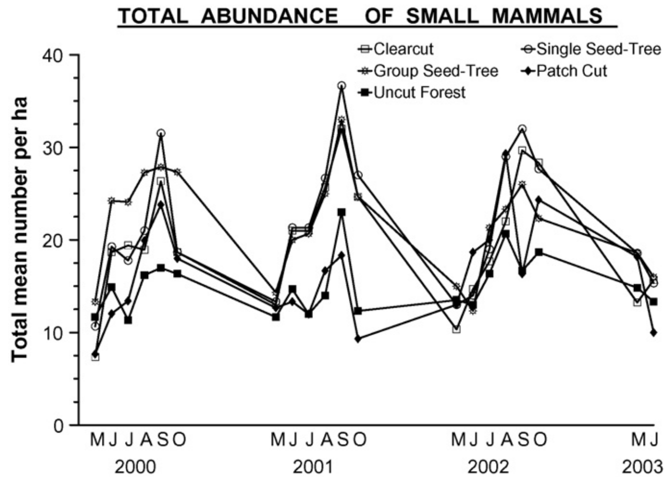

Fig. 2. Mean ($n = 3$) total abundance of small mammals/ha in clearcut, single seed-tree, group seed-tree, patch cut, and uncut forest sites in 2000–2003, 5–8 years post-harvest.

3.5. Relative habitat use by deer

Relative habitat use by mule deer, as indexed by fecal pellet-groups, was based on mean pellet counts for summer and winter periods. Habitat use by deer was similar among sites in summer ($F_{4,10} = 1.70$; $P = 0.23$) and winter ($F_{4,10} = 0.51$; $P = 0.73$) periods (Table 7). However, in terms of the effect size, overall mean ($n = 15$) pellet-group counts appeared highest in the seed-tree sites in summer according to non-overlapping 95% CI (Fig. 6). Similarly, in winter, overall mean ($n = 15$) pellet counts were highest in group seed-tree, patch cut, and uncut forest sites (Fig. 6).

4. Discussion

4.1. Variable retention harvests

This 8-year study is the first detailed investigation of diversity of stand structure attributes and mammal communities over a range of variable retention, from the time of harvest, in replicate sites of mixed Douglas-fir-lodgepole pine forest. Variable retention harvests in temperate zone coniferous forests are a method to integrate both ecological and economic objectives in forest management. Retention of green trees can (1) structurally enrich the subsequent forest stand, (2) maintain

Table 5
Mean ($n = 3$ replicate sites) ± SE total abundance, species richness, and species diversity of small mammal communities in the five treatments during 2000–2003 (5–8 years post-harvest) and results of RM-ANOVA

Parameter and year	Treatment					Overall analysis					
	Clearcut	Single seed-tree	Group seed-tree	Patch cut	Uncut forest	Treatment		Time		Treatment × time	
						$F_{4,10}$	P	$F_{3,30}$	P	$F_{12,30}$	P
Total abundance						2.21	0.14	25.89	<0.01	2.07	0.05
2000	18.9 ± 2.4ab	23.5 ± 3.6ab	30.1 ± 4.1a	17.0 ± 3.2b	16.2 ± 3.0b						
2001	28.1 ± 5.1a	32.0 ± 1.3a	30.3 ± 1.3a	18.0 ± 3.0b	17.2 ± 2.2b						
2002	24.0 ± 2.5	26.6 ± 2.4	26.1 ± 2.0	28.4 ± 2.2	20.8 ± 4.6						
2003	14.5 ± 2.7	17.0 ± 1.6	17.3 ± 3.6	14.1 ± 1.3	14.1 ± 3.1						
Species richness						0.53	0.71	15.45	<0.01	0.89	0.57
2000	3.4 ± 0.4	3.6 ± 0.3	3.4 ± 0.3	3.5 ± 0.6	3.3 ± 0.4						
2001	4.0 ± 0.7	4.4 ± 0.5	3.6 ± 0.4	2.9 ± 0.5	3.0 ± 0.1						
2002	3.4 ± 0.8	3.6 ± 0.1	3.7 ± 0.3	3.2 ± 0.3	3.3 ± 0.1						
2003	2.8 ± 0.6	2.5 ± 0.3	2.3 ± 0.3	2.2 ± 0.2	2.5 ± 0.3						
Shannon–Wiener species diversity						0.22	0.92	7.12	<0.01	0.46	0.92
2000	1.3 ± 0.2	1.4 ± 0.1	1.3 ± 0.1	1.4 ± 0.3	1.5 ± 0.2						
2001	1.4 ± 0.3	1.6 ± 0.2	1.4 ± 0.2	1.2 ± 0.2	1.3 ± 0.2						
2002	1.3 ± 0.2	1.4 ± 0.1	1.3 ± 0.1	1.2 ± 0.1	1.3 ± 0.0						
2003	1.1 ± 0.3	1.0 ± 0.1	0.9 ± 0.1	1.0 ± 0.1	1.1 ± 0.2						
Log series alpha species diversity						0.40	0.80	7.39	<0.01	0.72	0.72
2000	1.4 ± 0.1	1.3 ± 0.2	1.1 ± 0.1	1.5 ± 0.2	1.3 ± 0.2						
2001	1.3 ± 0.2	1.4 ± 0.2	1.1 ± 0.2	1.0 ± 0.2	1.1 ± 0.1						
2002	1.2 ± 0.4	1.2 ± 0.1	1.3 ± 0.2	1.0 ± 0.1	1.2 ± 0.2						
2003	1.1 ± 0.2	0.9 ± 0.2	0.7 ± 0.1	0.8 ± 0.1	0.9 ± 0.1						

Columns of mean values with different letters are significantly different by Duncan's multiple range test (adjusted for multiple contrasts).

some species and ecological processes from the original forest, particularly in aggregated or group seed-tree patterns, and (3) maintain some connectivity in the managed forest landscape (Franklin et al., 1997). The major theme of our study was to address the overall question with respect to plant and mammal communities: are there changes in abundance and diversity of these attributes in stands with structural retention compared with those that are clearcut?

Franklin et al. (1997) defined the structural components of variable retention, whether dispersed or aggregated, to include live large-diameter Douglas-fir trees, some snags (5–10/ha), understory vegetation, fallen wood representing a range of decay classes, and relatively undisturbed layers of forest floor. As discussed by Sullivan et al. (2001a), our study sites incorporated these components, except for the clearcut and seed-tree sites that had mechanical site preparation of the forest

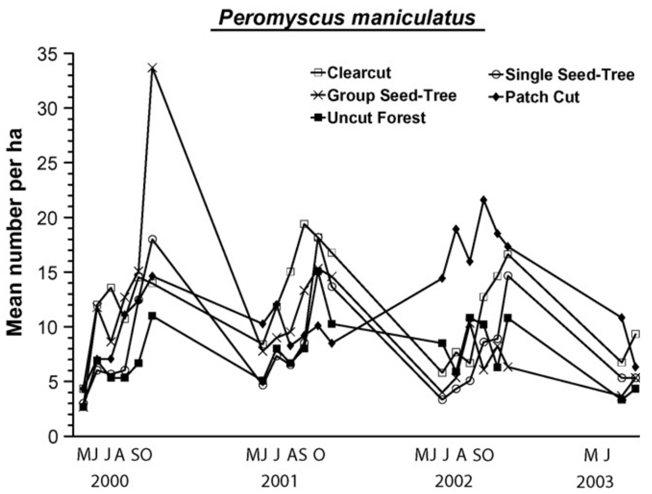

Fig. 3. Mean ($n = 3$) abundance of deer mice (*Peromyscus maniculatus*)/ha in clearcut, single seed-tree, group seed-tree, patch cut, and uncut forest sites in 2000–2003, 5–8 years post-harvest.

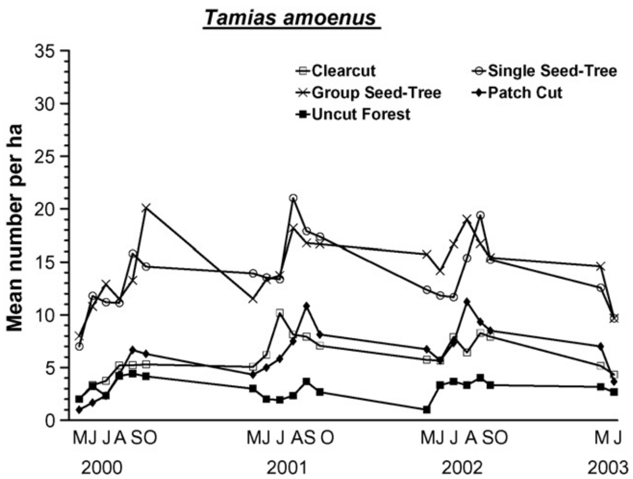

Fig. 4. Mean ($n = 3$) abundance of northwestern chipmunks (*Tamias amoenus*)/ha in clearcut, single seed-tree, group seed-tree, patch cut, and uncut forest sites in 2000–2003, 5–8 years post-harvest.

Table 6
Mean ($n = 3$ replicate sites) ± SE abundance per ha of small mammal species in the five treatments during 2000–2003 (5–8 years post-harvest) and results of RM-ANOVA

Species and year	Treatment					Overall analysis					
	Clearcut	Single seed-tree	Group seed-tree	Patch cut	Uncut forest	Treatment		Time		Treatment × time	
						$F_{4,10}$	P	$F_{3,30}$	P	$F_{12,30}$	P
Peromyscus maniculatus						2.05	0.16	10.40	<0.01	1.62	0.14
2000	11.5 ± 0.6	8.5 ± 3.3	14.1 ± 5.2	9.4 ± 0.5	6.3 ± 1.2						
2001	14.9 ± 2.5	9.8 ± 1.3	11.6 ± 0.7	9.7 ± 0.6	8.8 ± 2.6						
2002	10.7 ± 3.4	7.5 ± 0.8	6.7 ± 1.0	17.8 ± 0.3	8.4 ± 4.2						
2003	8.0 ± 0.8	5.3 ± 0.9	4.5 ± 1.0	8.6 ± 0.1	3.8 ± 1.7						
Tamias amoenus	AB	A	A	AB	B	3.00	0.07	5.17	<0.01	0.95	0.51
2000	4.1 ± 1.7	11.9 ± 1.9	12.8 ± 3.1	3.7 ± 1.1	3.4 ± 1.8						
2001	7.4 ± 3.5	16.2 ± 1.7	14.0 ± 2.8	6.9 ± 1.7	2.6 ± 1.4						
2002	7.0 ± 3.4	14.3 ± 1.4	16.3 ± 1.7	8.1 ± 1.0	3.4 ± 1.7						
2003	4.8 ± 2.2	11.1 ± 1.1	12.1 ± 2.3	5.3 ± 1.4	2.9 ± 1.7						
Phenacomys intermedius	A	BC	AB	BC	C	5.09	0.02	1.74	0.18	0.74	0.71
2000	0.3 ± 0.2	0.3 ± 0.1	0.1 ± 0.1	0.0	0.0						
2001	0.5 ± 0.5	0.2 ± 0.1	0.3 ± 0.1	0.0	0.0						
2002	0.4 ± 0.2	0.0	0.4 ± 0.2	0.3 ± 0.1	0.0						
2003	0.2 ± 0.2	0.0	0.0	0.0	0.0						
Microtus longicaudus						0.39	0.81	4.02*	0.02	1.18*	0.34
2000	0.9 ± 0.9	0.6 ± 0.5	1.4 ± 1.4	0.6 ± 0.6	0.0						
2001	2.1 ± 1.9	0.8 ± 0.5	0.8 ± 0.8	0.2 ± 0.2	0.0						
2002	0.9 ± 0.9	0.0	0.7 ± 0.7	1.2 ± 0.5	0.1 ± 0.1						
2003	0.0	0.0	0.0	0.0	0.0						
Microtus pennsylvanicus	AB	A	AB	B	B	3.12	0.07	3.47	0.03	1.10	0.40
2000	0.5 ± 0.5	0.5 ± 0.3	0.1 ± 0.1	0.2 ± 0.2	0.0						
2001	1.4 ± 1.0	2.4 ± 2.0	0.4 ± 0.4	0.0	0.0						
2002	4.4 ± 3.1	3.0 ± 1.6	0.3 ± 0.3	0.0	0.0						
2003	0.5 ± 0.5	0.5 ± 0.3	0.0	0.0	0.0						
Clethrionomys gapperi	BC	C	BC	B	A	26.76	<0.01	0.68	0.57	1.44	0.20
2000	0.1 ± 0.1	0.0	0.6 ± 0.5	2.7 ± 1.2	5.7 ± 0.5						
2001	0.2 ± 0.2	0.1 ± 0.1	0.3 ± 0.2	0.9 ± 0.5	5.1 ± 0.4						
2002	0.1 ± 0.1	0.1 ± 0.1	0.3 ± 0.1	1.0 ± 0.8	8.4 ± 1.5						
2003	0.7 ± 0.7	0.0	0.7 ± 0.7	0.2 ± 0.2	7.3 ± 2.8						
Sorex monticolus	AB	A	A	C	BC	7.94	<0.01	22.56	<0.01	2.51	0.02
2000	1.4 ± 0.4a	1.6 ± 0.3a	1.0 ± 0.3ab	0.3 ± 0.2b	0.3 ± 0.2b						
2001	1.3 ± 0.5abc	2.1 ± 0.5a	1.8 ± 0.8ab	0.2 ± 0.2c	0.4 ± 0.4bc						
2002	0.4 ± 0.2b	1.6 ± 0.3a	1.3 ± 0.1a	0.0b	0.3 ± 0.2b						
2003	0.0	0.0	0.0	0.0	0.0						
Sorex cinereus						0.96	0.47	5.62	<0.01	0.81	0.64
2000	0.0	0.0	0.1 ± 0.1	0.1 ± 0.1	0.2 ± 0.1						
2001	0.1 ± 0.1	0.2 ± 0.1	0.1 ± 0.1	0.1 ± 0.1	0.2 ± 0.1						
2002	0.0	0.0	0.0	0.0	0.1 ± 0.1						
2003	0.0	0.0	0.0	0.0	0.0						

Columns of mean values with different letters are significantly different by Duncan's multiple range test (adjusted for multiple contrasts). F-values identified by * were calculated using the H-F correction factor, which decreased the stated degrees of freedom due to correlation of data among repeated measures (years).

floor prior to planting of tree seedlings. The seed-tree harvesting technique (Smith, 1986) is commonly used in mixed Douglas-fir-lodgepole pine and western larch (*Larix occidentalis*)-lodgepole pine forests in inland parts of the PNW. This strategy attempts to emulate the pre-suppression wildfire regime of relatively high-frequency, variable-intensity fires of interior regions (Agee, 1993). Pockets of live trees were often left after such fires and subsequent multi-aged stands provided a template for green-tree retention systems (Franklin and Waring, 1979; Morrison and Swanson, 1990). The range of ‘‘legacy trees’’ (Franklin et al., 2000) on our seed-tree sites was based on the number and distribution of Douglas-fir in the original late successional stands. Patch-cutting is often used to harvest multi-aged forests such as interior Douglas-fir ecosystems, and are typically $\leq$1.0 ha in area (Vyse et al., 1998).

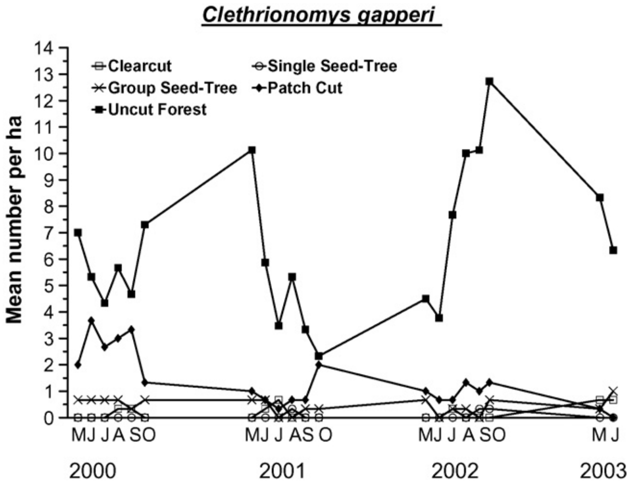

Fig. 5. Mean ($n = 3$) abundance of southern red-backed voles (*Clethrionomys gapperi*) in clearcut, single seed-tree, group seed-tree, patch cut, and uncut forest sites in 2000–2003, 5–8 years post-harvest.

4.2. Understory vegetation

In terms of hypothesis (i), that abundance and species diversity of plant communities would decline with decreasing levels of tree retention, abundance of herbs and shrubs was similar among treatment sites, at least 5–8 years post-harvest. This result was similar to years 1–4 post-harvest on these same sites, but herb volume declined (years 5–8) rather than increased (years 1–4). Shrub volume was higher in 2001 and 2002 than in 2000 or 2003. In terms of coniferous regeneration, clearcut and seed-tree sites had the highest abundance of understory conifers. Thus, at least for abundance of understory vegetation, hypothesis (i) was not supported.

The species diversity component of hypothesis (i) had conflicting evidence: species richness of herbs, shrubs, and total vascular plants was similar among harvested sites. Species diversity of herbs followed this pattern but shrubs did not, nor did total species diversity (2003, 8 years post-harvest) and total structural diversity of plants. Thus, hypothesis (i), with respect to species diversity of understory vegetation, was not supported. These results are contrary to those of Beese and Bryant (1999), Jalonen and Vanha-Majamaa (2001), and Halpern et al. (2005) who reported declines in abundance and richness of vascular plants up to 1–3 years post-harvest, particularly in sites with low retention levels of residual trees. Similarly, in a retrospective study, Deal (2001) reported significant changes in plant community structure in sites where > 50% BA was cut. Alternatively, Fredericksen et al. (1999) reported no significant short-term changes in understory plant richness or diversity, regardless of harvest intensity of northern hardwood and oak-hickory stands. In addition, North et al. (1996) found herb and shrub richness and evenness to be highest in a green-tree retention stand compared with a clearcut and intact 65-year-old forest.

Despite having no effect on total species richness of plants, retention of live trees did provide suitable conditions for some plant species considered to be associated with forest interior conditions. For example, both *A. formosa* and *O. chilensis* (forest species) were able to persist up to 8 years post-harvest within either the single or group seed-tree, but not clearcut sites. Similarly, *G. oblongifolia* (a forest species) was also able to persist within patch cut sites up to 8 years post-harvest, but was lost within clearcut sites by 1 year post-harvest. Forest species such as *C. bulbosa*, *C. uniflora*, *P. bracteosa*, *P. racemosa*, and *T. occidentale*, while absent from all sites immediately following harvest, were present within seed-tree and/or patch cut sites 5–8 years post-harvest, but not in clearcut sites. Conversely, some forest interior plants such as *A. cordifolia*, bunchberry (*Cornus canadensis*), *O. secunda*, and prince's pine (*Chimaphila umbellata*) were maintained on clearcuts during this period.

Table 7
Mean ($n = 3$ replicate sites) ± SE number of mule deer pellet-groups per ha in five consecutive summer and winter periods and results of RM-ANOVA

Season and year	Treatment					Overall analysis					
	Clearcut	Single seed-tree	Group seed-tree	Patch cut	Uncut forest	Treatment		Time		Treatment × time	
						$F_{4,10}$	P	$F_{4,40}$	P	$F_{16,40}$	P
Summer						1.70	0.23	4.12	<0.01	0.76	0.72
1999	146.67 (63.60)	233.33 (6.67)	266.67 (78.60)	146.67 (76.88)	100.00 (52.92)						
2000	80.00 (11.55)	260.00 (90.18)	333.33 (121.29)	73.33 (37.12)	73.33 (63.60)						
2001	53.33 (35.28)	100.00 (30.55)	160.00 (30.55)	40.00 (11.55)	40.00 (23.09)						
2002	80.00 (11.55)	320.00 (30.55)	300.00 (80.00)	146.67 (75.13)	120.00 (61.10)						
2003	233.33 (26.67)	300.00 (50.33)	273.33 (76.88)	126.67 (26.67)	86.67 (59.25)						
Winter						0.51	0.73	1.34*	0.27	1.47*	0.16
1999–2000	120.00 (30.55)	113.33 (35.28)	240.00 (102.63)	413.33 (26.67)	380.00 (253.25)						
2000–2001	80.00 (30.55)	153.33 (29.06)	200.00 (57.74)	426.67 (92.62)	373.33 (186.67)						
2001–2002	120.00 (11.55)	220.00 (83.27)	366.67 (56.96)	313.33 (33.33)	260.00 (130.13)						
2002–2003	220.00 (50.33)	200.00 (113.72)	306.67 (29.06)	393.33 (35.28)	360.00 (183.30)						
2003–2004	66.67 (6.67)	106.67 (48.07)	60.00 (20.00)	280.00 (50.33)	266.67 (133.83)						

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

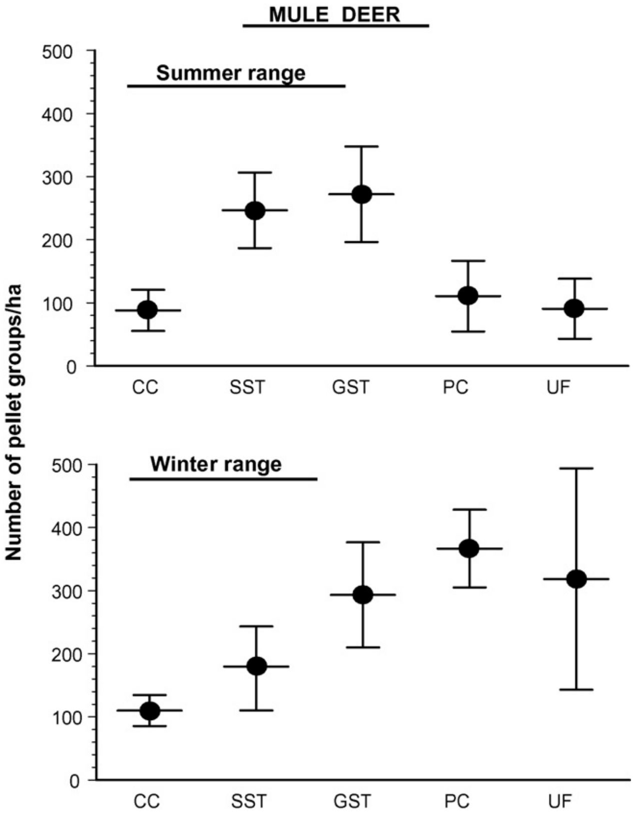

Fig. 6. Relative habitat use by mule deer, based on overall mean ($n = 15$; 3 replicates × 5 years) number of fecal pellet groups per ha and 95% CI, during summer and winter periods. Clearcut (CC), single seed-tree (SST), group seed-tree (GST), patch cut (PC), and uncut forest (UF).

4.3. Small mammal communities

Abundance, species richness, and species diversity of small mammals were maintained on all harvested sites, primarily because of habitat generalist and early successional species. Thus, with respect to hypothesis (ii), our results do not support the prediction that abundance and diversity of small mammals will decline with decreasing levels of tree retention. These results are contrary to those of Sullivan and Sullivan (2001) who reported higher richness and diversity of small mammals in all sites than uncut forest at 1–4 years post-harvest. In general, measurements of abundance and species richness and diversity were higher in 1997 and 1998 (1 and 2 years post-harvest) than in any of the subsequent 5 post-harvest years (see Table 5 and Sullivan and Sullivan, 2001).

There were three striking results in the current study. First, there was the significant reduction in abundance of *C. gapperi* after its relatively high numbers on group seed-tree sites at 1–3 years post-harvest (Sullivan and Sullivan, 2001). Maintenance of habitat conditions for *C. gapperi* in partially cut forests with retention levels of > 15 m^2/ha BA or 30% uncut forest has been reported across a variety of forest conditions (Martell, 1983; Medin and Booth, 1989; Steventon et al., 1998; Von Trebra et al., 1998; Moses and Boutin, 2001; Gitzen and West, 2002; Klenner and Sullivan, 2003; Fuller et al., 2004). This microtine prefers mesic to moist habitats in coniferous, deciduous, and mixed forests with relatively heavy cover of down wood in various stages of decomposition (Merritt, 1981; Yahner, 1986) and dense cover of coniferous or deciduous trees (Martell and Radvanyi, 1977; Moses and Boutin, 2001). These conditions provide substrates for hypogeous ectomycorrhizal fungi, berry production (e.g., *Vaccinium* spp.), and seed-fall from overstory trees that may act as food sources for *C. gapperi* (Maser et al., 1978; Merritt, 1981). As discussed by Sullivan et al. (1999), at least in western North America, *C. gapperi* seems to disappear from clearcuts when these habitat attributes are altered, by loss of moisture, over the first 5 years after forest harvesting. Thus, after the third post-harvest year, conditions for *C. gapperi* presumably became intolerable for this species to persist at numbers > 1/ha in the clearcut or seed-tree sites up to 8 years post-harvest.

Second, *T. amoenus*, a habitat generalist, showed a consistent pattern of preference for the seed-tree sites over the other sites. This sciurid generally occurs in relatively ‘‘open’’ and some shrub-covered habitats associated with coniferous forests, particularly sites with fruit-bearing and seed-producing shrubs and trees (Sutton, 1992). This chipmunk also disperses mycorrhizal fungi (Maser et al., 1978; McIntire, 1984) which likely remained viable and symbiotic with tree roots of residual Douglas-fir (and other woody plants) in the seed-tree sites (Hagerman et al., 2001; Lazaruk et al., 2005). Thus, we postulate that the relatively high numbers of *T. amoenus* on seed-tree sites was related to their ‘‘openness’’ combined with high species diversity of shrubs and the presumed presence of mycorrhizal fungal networks maintained by residual trees. This continuity of mycorrhizal legacies, via residual conifers, probably did not occur on the clearcut sites. Enhanced flower and fruit production of understory shrubs on sites with reduced overstory trees (Wender et al., 2004) may also have contributed to the abundance of *T. amoenus* on seed-tree sites. However, this is speculative as vegetation measurements were quantitative only, and hence did not assess fruit production of shrub species. Patch cut openings provided some habitat opportunities for *T. amoenus*, similar to clearcut sites, but supported less than one-half the abundance recorded on seed-tree sites.

Third, numbers of *Microtus* spp. were substantially reduced to a maximum of < 10/ha in the peak year of 2002 compared with ca. 35/ha in 1998 (Sullivan and Sullivan, 2001). *M. pennsylvanicus*, in particular, has shown a clear pattern of high numbers every 3–4 years from 1994 to 2002 in the south-central interior of BC (Sullivan and Sullivan, unpublished). Thus, the early successional habitats created by clearcutting and seed-tree harvest methods, that are optimum for *M. pennsylvanicus* and *M. longicaudus* (Reich, 1981; Getz, 1985), seemed less conducive to population build-ups by these microtines during the 5–8 years post-harvest. The significant decline in abundance of herbaceous vegetation may have contributed to the relatively low numbers of *Microtus* spp., or perhaps owing to another aspect of their multi-annual population fluctuations.

In terms of individual species responses to a gradient of tree retention, the late successional forest species *C. gapperi* showed a clear trend for increased overall abundance per ha,

Table 8
Responses (overall mean values, $n = 20$ trapping periods) of small mammal communities to variable retention harvests 2000–2003, 5 to 8 years post-harvest

Parameter	Clearcut	Single seed-tree	Group seed-tree	Patch cut	Uncut forest
Mean abundance per ha					
Peromyscus maniculatus	11.95	8.28	10.17	11.95	7.48
Tamias amoenus	6.04	13.84	14.44	6.17	3.10
Phenacomys intermedius	0.04	0.13	0.25	0.08	0.00
Microtus longicaudus	1.17	0.43	0.88	0.58	0.02
Microtus pennsylvanicus	1.94	1.83	0.22	0.05	0.00
Clethrionomys gapperi	0.17	0.05	0.45	1.38	6.46
Sorex monticolus	0.95	1.58	1.23	0.13	0.34
Sorex cinereus	0.03	0.05	0.03	0.03	0.17
Zapus princeps	0.03	0.02	0.00	0.00	0.03
Mustela erminea	0.03	0.12	0.00	0.05	0.07
Total	22.72	26.33	27.68	20.43	17.66
Species Richness	3.53	3.73	3.47	3.12	3.12
Species Diversity					
Shannon–Wiener	1.31	1.40	1.28	1.21	1.31
Log-series	1.27	1.24	1.12	1.11	1.18

ranging from 0.17 (clearcut) to 6.46 (uncut forest) (Table 8). *S. cinereus* also followed this preference for uncut forest. *T. amoenus*, *P. intermedius*, and *S. monticolus* were relatively more abundant in the seed-tree sites than other sites (Table 8). *Microtus* spp. were generally more abundant with less retention of residual trees. These overall comparisons highlight the need to evaluate small mammals on an individual and species-habitat association basis (Lehmkuhl et al., 1999). Thus, with respect to hypothesis (ii), *C. gapperi* and *S. cinereus* support the prediction that abundance will decline with decreasing tree retention. Conversely, *T. amoenus*, *P. intermedius*, *S. monticolus*, and the two *Microtus* species tend to fit the opposite trend and do not support the hypothesis. *P. maniculatus* was present at similar numbers in all sites (Table 8).

4.4. Relative habitat use by deer

Seed-tree sites appeared to provide both summer and winter habitat for mule deer. Forage production and species diversity (herbs) may have been higher in the favorable microclimatic conditions within and near residual Douglas-fir trees during summer months. Unfortunately, we did not compare herb communities within or near single and group residual trees and in more open parts of the harvested seed-tree sites. Nelson and Halpern (2005) described initial (1–2 years) edge-related responses and maintenance of plant species richness and composition in 1-ha aggregates of intact forest. Chen et al. (1992) concluded that some microclimatic benefits may be achieved even with small aggregates (<1 ha in size), such as our group seed-tree sites that averaged 0.70 ha in size.

In winter, some snow interception by crowns of fir trees on group seed-tree sites, along with understory forage, may have provided habitat conditions similar to those found in patch cut and uncut forest sites. Late successional closed-canopy Douglas-fir forests seem to provide winter range for mule deer via snow interception and forage accumulations from herbs, shrubs, and litterfall composed of arboreal lichens and Douglas-fir (Dawson et al., 1990; Armleder et al., 1994). Thus, our group seed-tree sites provided comparable levels of relative habitat use by deer to those recorded in patch cut and uncut forest sites. It is important to note that the forest aggregate, in all three group seed-tree sites, was located near the edge of a much larger area of intact mature or old-growth forest. This juxtaposition may have contributed to high use of the group seed-tree sites, particularly in winter. Thus, our hypothesis (iii), that relative habitat use by mule deer will decline with decreasing levels of tree retention, is not supported for summer range use but seems to be supported for winter range use. However, the prediction that the response variable of habitat use should be greater in sites with green-tree retention than in clearcuts is supported for summer range use.

5. Management implications

Variable retention harvests in temperate zone coniferous forests are designed to maintain some species and ecological processes from the original forest. This premise should be particularly true in aggregated or group seed-tree patterns. Green-tree retention over the 5–8 post-harvest years of this study, and the earlier 1–4 years post-harvest reported by Sullivan et al. (2001a) and Sullivan and Sullivan (2001), maintained a range of BA and density of residual trees across treatment sites. In general, our harvesting regimes did not have a significant effect on the abundance or species richness of plant and forest floor small mammal communities. However, there were several species- and group-specific responses to the range of harvesting treatments.

Clearcutting favored an abundance of coniferous regeneration, whereas species diversity of understory conifers was highest in seed-tree and patch cut sites. Retention of live trees did provide suitable conditions for some plant species considered to be associated with forest interior conditions, such as *C. bulbosa*, *C. uniflora*, *P. bracteosa*, *P. racemosa*, and *T. occidentale*. These herbaceous species were present within seed-tree and/or patch cut sites 5–8 years post-harvest, but not in clearcut sites. Forest specialist species such as *C. gapperi* declined on clearcut and seed-tree sites, whereas the generalist *T. amoenus* was abundant in the seed-tree sites. Early successional species such as *M. pennsylvanicus* were abundant in clearcut and seed tree sites but not in patch cut or uncut forest sites. Monitoring of these sites over future decades will determine if these patterns continue.

Thus, an array of harvesting systems, including green-tree retention, may be used to maintain different species and groups of species of plants and mammals in commercial forest landscapes. Diverse habitat conditions derived from a range of harvesting systems should be able to maintain the various components of biodiversity.

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