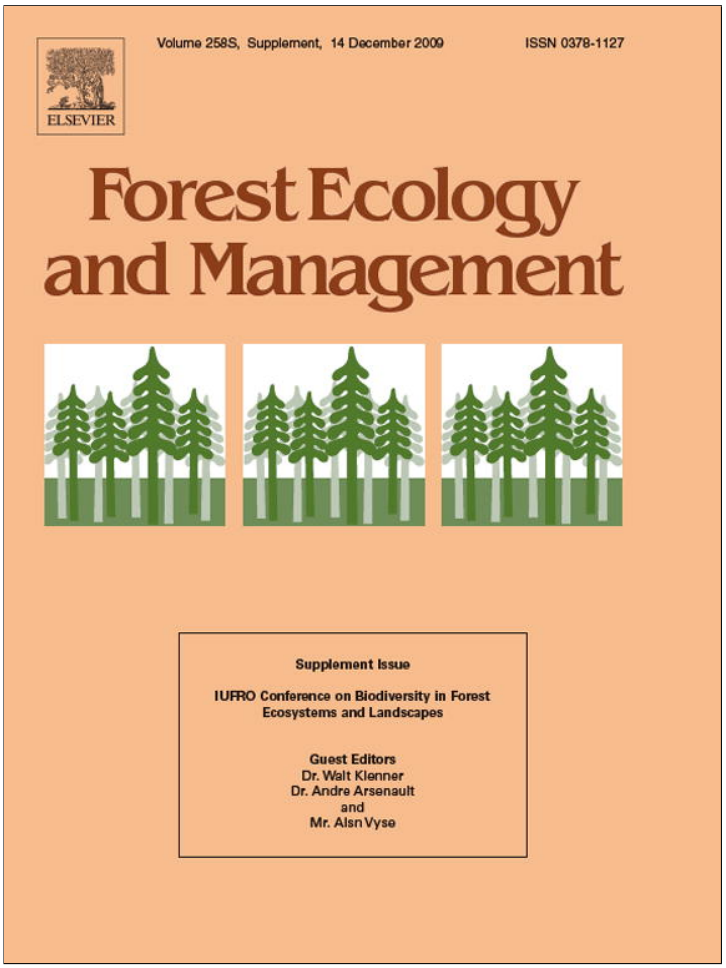

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Stand structure and the abundance and diversity of plants and small mammals in natural and intensively managed forests

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ABSTRACT

Little attention has been given to investigating biodiversity in managed forests. Pre-commercial thinning (PCT) and fertilization have been used successfully to increase growth of coniferous trees, vegetative succession, and overall stand structure in second-growth stands. This study was designed to test the hypotheses (H) that PCT and repeated fertilization of young (20–25 years) even-aged lodgepole pine (*Pinus contorta*) stands would enhance (H1) coniferous stand structure; (H2) abundance and diversity of understory vegetation; and (H3) abundance and diversity of forest-floor small mammals, to levels found in mature and old-growth forests. Replicate study areas were located near Summerland and Kelowna in south-central British Columbia, Canada. Each study area had six stands: young plantation, thinned stand (1000 stems/ha), thinned–fertilized stand (1000 stems/ha), unthinned stand, mature forest, and old-growth forest. Coniferous stand structure, understory vegetation, and forest-floor small mammals were sampled during a 5-year period from 1999 through 2003.

The smaller tree sizes (diameter, height, basal area) in the young lodgepole pine stands did not support the tree size part of H1. Similar abundance of overstory and total conifers did support the abundance part of H1. The diversity component was supported by the similarity in species and structural diversity of total conifers among the intensively managed and older unmanaged stands. Response of understory vegetation was dominated by the abundance of herbs in the thinned–fertilized stands. There was no difference in shrub abundance among stands, but mosses and terrestrial lichens were most numerous in the mature and old-growth stands. Our results supported the abundance part of H2, at least for herbs and shrubs. Species richness and diversity of vascular plants were similar in managed and old-growth forests, and richness was lowest in the mature stands.

H3 was supported for total abundance, species richness, and diversity of small mammals, and for the generalist species *Peromyscus maniculatus* and *Tamias amoenus*, but not for the old forest specialist *Myodes gapperi*. Two insectivores, *Sorex monticolus* and *Sorex cinereus*, were at comparable or higher abundance in the managed stands than in the older unmanaged forests. Three other microtines: *Microtus pennsylvanicus*, *Microtus longicaudus*, and *Phenacomys intermedius* were early successional vegetation specialists, and hence did not fit the prediction of H3. Thus, despite overall quantitative differences in stand structure and species-specific variability between our intensively managed and older natural stands, old-growth attributes seem to be developing in a time-span of decades rather than the centuries depicted by long rotations.

1. Introduction

Forest management should conserve biological diversity by maintaining a variety of tree species, age classes, successional stages, harvesting strategies, and protected areas in a 'mosaic' of habitats (Hunter, 1999; Kohm and Franklin, 1997). Inherent in this plan is the need to meet presumed increases in global demand for wood (Brooks, 1997; Moore and Allen, 1999; Hartley, 2002). Integrating conservation and wood production in managed landscapes may alleviate harvesting pressure on old-growth forests and augment the role of reserves in protecting biodiversity (Angelstam et al., 1997; Sedjo and Botkin, 1997; Hunter, 1999).

Even-aged forests, regenerated naturally or by planting, are generally considered to negatively affect biodiversity (Peterken, 1996; Betts et al., 2005). Much of this criticism relates to forest simplification through loss of both horizontal (spatial hetero-

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geneity) and vertical (stratification) structural diversity (Lust et al., 1998; Lindenmayer and Franklin, 2002). Stand structure is one component of biodiversity because the layers of vegetation and array of tree sizes provide habitats for a range of plant and animal species (Lindenmayer et al., 2000; Tews et al., 2004).

Although plantations are commonly viewed less favourably than naturally regenerated even-aged forests, both have been criticized by some conservation biologists because they originate primarily from clearcut harvesting (Kimmins, 1996). This concern exists despite the limited understanding of the relationship between wood production and biodiversity (Barbour et al., 1997; Moore and Allen, 1999). For example, stand tending in the first half of a rotation is crucial to both wood production and biodiversity (Bailey and Tappeiner, 1998). Nevertheless, forest harvesting over large areas and time seems to reduce structural diversity because young second-growth stands have yet to converge with those in mature and old-growth forests (Lomolino and Perault, 2000).

Most of the controversy surrounding even-aged second-growth stands and presumed loss of biodiversity is focussed on plantations (Carnus et al., 2006), rather than intensive silvicultural practices such as pre-commercial thinning (PCT) and fertilization. These latter activities are designed to increase fibre production while maintaining or reducing production costs (Allen et al., 1990). Soil preparation, planting selected genotypes, vegetation management, thinning (both pre-commercial and commercial), and nutrient additions are silvicultural treatments that have been used successfully around the world (Allen et al., 1990; Oliver and Larson, 1996). Intensively managed young stands may produce three to seven times the usable wood per hectare compared to unmanaged stands (Sedjo, 1999; Jokela et al., 2004), although this production potential varies among forest types (Sedjo et al., 1998). Surprisingly, the actual impacts of these intensive practices on biodiversity have received little research attention (Lautenschlager, 2000).

Studies on PCT have indicated a higher diversity of plant species (herbs, shrubs, trees) in heavily thinned stands than in unthinned stands or old-growth forests at 10 years post-thinning (Sullivan et al., 2001). In addition, species diversity and structural diversity of understory coniferous trees were higher in heavily thinned (500 and 1000 stems/ha) stands than in unthinned stands at 15 years post-thinning (Sullivan et al., 2006). Other old-growth attributes such as large-diameter trees and crown volumes have also developed in managed young (32–42 years) stands (Sullivan et al., 2006), as well as in other thinning regimes in older (60–70 years) stands (Carey and Wilson, 2001).

PCT and fertilization can enhance growth of naturally regenerated lodgepole pine (*Pinus contorta*) in inland areas of the Pacific Northwest of North America (Sullivan et al., 2001; Lindgren et al., 2007). Lodgepole pine often regenerates overabundantly after clearcut harvesting or wildfire, resulting in reduced tree growth. PCT concentrates growth on fewer stems with subsequent control of the yield, rotation, and value of the future crop (Johnstone, 1985). Lodgepole pine also responds well to single-application fertilization with nitrogen alone or in combination with other elements (Brockley, 1996). Sustained growth responses to repeated fertilization have been demonstrated in field studies with lodgepole pine (see review by Lindgren et al., 2007).

Positive biomass responses of understory vegetation have been reported for stand thinning (Crouch, 1986; Sullivan et al., 2001; Lindgren et al., 2006) and fertilization (Thomas et al., 1999; VanderSchaaf et al., 2000). Others have suggested that these silvicultural tools could accelerate stand development, perhaps creating old-growth structural features in intensively managed stands (Carey and Curtis, 1996; Hayes et al., 1997). However, it is uncertain whether wildlife species associated with late-seral forests will respond positively to their development in intensively managed young even-aged stands. Forest-floor small mammals are useful indicators of habitat suitability in managed forests (Carey and Harrington, 2001; Pearce and Venier, 2005) because of their varied functional roles as seed disseminators (Maser et al., 1978; Sullivan et al., 1990), prey for various carnivores (Carey and Johnson, 1995), and regulation of some invertebrate populations (Carey and Harrington, 2001).

We know of no studies that have investigated the use of PCT and fertilization for enhancing tree growth, vegetative succession, and stand structure in even-aged stands with a goal of developing old-growth attributes, and how intensively managed stands compare to unmanaged stands. Therefore, we tested the hypotheses (H) that PCT and repeated fertilization of young (20–25 years) even-aged lodgepole pine stands would enhance (H1) coniferous stand structure (e.g. tree sizes, abundance, species diversity, and structural diversity of coniferous tree layers); (H2) abundance (crown volume index) and diversity (e.g. species richness and diversity of herb, shrub, and tree layers) of vegetation; and (H3) abundance and diversity of forest-floor small mammals, to levels found in mature and old-growth forests.

2. Methods

2.1. Study areas

Each mosaic consisted of six habitats which represented common habitat types in these forest management areas: (1) young plantation; (2) thinned stand; (3) thinned and fertilized stand; (4) unthinned stand; (5) mature stand; and (6) old-growth stand. Three replicate blocks were chosen in south-central British Columbia (BC), Canada, at the Kelowna (replicate 1, medium sites; replicate 2, wet sites) and Summerland (replicate 3) study areas.

The Kelowna study area was located 37 km northwest of Kelowna, BC (50°04′N; 119°34′W) in the Montane Spruce (MS_{dm}) biogeoclimatic subzone (Meidinger and Pojar, 1991). Topography is rolling to flat with sandy loam soil at 1240–1260 m elevation. The MS has a cool, continental climate with cold winters and moderately short, warm summers. Mean annual temperature is 0.5–4.7 °C and precipitation ranges from 380 to 900 mm. The MS landscape has extensive young and maturing seral stages of lodgepole pine, which have regenerated after wildfire. Hybrid interior spruce (*Picea glauca* × *P. engelmannii*) and subalpine fir (*Abies lasiocarpa*) are the dominant shade-tolerant climax trees. Douglas-fir (*Pseudotsuga menziesii*) 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*) is a common seral species and black cottonwood (*Populus trichocarpa*) occurs on some moist sites (Meidinger and Pojar, 1991).

At Kelowna, two plantations (YP_1 and YP_2; Fig. 1a) were clearcut harvested in 1995 and were 13.2 and 9.2 ha in area, respectively. These sites regenerated naturally to lodgepole pine. Previous forest cover was 99–101-year-old lodgepole pine with mean dbh of 19.5–20.0 cm and mean height of 20.0–20.5 m. The juvenile lodgepole pine stands were clearcut harvested in 1979 and 1982 and regenerated naturally to lodgepole pine with the other coniferous species, including western larch (*Larix occidentalis*), as minor components. Two of these juvenile stands were PCT thinned (1993) to 1000 stems/ha (Th_1 and Th_2; Fig. 2a), thinned (1993) to 1000 stems/ha and fertilized in fall 1994, spring 1997, fall 1998, fall 2000, and spring 2003 ($Th + F_1$ and $Th + F_2$; Fig. 2b), or were left unthinned ($Unth_1$ and $Unth_2$; Fig. 1b). Stand areas ranged from 9.5 to 12.6 ha at 17–18 years of age.

The mature forest stands (MF_1 and MF_2; Fig. 3a) were composed primarily of lodgepole pine with a minor component of Douglas-fir

Fig. 1. Photographs (summer 1999) of (a) a young lodgepole pine plantation and (b) an unthinned lodgepole pine stand.

Fig. 2. Photographs (summer 1999) of (a) a lodgepole pine stand thinned to 1000 stems/ha in 1993 and pruned in 1998 and (b) a lodgepole pine stand thinned to 1000 stems/ha in 1993, fertilized five times from 1994 to 2002, and pruned in 1998.

and interior spruce at 80–120 years of age. Each stand was located near the young plantation units (YP_1 and YP_2). The old-growth forest stands (OG_1 and OG_2; Fig. 3b) were in the 140–250 year age class. Stand OG_1 was dominated by Douglas-fir and stand OG_2 by subalpine fir, Douglas-fir, and interior spruce.

The Summerland study area was located 25 km west of Summerland (49°40′N; 119°53′W) in the MS_{dm} subzone at an elevation range of 1450–1520 m with gently rolling topography and sandy loam soil. The 12.8-ha young plantation (YP_3) was clearcut harvested in winter 1995–1996 and was planted with lodgepole pine in spring 1997. There was ingress of naturally regenerated lodgepole pine in subsequent years. Previous forest cover was 140–250-year-old lodgepole pine.

The juvenile lodgepole pine stands were located on units clearcut harvested in 1978: unthinned ($Unth_3$), PCT (1993) to 1000 stems/ha (Th_3), and PCT (1993) to 1000 stems/ha and fertilized in fall 1994, spring 1997, fall periods of 1998, 2000, and spring 2003 ($Th + F_3$). Naturally regenerated lodgepole pine was the dominant tree species. Stand areas ranged from 4.4 to 11.3 ha at 17–19 years of age. Minor components of the stands included Douglas-fir, interior spruce, subalpine fir, ponderosa pine (*Pinus ponderosa*), willow (*Salix* sp.), Sitka alder (*Alnus sinuata*), and trembling aspen.

The mature forest stand (MF_3) in this replicate was composed of 80–120-year-old lodgepole pine with minor components of Douglas-fir and subalpine fir. There were some veteran Douglas-fir (140–250 years old) dispersed through the stand. The old-growth forest stand (OG_3) had 120–140-year-old lodgepole pine and Douglas-fir with subalpine fir and spruce as minor components. Douglas-fir also occurred throughout the stand in the veteran age class of 251^+ years. These stands covered several hundred ha.

2.2. Stand treatments

The PCT treatment of the juvenile stands (Th_{1-3} and $Th + F_{1-3}$) occurred at an appropriate time to maximize growth response. Thinning to 1000 stems/ha was done operationally at all study areas in the late summer–early fall of 1993.

The fertilization treatments were designed as large-scale applications of established "optimum nutrition" field experiments in Sweden (Tamm et al., 1999) and BC (Brockley, 2005). Fertilizer was applied at 2-year intervals for 10 years (total of 5 applications), using formulations developed from annual nutrient diagnosis of lodgepole pine foliage samples. The objective was to maintain elevated foliar N levels (~1.3%), with levels of all other nutrients in proportional balance with N. Fertilization was initiated in November 1994 and provided 100 kg/ha nitrogen (100 N), 100 kg/ha phosphorus (100 P), 100 kg/ha potassium (100 K), 50 kg/ha sulfur (50 S), 25 kg/ha magnesium (25 Mg), and 1.5 kg/ha boron (1.5 B). The blended product (11-25-13-5.5S-2.7Mg-0.17B) was applied aerially (helicopter) at 906 kg/ha.

Stands were re-fertilized in May 1997 with 36-0-0-9S at 547 kg/ha, the blend delivered 200 N and 50 S. Stands were fertilized again in October 1998. Targeted application rates were 150 N, 25 S, and 3 B, using 37-0-0-6.1S-0.7B applied at 404 kg/ha. In 2000, targeted application rates were 150 N and 50 S, using 31.1-0-0-11.3S applied at 439.4 kg/ha. In 2003, targeted application rates were 150 N and 1.5 B, 44.6-0-0-0.45B applied at 336.1 kg/ha. Additional details of the PCT and fertilization treatments are reported in Lindgren et al. (2007). Pruning of all pole-sized lodgepole pine and Douglas-fir crop trees in the thinned and thinned–fertilized stands, to a height of 3.0 m, was conducted in September to December

Fig. 3. Photographs (summer 1999) of (a) a mature lodgepole pine stand and (b) an old-growth stand.

1998. This practice was designed to improve stem form and wood quality without sacrificing stem growth (Lindgren et al., 2007).

2.3. Coniferous stand structure

Sampling of coniferous tree species in layers in 0–1, 1–2, 2–3, and >3 m height classes was done in a 5.64-m radius circular plot (100 m^2) located systematically at 50-m intervals throughout each stand in 2003. In each plot, we tallied species, dbh (diameter at breast height, 1.3 m above soil surface), and total height. In the young plantation stands, we only counted trees in each height class because of the small average size (diameters <3 cm) of trees.

2.4. Vegetation communities

Three 25-m transects, consisting of five 5-m × 5-m plots, were systematically located in each habitat type (Stickney, 1980). Each plot contained three nested sub-plots: a 5-m × 5-m plot for sampling trees, a 3-m × 3-m sub-plot for sampling shrubs; and a 1-m × 1-m sub-plot for sampling herbaceous species, mosses, and terrestrial lichens. Tree, shrub, and herb layers were subdivided into height classes (0–0.25, 0.25–0.5, 0.5–1.0, 1.0–2.0, 2.0–3.0, and 3.0–5.0 m). A visual estimate of percentage cover of the ground was made for each species height class combination within the appropriate sub-plot. Total percentage cover for each layer was also estimated. These data were summarized in terms of absolute crown volume (m^3/0.01 ha) for each plant 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. Volume values were averaged by species for each plot size and converted to a 0.01-ha base to produce a tabular value given for each species and life-form group. Sampling was done annually in July–August 1999 to 2003 (6–10 years post-thinning) by the same person. Plant species were identified in accordance with Hitchcock and Cronquist (1973) and Parish et al. (1996). Mosses and terrestrial lichens were not identified to species.

2.5. Small mammal communities

Forest-floor small mammal populations were sampled at 4-week intervals from May to October 1999, 2000, 2001, 2002, and May–June 2003 for a total of 25 sampling periods over the study. Trapping grids (1 ha) 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. Small mammals sampled included the southern red-backed vole (*Myodes gapperi*), deer mouse (*Peromyscus maniculatus*), northwestern chipmunk (*Tamias amoenus*), meadow vole (*Microtus pennsylvanicus*), long-tailed vole (*Microtus longicaudus*), heather vole (*Phenacomys intermedius*), western jumping mouse (*Zapus princeps*), montane shrew (*Sorex monticolus*), common shrew (*Sorex 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). The overnight trapping technique resulted in a high mortality rate for shrews. Therefore, shrews were collected and identified according to Nagorsen (1996). All handling of animals was in accordance with the principles of the Animal Care Committee, University of British Columbia.

To determine the effects of treatments on abundance of the major species, we measured trappability and population density. Jolly estimates of trappability were calculated according to Krebs and Boonstra (1984). Population estimates of the southern red-backed vole, deer mouse, northwestern chipmunk, meadow vole, and long-tailed vole were derived from the Jolly–Seber stochastic model (Seber, 1982), with correction for small sample sizes (Krebs, 1991). The reliability of the Jolly–Seber model declines when population sizes are very low and no marked animals are captured. In these cases, the total number of individuals captured was used to compare populations of the heather vole, western jumping mouse, montane shrew, common shrew, and short-tailed weasel.

2.6. Diversity measures

Diversity of vascular 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. Species diversity was based on the Shannon–Wiener index (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 1999–2003), and understory and overstory 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 species richness and diversity with the height classes of the coniferous tree layers acting as "species" (Sullivan et al., 2001). This measure of foliage height diversity used the Shannon–Wiener index with tree species represented by height classes and the number of conifers in each class. Diversity of overstory (>3 m) and understory (<3 m) coniferous stand structure was evaluated in the four height classes. In addition, we used the coefficient of variation (CV) of tree size, based on mean diameter and height of lodgepole pine, as a measure of overstory tree-size diversity (Edgar and Burk, 2001; Staudhammer and LeMay, 2001).

2.7. Statistical analysis

A repeated measures analysis of variance (RM-ANOVA) (SPSS Institute Inc., 2007) was conducted to determine the effects of treatment and time (1999–2003) on mean crown volume index of herbs, shrubs, trees, mosses, and terrestrial lichens, and mean species richness and species diversity of the herb, shrub, and tree layers. This RM-ANOVA model was also used to test for differences in mean total abundance, mean species richness, and mean species diversity of the small mammal communities and mean abundance of each species, across the six treatment stands. Before 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 (Huynh and Feldt, 1976).

A randomized block two-way analysis of variance (ANOVA)-Model III (Zar, 1999) with factor stand treatment (six habitats) as a fixed effect and factor block as a random effect was used to evaluate differences in mean abundance, mean species diversity, and mean structural diversity of coniferous tree layers in 2003. This ANOVA was also used to compare mean basal area (BA) of total overstory conifers and mean diameter, mean height, and mean CVs of tree size (based on mean diameter and height) of overstory lodgepole pine.

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

Mean diameter of lodgepole pine, the dominant tree species, was significantly ($F_{4,8} = 45.63$; $P < 0.01$) different among stands and ranged from 8 cm in the unthinned stands to 11–13 cm in the thinned and thinned–fertilized stands, 16–17 cm in the mature forest, and 19–23 cm in the old-growth stands (Table 1). Mean total tree heights (m) of lodgepole pine also followed this pattern of significance ($F_{4,8} = 130.13$; $P < 0.01$) but with up to 2 m greater height in the thinned, thinned–fertilized, and unthinned stands at the Kelowna sites than Summerland sites. Mean tree heights of pine ranged from 18–20 m for pine in the mature and old-growth stands to 6–8 m in the three young pine stands (Table 1). The other overstory coniferous species were in the mature and old-growth stands with mean diameters ranging from 11 to 33 cm and mean

Table 1
Mean ($n = 3$ replicate sites) ± SE diameter (cm), height (m), basal area (m^2/ha), and stand density of overstory (>3 m height) coniferous trees, and abundance and composition of understory (<3 m height) conifers and results of analyses at the three study areas, British Columbia. Mean values followed by different letters are significantly different by DMRT.

Parameter and species[a]	YP	Th	Th + F	UnTh	MF	OG	Analysis	
							$F_{4,8}$	P
Overstory conifers								
Mean diameter								
Pl	–	11.2 c ± 0.4	13.4 c ± 0.3	8.0 d ± 0.7	16.9 b ± 0.5	21.2 a ± 1.3	45.63	<0.01
DF	–	–	–	–	23.1 ± 1.8	31.4 ± 4.1	–	–
Sal	–	–	–	–	11.4 ± 1.0	22.2 ± 1.5	–	–
Sp	–	–	–	–	12.7 ± 1.9	33.5	–	–
Mean height								
Pl	–	7.2 c ± 0.5	7.9 c ± 0.6	6.6 c ± 0.6	18.0 b ± 0.6	20.0 a ± 0.8	130.13	<0.01
DF	–	–	–	–	19.0 ± 1.7	21.5 ± 1.2	–	–
Sal	–	–	–	–	11.5 ± 1.3	19.9 ± 2.9	–	–
Sp	–	–	–	–	13.2 ± 2.1	23.9	–	–
Basal area	–	9.51 c ± 0.26	12.72 c ± 1.40	27.31 b ± 4.85	41.20 a ± 3.85	41.67 a ± 4.91	30.81	<0.01
Density (stems/ha)	–	1078 b ± 34	1082 b ± 89	6263 a ± 2033	2217 b ± 226	830 b ± 95	6.65	<0.01

Parameter and species[a]	YP	Th	Th + F	UnTh	MF	OG	Analysis	
							$F_{5,10}$	P
Understory conifers								
0–1 m height class	7657 ± 5742	853 ± 164	188 ± 46	235 ± 81	433 ± 268	3330 ± 1695	1.51	0.27
1–2 m height class	2620 a ±1063	829 b ±222	504 b ±175	505 b ±194	533 b ±115	423 b ±294	3.54	0.04
2–3 m height class	393 ± 231	291 ± 76	307 ± 43	997 ± 500	293 ± 33	143 ± 114	1.53	0.27
Total conifers	10673 ± 4696	3051 ± 416	2082 ± 341	8000 ± 2682	3476 ± 339	4726 ± 2059	2.60	0.09
Composition (%)								
Lodgepole pine	94.8	68.3	68.9	84.1	37.7	4.3	–	–
Douglas-fir	0.5	4.0	3.2	1.0	2.9	34.9	–	–
Subalpine fir	4.0	22.2	19.5	11.9	46.5	60.5	–	–
Interior spruce	0.7	3.7	2.1	1.5	12.9	0.3	–	–
Western larch	0.0	1.8	6.3	1.5	0.0	0.0	–	–

YP, young plantation; Th, thinned; Th + F, thinned and fertilized; UnTh, unthinned; MF, mature forest; OG, old-growth.
[a] Pl, lodgepole pine; DF, Douglas-fir; Sal, subalpine fir; Sp, spruce.

heights ranging from 11 to 24 m. Subalpine fir and interior spruce had smaller mean diameters and heights in the mature than old-growth stands (Table 1).

Mean BA of all overstory coniferous trees was significantly ($F_{4,8}$ = 30.81; $P < 0.01$) different among stands with the highest (DMRT; P = 0.05) BA in the mature and old-growth stands (Table 1). Mean overall densities of coniferous trees were similar ($P > 0.05$) among treatment stands in the 0–1 m and 2–3 m height classes but were significantly different in the 1–2 m ($F_{5,10}$ = 3.54; P = 0.04) and >3 m ($F_{4,8}$ = 6.65; $P < 0.01$) height classes (Table 1). The young plantation and old-growth stands had very high but variable densities of lodgepole pine and subalpine fir, respectively, in the 0–1 m height class (Table 1). In the >3 m height class (overstory trees), mean tree density (stems/ha) was significantly higher (DMRT; P = 0.05) in the unthinned (6263) stand than the other stands. Lodgepole pine was the dominant tree species in the four young stand treatments, with pine and subalpine fir prominent in the mature forest, and Douglas-fir and subalpine fir in the old-growth stands (Table 1).

Mean species diversity of all coniferous tree layers was significantly ($F_{5,10}$ = 5.47; $P < 0.01$) different among stands with the thinned, thinned–fertilized, and mature forest stands having the highest (DMRT; P = 0.05) diversity, followed by the unthinned, old-growth, and young plantation sites (Fig. 4a). Mean structural diversity of all conifers also was significantly ($F_{5,10}$ = 3.60; P = 0.04) different among stands with the thinned and thinned–fertilized stands having a similar diverse assemblage of coniferous stand structure as the mature and old-growth forests (Fig. 4b).

Mean species diversity of overstory conifers was similar ($F_{4,8}$ = 1.67; P = 0.25) among stands (Fig. 5a). Another measure of structural diversity is variation in tree sizes for the conifers in each stand, based on the coefficient of variation in diameter and height. The mean coefficient of variation for diameter was significantly ($F_{4,8}$ = 16.20; $P < 0.01$) different among stands. The unthinned stand had the highest (DMRT; P = 0.05) variation in tree diameters, followed by the thinned, thinned–fertilized, and mature stands (Fig. 5b). The old-growth stands had the lowest (DMRT; P = 0.05) range of tree diameters, similar to that of the thinned–fertilized stands. Mean coefficient of variation for tree height was similar ($F_{4,8}$ = 2.77; P = 0.10) among stands (Fig. 5c).

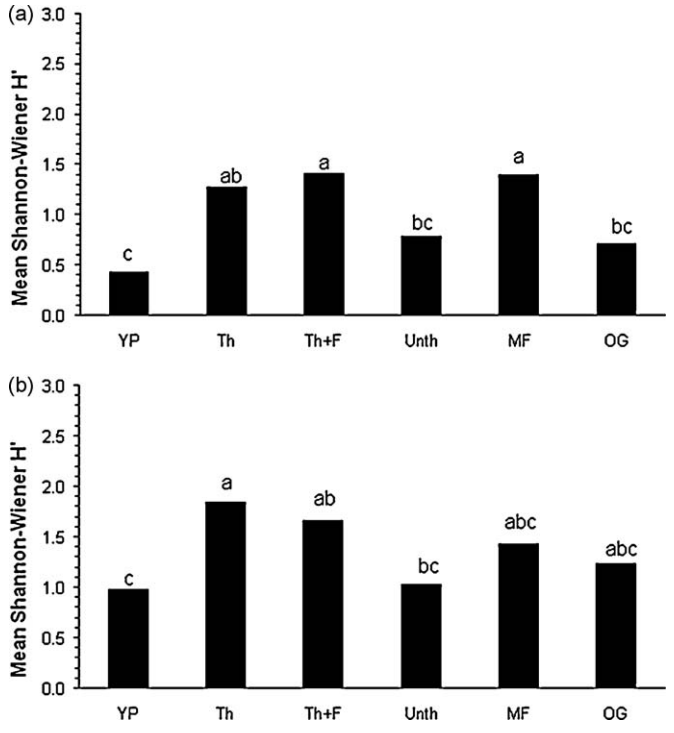

Fig. 4. Mean Shannon–Wiener (H′) diversity of (a) all conifer species and (b) structural diversity of all conifers. Histograms with different letters are significantly different by Duncan's multiple range test (DMRT). YP, Young plantation. Th, thinned; Th + F, thinned and fertilized; Unth, unthinned; MF, mature forest; OG, old-growth forest.

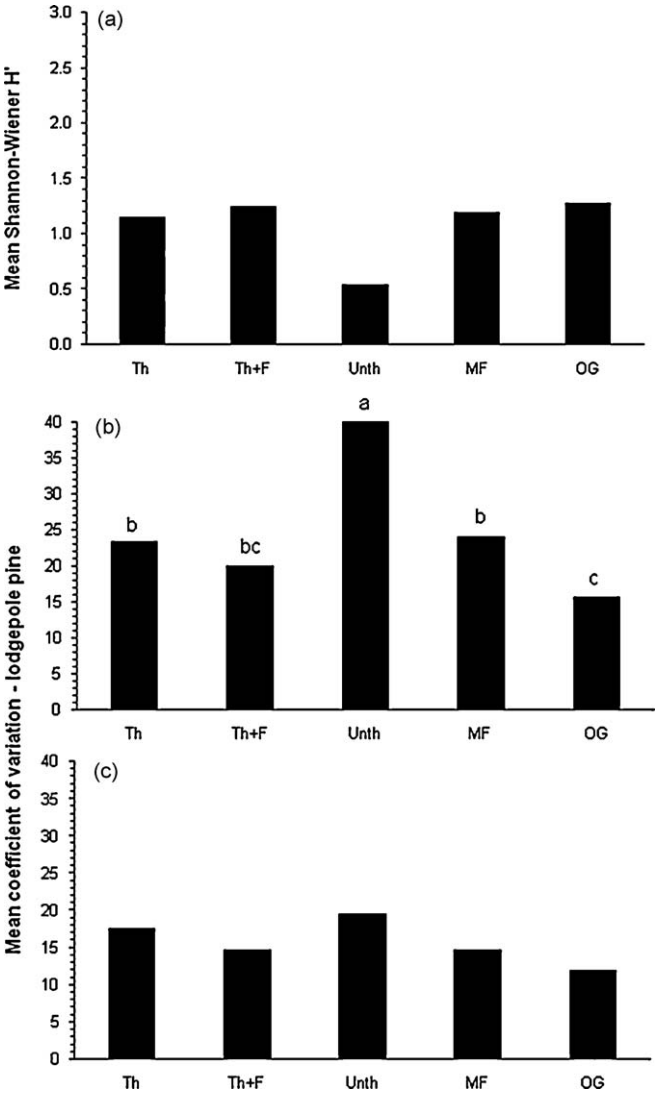

Fig. 5. (a) Mean Shannon–Wiener (H′) species diversity of the >3 m layer, plus mean coefficient of variation of lodgepole pine (b) diameter, and (c) height in the >3 m layer. Histograms with different letters are significantly different by Duncan's multiple range test (DMRT). Th, thinned; Th + F, thinned and fertilized; Unth, unthinned; MF, mature forest; OG, old-growth forest.

3.2. Understory vegetation

Mean total crown volume index of herbs was significantly ($F_{5,10}$ = 5.31; P = 0.01) different among stands, and seemed to change significantly ($F_{4,48}$ = 10.05; $P < 0.01$) with time, initially increasing and then declining (Table 2). The thinned–fertilized stands had the highest (DMRT; P = 0.05) volume of herbs with the unthinned stands similar in herb volume, but intermediate with the other four stands. Mean volume of herbs ranged from 1.7 to 2.3 times as much in the thinned–fertilized than unthinned stands. Similarly, this range expanded from 3.6 to 175.4 times as much herb biomass in the thinned–fertilized than other four stands (Table 2).

Prominent herbaceous species in the four young managed stands included fireweed (*Epilobium angustifolium*), yarrow (*Achillea*

Table 2
Mean ± SE (n = 3 replicate sites) abundance (crown volume index) in each year and results of repeated measures analysis of variance (RM-ANOVA). Columns of mean values with different letters are significantly different by Duncan's multiple range test (DMRT), adjusted for multiple contrasts. F-values identified by '*' were calculated using an H–F correction factor, which decreased the stated degrees of freedom due to correlation among repeated measures.

Attribute and year	Site						RM-ANOVA results					
	YP	Th	Th + F	UnTh	MF	OG	Site		Time		Site × time	
							$F_{5,10}$	P	$F_{4,48}$	P	$F_{20,48}$	P
Herbs	**BC**	**BC**	**A**	**AB**	**C**	**BC**	5.31	0.01	10.05	<0.01	1.18	0.31
1999	7.11 ± 1.00	7.43 ± 0.54	40.65 ± 18.76	24.41 ± 6.93	0.18 ± 0.10	6.98 ± 3.49						
2000	16.32 ± 1.75	17.72 ± 3.94	63.15 ± 24.78	27.95 ± 3.33	0.36 ± 0.23	10.39 ± 5.27						
2001	14.51 ± 1.76	14.86 ± 2.56	57.13 ± 25.13	27.80 ± 7.15	0.33 ± 0.18	9.44 ± 5.09						
2002	12.20 ± 3.59	10.34 ± 0.96	34.52 ± 14.90	16.06 ± 1.80	0.24 ± 0.12	5.90 ± 3.33						
2003	9.23 ± 2.15	7.96 ± 0.78	35.81 ± 18.59	16.70 ± 3.14	0.20 ± 0.10	5.20 ± 2.49						
Shrubs							1.50	0.27	6.29	<0.01	0.82	0.68
1999	2.72 ± 0.74	11.51 ± 4.78	5.49 ± 1.26	14.71 ± 8.02	2.30 ± 0.68	6.44 ± 2.37						
2000	4.95 ± 0.35	13.98 ± 5.63	8.86 ± 1.98	16.54 ± 8.62	2.93 ± 0.78	6.88 ± 1.90						
2001	7.95 ± 1.15	16.04 ± 4.68	11.48 ± 3.82	18.40 ± 9.39	3.56 ± 0.72	8.92 ± 2.85						
2002	9.30 ± 2.84	15.82 ± 4.05	7.81 ± 1.10	14.07 ± 7.21	3.74 ± 1.03	7.65 ± 1.80						
2003	8.48 ± 1.65	14.77 ± 4.64	11.47 ± 3.85	14.85 ± 8.34	2.78 ± 0.62	7.66 ± 2.02						
Trees	**E**	**D**	**CD**	**AB**	**A**	**BC**	33.65	<0.01	18.56	<0.01	1.35	0.19
1999	3.22 ± 1.83	46.54 ± 7.62	57.43 ± 5.86	136.73 ± 34.25	181.40 ± 18.29	137.97 ± 14.90						
2000	4.40 ± 0.30	70.99 ± 10.63	90.28 ± 9.77	192.63 ± 31.14	235.07 ± 45.63	152.57 ± 8.73						
2001	6.82 ± 0.77	102.41 ± 22.41	134.32 ± 16.59	200.61 ± 24.85	288.22 ± 22.84	198.49 ± 19.86						
2002	12.11 ± 1.34	94.73 ± 13.96	119.06 ± 8.55	201.97 ± 18.46	246.16 ± 7.36	165.78 ± 16.44						
2003	20.52 ± 5.21	101.98 ± 11.28	149.79 ± 13.12	204.06 ± 28.08	246.07 ± 22.46	141.06 ± 9.93						
Mosses							2.90*	0.07	1.20	0.31	0.35	0.98
1999	0.91 ± 0.63	2.95 ± 1.19	0.63 ± 0.14	1.90 ± 0.50	7.90 ± 1.86	6.15 ± 3.29						
2000	0.96 ± 0.54	2.07 ± 1.28	0.38 ± 0.10	1.92 ± 0.74	7.75 ± 2.26	5.36 ± 3.56						
2001	1.65 ± 0.96	3.46 ± 1.77	0.48 ± 0.25	1.72 ± 0.41	7.25 ± 1.26	5.67 ± 3.57						
2002	1.75 ± 1.03	2.12 ± 1.47	0.35 ± 0.10	0.83 ± 0.18	6.41 ± 1.11	5.19 ± 3.80						
2003	1.46 ± 0.86	2.27 ± 1.66	0.23 ± 0.06	0.98 ± 0.30	6.07 ± 1.75	5.42 ± 3.64						
Lichens	**B**	**B**	**B**	**B**	**A**	**A**	8.91*	<0.01	1.89	0.17	2.09	0.07
1999	0.13 ± 0.11	0.22 ± 0.00	0.15 ± 0.03	0.22 ± 0.07	1.26 ± 0.41	0.86 ± 0.24						
2000	0.22 ± 0.09	0.23 ± 0.02	0.18 ± 0.02	0.28 ± 0.03	0.67 ± 0.16	0.41 ± 0.04						
2001	0.22 ± 0.01	0.27 ± 0.04	0.14 ± 0.04	0.26 ± 0.02	0.53 ± 0.10	0.45 ± 0.08						
2002	0.23 ± 0.00	0.22 ± 0.03	0.16 ± 0.04	0.25 ± 0.03	0.46 ± 0.04	0.34 ± 0.06						
2003	0.24 ± 0.02	0.26 ± 0.01	0.14 ± 0.03	0.26 ± 0.01	0.45 ± 0.08	0.31 ± 0.03						

YP, young plantation; Th, thinned; Th + F, thinned and fertilized; UnTh, unthinned; MF, mature forest; OG, old-growth.

millefolium), wild strawberry (*Fragaria virginiana*), pinegrass (*Calamagrostis rubescens*), other grasses, and arctic lupine (*Lupinus arcticus*). Herb species found in the mature or old-growth stands only included Queen's cup (*Clintonia uniflora*), rattlesnake plantain (*Goodyera oblongifolia*), slender hawkweed (*Hieracium gracile*), rein-orchid (*Plantanthera* spp.), pink wintergreen (*Pyrola asarifolia*), large-leaved avens (*Geum macrophyllum*), and one-leaved foamflower (*Tiarella unifoliata*). Species of herbs common to the natural unmanaged stands and the intensively managed stands were rosy pussytoes (*Antennaria microphylla*), field pussytoes (*Antennaria neglecta*), racemose pussytoes (*Antennaria racemosa*), heart-leaved arnica (*Arnica cordifolia*), purple-leaved willow-herb (*Epilobium ciliolatum*), northern gentian (*Gentianella amarella*), white-flowered hawkweed (*Hieracium albiflorum*), orange hawkweed (*Hieracium aurantiacum*), one-sided wintergreen (*Orthilia secunda*), mountain sweet-cicely (*Osmorhiza chilensis*), violet (*Viola* spp.), and three-leaved foamflower (*Tiarella trifoliata*).

Mean total crown volume index of shrubs was similar ($F_{5,10}$ = 1.50; P = 0.27) among stands, but with a significant ($F_{4,48}$ = 6.29; $P < 0.01$) increase in biomass through time (Table 2). Several prominent shrub species were common to the natural unmanaged and intensively managed stands, including Sitka alder, willow, kinnikinnick (*Arctostapylos uva-ursi*), Prince's pine (*Chimaphila umbellata*), twinflower (*Linnaea borealis*), red twinberry (*Lonicera utahensis*), falsebox (*Paxistima myrsinites*), birch-leaved spiraea (*Spiraea betulifolia*), black huckleberry (*Vaccinium membranaceum*), and grouseberry (*V. scoparium*).

Mean total crown volume index of trees was significantly ($F_{5,10}$ = 33.65; $P < 0.01$) different among stands, and also generally increased significantly ($F_{4,48}$ = 18.56; $P < 0.01$) from 1999 to 2003 (Table 2). Not surprisingly, tree crown volume index was highest (DMRT; P = 0.05) in the unthinned, mature, and old-growth stands than the other three stands. However, mean crown volume index was similar in the thinned–fertilized and old-growth stands, particularly as these managed stands continued to grow from 1999 to 2003.

Mean abundance of mosses appeared highest in the mature and old-growth stands, but this difference was not formally significant (P = 0.07). However, moss volume ranged from 2.8 to 17.3 times higher in the mature and old-growth stands than other stands (Table 2). Mean abundance of terrestrial lichens was significantly ($F_{5,10}$ = 8.91; $P < 0.01$) different among stands, following the pattern of moss abundance, being highest (DMRT; P = 0.05) in the mature and old-growth stands (Table 2).

There was a total of 73 species of herbs, 32 species of shrubs, and 10 species of trees sampled during 1999–2003. Mean species richness of herbs was similar ($F_{5,10}$ = 2.84; P = 0.08) among stands, and changed significantly ($F_{4,48}$ = 2.79; P = 0.05) with time, increasing initially and then declining (Table 3). Mean species richness of shrubs was significantly ($F_{5,10}$ = 3.48; P = 0.04) different among stands with the lowest (DMRT; P = 0.05) number of species in the mature stand than other stands. Mean species richness of trees was similar ($F_{5,10}$ = 1.47; P = 0.28) among stands (Table 3). Mean total species richness of vascular plants was significantly ($F_{5,10}$ = 4.44; P = 0.02) different among stands, being highest (DMRT; P = 0.05) in the young plantation and young pine stands and lowest in the mature stands (Table 3).

Mean species diversity of herbs ($F_{5,10}$ = 1.37; P = 0.31) and trees ($F_{5,10}$ = 2.18; P = 0.14) were similar among stands (Table 4). Mean

Table 3
Mean ± SE (n = 3 replicate sites) species richness of herbs, shrubs, trees and total vascular plants in each year and results of repeated measures analysis of variance (RM-ANOVA). Columns of mean values with different letters are significantly different by Duncan's multiple range test (DMRT), adjusted for multiple contrasts. F-values identified by '*' were calculated using an H–F correction factor, which decreased the stated degrees of freedom due to correlation among repeated measures.

Attribute and year	Site						RM-ANOVA results					
	YP	Th	Th + F	UnTh	MF	OG	Site		Time		Site × time	
							$F_{5,10}$	P	$F_{4,48}$	P	$F_{20,48}$	P
Herbs							2.84*	0.08	2.79	0.05	0.85	0.63
1999	6.89 ± 1.57	8.22 ± 2.04	8.78 ± 0.99	8.22 ± 0.45	1.66 ± 0.88	4.67 ± 1.84						
2000	7.22 ± 1.75	9.78 ± 2.51	11.56 ± 1.06	11.55 ± 1.35	2.33 ± 1.15	5.44 ± 2.16						
2001	7.33 ± 1.02	9.89 ± 1.93	10.67 ± 2.72	9.67 ± 1.07	3.00 ± 0.84	5.22 ± 2.06						
2002	7.00 ± 1.65	9.00 ± 1.83	9.56 ± 2.51	9.89 ± 1.42	2.89 ± 0.97	5.33 ± 2.03						
2003	6.22 ± 1.83	7.11 ± 1.96	6.34 ± 2.33	8.67 ± 0.58	2.56 ± 1.16	4.78 ± 2.06						
Shrubs	**A**	**A**	**A**	**A**	**B**	**AB**	3.48	0.04	1.03	0.40	0.33	1.00
1999	7.33 ± 0.70	7.22 ± 0.11	6.78 ± 0.40	8.11 ± 0.80	4.78 ± 0.62	6.33 ± 0.84						
2000	8.00 ± 0.88	7.78 ± 0.22	7.00 ± 0.19	8.55 ± 0.78	4.67 ± 0.51	6.56 ± 0.68						
2001	7.11 ± 0.97	7.67 ± 0.51	7.11 ± 0.56	8.89 ± 0.67	5.11 ± 0.95	7.11 ± 0.73						
2002	8.00 ± 0.84	7.56 ± 0.29	7.22 ± 0.11	8.34 ± 0.88	5.00 ± 0.84	7.00 ± 0.77						
2003	7.44 ± 1.11	7.56 ± 0.68	6.56 ± 0.29	8.22 ± 0.49	4.89 ± 1.06	6.89 ± 0.67						
Trees							1.47	0.28	0.85	0.50	0.90	0.59
1999	2.78 ± 0.22	4.22 ± 1.13	4.00 ± 1.07	3.78 ± 0.29	3.44 ± 0.29	2.33 ± 0.38						
2000	3.22 ± 0.40	4.44 ± 1.06	3.78 ± 0.91	3.78 ± 0.29	3.67 ± 0.33	2.34 ± 0.33						
2001	3.00 ± 0.33	4.78 ± 1.24	4.00 ± 0.88	4.00 ± 0.33	3.56 ± 0.29	2.34 ± 0.33						
2002	3.33 ± 0.38	4.45 ± 1.22	4.11 ± 0.97	3.55 ± 0.40	3.33 ± 0.33	2.22 ± 0.29						
2003	3.44 ± 0.48	4.44 ± 1.06	4.22 ± 1.06	3.44 ± 0.29	3.44 ± 0.29	2.45 ± 0.40						
Total	**AB**	**AB**	**AB**	**A**	**C**	**BC**	4.44	0.02	7.37	<0.01	0.82	0.68
1999	17.00 ± 2.34	19.67 ± 0.88	19.55 ± 0.89	20.11 ± 1.28	9.88 ± 1.28	13.33 ± 2.80						
2000	18.44 ± 2.94	22.00 ± 1.65	22.33 ± 0.70	23.88 ± 2.42	10.66 ± 1.26	14.34 ± 2.59						
2001	17.44 ± 2.00	22.33 ± 1.20	21.78 ± 1.75	22.55 ± 2.05	11.67 ± 1.50	14.67 ± 2.65						
2002	18.33 ± 2.73	21.00 ± 1.17	20.89 ± 2.11	21.78 ± 2.47	11.22 ± 1.66	14.56 ± 2.51						
2003	17.11 ± 3.21	19.11 ± 1.28	17.11 ± 2.08	20.33 ± 1.17	10.89 ± 1.98	14.12 ± 2.51						

YP, young plantation; Th, thinned; Th + F, thinned and fertilized; UnTh, unthinned; MF, mature forest; OG, old-growth.

species diversity of shrubs was significantly ($F_{5,10}$ = 4.61; P = 0.02) different among stands with the mature forests again having the consistently lowest (DMRT; P = 0.05) values than the other stands. For the three years (2001–2003) that total species diversity of vascular plants was calculated, there seemed to be a gradient from highest diversity in the young plantations to lowest in the old-growth forests, but this result was not formally significant (P = 0.06) (Table 4).

Table 4
Mean ± SE (n = 3 replicate sites) species diversity of herbs, shrubs, trees, and total vascular plants in each year and results of repeated measures analysis of variance (RM-ANOVA). Columns of mean values with different letters are significantly different by Duncan's multiple range test (DMRT), adjusted for multiple contrasts. F-values identified by '*' were calculated using an H–F correction factor, which decreased the stated degrees of freedom due to correlation among repeated measures.

Attribute and year	Site						RM-ANOVA results					
	YP	Th	Th + F	UnTh	MF	OG	Site		Time		Site × time	
							$F_{5,10}$	P	$F_{4,48}$	P	$F_{20,48}$	P
Herbs							1.37	0.31	2.06	0.10	1.18	0.31
1999	1.26 ± 0.23	2.06 ± 0.28	1.61 ± 0.43	1.41 ± 0.25	0.53 ± 0.38	0.97 ± 0.43						
2000	1.09 ± 0.23	1.99 ± 0.33	1.58 ± 0.47	1.58 ± 0.09	0.97 ± 0.53	1.01 ± 0.43						
2001	1.03 ± 0.18	2.01 ± 0.29	1.59 ± 0.49	1.29 ± 0.23	1.15 ± 0.28	0.98 ± 0.37						
2002	1.15 ± 0.33	2.00 ± 0.30	1.59 ± 0.62	1.52 ± 0.12	1.02 ± 0.39	1.39 ± 0.35						
2003	0.97 ± 0.36	1.82 ± 0.20	1.32 ± 0.43	1.21 ± 0.29	0.84 ± 0.46	1.24 ± 0.45						
Shrubs	**A**	**A**	**AB**	**A**	**B**	**A**	4.61	0.02	1.94	0.12	0.94	0.54
1999	2.35 ± 0.23	1.93 ± 0.20	1.91 ± 0.18	2.16 ± 0.06	1.44 ± 0.13	1.90 ± 0.09						
2000	2.08 ± 0.17	2.05 ± 0.14	1.86 ± 0.07	2.18 ± 0.08	1.51 ± 0.08	2.00 ± 0.06						
2001	1.89 ± 0.19	1.84 ± 0.17	1.81 ± 0.06	2.16 ± 0.04	1.48 ± 0.09	2.02 ± 0.05						
2002	1.94 ± 0.17	1.84 ± 0.11	1.75 ± 0.08	2.09 ± 0.04	1.43 ± 0.11	2.00 ± 0.11						
2003	2.00 ± 0.18	1.90 ± 0.22	1.66 ± 0.04	2.10 ± 0.13	1.49 ± 0.12	1.93 ± 0.02						
Trees							2.18	0.14	1.44	0.24	0.61	0.88
1999	1.01 ± 0.21	0.80 ± 0.36	0.75 ± 0.27	0.66 ± 0.25	1.38 ± 0.10	0.70 ± 0.25						
2000	1.16 ± 0.15	0.82 ± 0.36	0.77 ± 0.28	0.67 ± 0.23	1.52 ± 0.09	0.61 ± 0.14						
2001	1.04 ± 0.18	0.73 ± 0.31	0.77 ± 0.26	0.74 ± 0.22	1.47 ± 0.09	0.68 ± 0.17						
2002	1.00 ± 0.17	0.70 ± 0.30	0.74 ± 0.22	0.75 ± 0.14	1.41 ± 0.11	0.61 ± 0.20						
2003	0.81 ± 0.20	0.71 ± 0.32	0.78 ± 0.30	0.61 ± 0.21	1.47 ± 0.08	0.61 ± 0.21						
Total							3.16	0.06	5.08	0.01	0.61	0.79
2001	2.67 ± 0.20	1.93 ± 0.15	1.91 ± 0.37	1.70 ± 0.47	1.58 ± 0.09	1.32 ± 0.24						
2002	2.65 ± 0.26	1.80 ± 0.17	1.75 ± 0.32	1.53 ± 0.31	1.52 ± 0.13	1.23 ± 0.22						
2003	2.39 ± 0.23	1.71 ± 0.18	1.67 ± 0.45	1.39 ± 0.42	1.57 ± 0.07	1.23 ± 0.11						

YP, young plantation; Th, thinned; Th + F, thinned and fertilized; UnTh, unthinned; MF, mature forest; OG, old-growth.

Table 5
Mean ± SE (n = 3 replicate stands) species richness and diversity of small mammals during 1999–2003 and results of RM-ANOVA. Columns of mean values with different letters are significantly different by Duncan's multiple range test (DMRT), adjusted for multiple contrasts. F-values identified by '*' were calculated using an H–F correction factor, which decreased the stated degrees of freedom due to correlation among repeated measures.

Attribute and year	Site						RM-ANOVA results					
	YP	Th	Th + F	UnTh	MF	OG	Site		Time		Site × time	
							$F_{5,10}$	P	$F_{4,48}$	P	$F_{20,48}$	P
Species richness							0.83	0.56	21.24	<0.01	0.99	0.49
1999	4.22 ± 0.24	3.28 ± 0.55	3.45 ± 0.36	3.50 ± 0.29	3.28 ± 0.15	2.67 ± 0.00						
2000	4.22 ± 0.40	3.89 ± 0.24	4.06 ± 0.31	4.45 ± 0.15	3.72 ± 0.20	3.50 ± 0.50						
2001	4.11 ± 0.49	4.22 ± 0.64	4.61 ± 0.70	3.78 ± 0.22	3.28 ± 0.39	3.78 ± 0.40						
2002	4.07 ± 0.59	3.60 ± 0.31	4.20 ± 0.72	3.73 ± 0.27	3.40 ± 0.20	3.20 ± 0.12						
2003	2.83 ± 0.60	2.00 ± 0.29	2.00 ± 0.00	2.17 ± 0.17	2.83 ± 0.17	2.50 ± 0.29						
Shannon–Wiener							0.50	0.77	10.35	<0.01	0.88	0.61
1999	1.63 ± 0.13	1.27 ± 0.11	1.31 ± 0.10	1.41 ± 0.12	1.48 ± 0.08	1.02 ± 0.00						
2000	1.64 ± 0.16	1.58 ± 0.06	1.65 ± 0.07	1.65 ± 0.19	1.55 ± 0.10	1.47 ± 0.18						
2001	1.60 ± 0.22	1.63 ± 0.20	1.67 ± 0.30	1.43 ± 0.16	1.32 ± 0.22	1.52 ± 0.16						
2002	1.50 ± 0.18	1.44 ± 0.18	1.64 ± 0.25	1.50 ± 0.15	1.47 ± 0.08	1.43 ± 0.13						
2003	1.22 ± 0.22	0.72 ± 0.18	0.90 ± 0.05	1.03 ± 0.09	1.36 ± 0.15	1.07 ± 0.23						
Log-series	**AB**	**A**	**A**	**A**	**AB**	**B**	3.23	0.05	4.96	<0.01	0.74	0.77
1999	1.78 ± 0.11	2.42 ± 0.17	1.88 ± 0.34	1.73 ± 0.20	1.64 ± 0.26	0.98 ± 0.00						
2000	1.55 ± 0.30	2.19 ± 0.06	1.80 ± 0.09	2.95 ± 0.99	1.57 ± 0.05	1.39 ± 0.18						
2001	1.32 ± 0.19	2.62 ± 0.42	2.31 ± 0.38	1.77 ± 0.34	1.21 ± 0.08	1.37 ± 0.10						
2002	1.44 ± 0.29	2.11 ± 0.47	2.17 ± 0.69	1.96 ± 0.36	1.36 ± 0.18	1.10 ± 0.11						
2003	0.91 ± 0.30	1.13 ± 0.14	1.29 ± 0.30	1.04 ± 0.19	0.99 ± 0.09	0.94 ± 0.04						

YP, young plantation; Th, thinned; Th + F, thinned and fertilized; UnTh, unthinned; MF, mature forest; OG, old-growth.

3.3. Small mammal communities

Ten species of small mammals were sampled yielding a total of 3607 individuals. *P. maniculatus* was the most common with a total of 1147 individuals captured. The next most abundant species, in terms of individuals, were *S. monticolus* (618), *M. gapperi* (502), *T. amoenus* (473), *M. pennsylvanicus* (325), *S. cinereus* (218), *M. longicaudus* (205), and *P. intermedius* (79). Seven individual *Z. princeps* and 33 individual *M. erminea* were also captured. Susceptibility to capture was measured by Jolly trappability estimates with mean values of 77.7% for *P. maniculatus*, 80.5% for *M. gapperi*, 58.9% for *T. amoenus*, 53.9% for *M. pennsylvanicus*, and 54.7% for *M. longicaudus*.

Mean species richness ($F_{5,10}$ = 0.83; P = 0.56) and Shannon–Wiener species diversity ($F_{5,10}$ = 0.05; P = 0.77) were similar among stands (Table 5). However, mean log-series species diversity was significantly ($F_{5,10}$ = 3.23; P = 0.05) different among stands, with the three young pine stands higher (DMRT; P = 0.05) than the old-growth stands, and the young plantation and mature forest at an intermediate level (Table 5). Again, the measures of species richness and diversity changed significantly ($P < 0.01$) with time in a similar pattern to total abundance.

Mean total abundance of small mammals per ha was significantly ($F_{5,10}$ = 6.08; $P < 0.01$) different among stands with the young plantations and old-growth stands having the highest (DMRT; P = 0.05) numbers and the thinned stands the lowest (Table 6). Mean numbers of animals changed significantly ($F_{4,48}$ = 6.28; $P < 0.01$) with time, increasing up to 2001 and then declining.

M. gapperi was the microtine species most likely to inhabit later successional stands and this pattern was clearly exhibited in their mean abundance being significantly ($F_{5,10}$ = 16.05; $P < 0.01$) higher (DMRT; P = 0.05) in the mature and old-growth stands than other stands (Table 6 and Fig. 6). Numbers of *M. gapperi* were <2/ha during all years in these younger stands, regardless of treatment. However, in 2000 and 2001, mean numbers of *M. gapperi* were similar in the unthinned and mature stands (Table 6).

Mean abundance of *P. maniculatus* was similar ($F_{5,10}$ = 2.50; P = 0.10) among stands, although mean numbers ranged from 1.1 to 2.6 times higher in the young pine than other stands in 1999 and 2000 (Table 6). *T. amoenus* appeared to have higher mean abundance in the young pine than other stands but this difference only approached significance ($F_{5,10}$ = 2.60; P = 0.09) (Table 6 and Fig. 7). Numbers of chipmunks generally increased from 1999 to 2003 and this change over time was significant ($F_{4,48}$ = 2.77; P = 0.04) (Fig. 7). There were, on average, 2.3–3.4 times as many *T. amoenus* in the young pine than other stands.

Conversely, the other three microtine species responded positively to the understory conditions in the younger stands, particularly mean abundance of *M. pennsylvanicus* which was significantly ($F_{5,10}$ = 7.74; $P < 0.01$) different among stands (Table 6). Meadow vole populations were highest (DMRT; P = 0.05) in the thinned–fertilized stands followed by the thinned stands and young plantations (Fig. 8). A somewhat similar pattern occurred for *M. longicaudus*, but was not significant (Table 6). Both species of *Microtus* declined ($P \leq 0.02$) in numbers each winter from 1999 to 2003. Mean abundance of *P. intermedius* was significantly ($F_{5,10}$ = 5.04; P = 0.01) higher (DMRT; P = 0.05) in all young stands than the mature and old-growth stands where it was not present (Table 6).

Of the two insectivore species, mean abundance of *S. monticolus* was significantly ($F_{5,10}$ = 4.77; P = 0.02) different among stands. Montane shrews were higher (DMRT; P = 0.05) in abundance in the thinned–fertilized stands than in the unthinned, mature, and old-growth stands, but at comparable levels with those populations in the young pine and thinned stands (Table 6 and Fig. 9). Populations of *S. cinereus* also exhibited this pattern in abundance but was not formally significant (P = 0.06) (Table 6). Abundance of insectivore species increased initially and then declined each winter and then significantly ($P < 0.01$) with time from 1999 to 2003. Numbers of *M. erminea* ranged from 4 to 7 individuals per treatment stand over the study.

4. Discussion

4.1. Coniferous stand structure

This study is the first investigation of the effects of PCT and fertilization on stand structure attributes of young (20–25 years)

Table 6
Mean ± SE (n = 3 replicate stands) total abundance per ha and for each species of small mammals during 1999–2003 and results of RM-ANOVA. Columns of mean values with different letters are significantly different by Duncan's multiple range test (DMRT), adjusted for multiple contrasts. F-values identified by '*' were calculated using an H–F correction factor, which decreased the stated degrees of freedom due to correlation among repeated measures.

Species and year	Site						RM-ANOVA results					
	YP	Th	Th + F	UnTh	MF	OG	Site		Time		Site × time	
							$F_{5,10}$	P	$F_{4,48}$	P	$F_{20,48}$	P
Total	**A**	**C**	**BC**	**BC**	**B**	**AB**	6.08	<0.01	6.28*	<0.01	0.85*	0.62
1999	20.82 ± 1.50	9.84 ± 4.02	15.95 ± 1.34	11.88 ± 0.81	12.08 ± 1.71	16.22 ± 0.00						
2000	24.74 ± 2.33	15.46 ± 1.87	18.49 ± 1.57	16.20 ± 3.41	16.71 ± 1.91	17.15 ± 3.31						
2001	31.97 ± 3.61	14.85 ± 3.10	18.78 ± 2.45	17.14 ± 2.04	19.12 ± 3.05	21.78 ± 3.93						
2002	25.05 ± 0.75	12.09 ± 1.64	19.24 ± 4.27	13.75 ± 1.50	16.85 ± 1.55	23.71 ± 6.04						
2003	23.10 ± 1.73	5.95 ± 1.59	6.75 ± 2.75	8.57 ± 1.57	18.62 ± 2.80	13.33 ± 3.93						
Myodes gapperi	**B**	**B**	**B**	**B**	**A**	**A**	16.05	<0.01	0.53*	0.60	2.55*	0.02
1999	0.00 d ± 0.00	0.00 d ± 0.00	0.06 d ± 0.06	1.78 c ± 0.93	4.78 b ± 2.17	10.22 a ± 0.00						
2000	0.11 c ± 0.11	0.00 c ± 0.00	0.00 c ± 0.00	2.39 b ± 1.27	4.00 ab ± 1.39	6.66 a ± 0.89						
2001	0.17 c ± 0.17	0.00 c ± 0.00	0.00 c ± 0.00	1.56 bc ± 0.87	3.08 b ± 1.26	7.84 a ± 2.59						
2002	0.07 b ± 0.07	0.00 b ± 0.00	0.00 b ± 0.00	1.00 b ± 0.53	5.09 a ± 2.12	8.25 a ± 2.05						
2003	0.67 bc ± 0.67	0.00 c ± 0.00	0.00 c ± 0.00	0.00 c ± 0.00	9.12 a ± 2.07	4.17 b ± 2.95						
Peromyscus maniculatus							2.50	0.10	4.24	<0.01	0.69	0.82
1999	7.43 ± 1.88	1.53 ± 0.87	0.56 ± 0.39	3.78 ± 1.02	3.09 ± 0.36	5.33 ± 0.00						
2000	11.00 ± 0.82	3.11 ± 1.59	1.67 ± 1.13	6.25 ± 4.43	7.23 ± 1.13	6.19 ± 0.83						
2001	14.30 ± 1.05	6.27 ± 1.00	3.09 ± 1.64	9.02 ± 3.50	10.54 ± 2.44	6.72 ± 0.74						
2002	6.58 ± 1.43	5.83 ±2.36	6.51 ± 3.26	4.93 ± 2.59	5.17 ± 1.51	7.91 ± 1.38						
2003	10.20 ± 0.85	3.70 ± 1.62	3.17 ± 0.73	4.33 ± 1.30	4.67 ± 2.09	6.33 ± 0.88						
Tamias amoenus							2.60	0.09	2.77	0.04	0.37	0.99
1999	6.77 ± 1.57	2.79 ± 1.27	3.10 ± 1.75	3.76 ± 1.72	3.33 ± 0.24	0.17 ± 0.00						
2000	8.35 ± 3.07	4.87 ± 1.34	3.45 ± 1.97	2.84 ± 0.93	3.81 ± 1.69	1.20 ± 1.04						
2001	11.21 ± 3.07	3.02 ± 1.22	5.20 ± 2.96	4.57 ± 1.75	4.50 ± 1.67	5.17 ± 3.19						
2002	13.40 ± 1.19	4.20 ± 0.64	6.93 ± 3.66	4.69 ± 1.70	6.13 ± 1.42	7.03 ± 3.79						
2003	11.57 ± 2.05	1.92 ± 0.79	3.58 ± 2.10	3.90 ± 0.78	4.83 ± 1.04	2.83 ± 1.74						
Microtus pennsylvanicus	**BC**	**AB**	**A**	**C**	**C**	**C**	7.74	<0.01	4.32	<0.01	1.68	0.07
1999	0.33 ± 0.19	2.96 ± 1.84	6.02 ± 2.07	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00						
2000	0.72 ± 0.64	4.77 ± 2.65	4.87 ± 2.37	0.33 ± 0.25	0.00 ± 0.00	0.00 ± 0.00						
2001	1.72 ± 0.96	2.94 ± 2.24	3.32 ± 1.63	0.45 ± 0.36	0.00 ± 0.00	0.00 ± 0.00						
2002	1.93 ± 0.98	0.20 ± 0.12	1.93 ± 0.74	0.33 ± 0.33	0.00 ± 0.00	0.00 ± 0.00						
2003	0.00 ± 0.00	0.17 ± 0.17	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00						
Microtus longicaudus							1.20	0.37	4.33*	0.02	0.92*	0.55
1999	3.90 ± 3.57	0.89 ± 0.89	3.17 ± 1.64	0.83 ± 0.83	0.00 ± 0.00	0.00 ± 0.00						
2000	1.17 ± 0.79	0.44 ± 0.29	2.33 ± 1.17	1.00 ± 0.76	0.00 ± 0.00	0.00 ± 0.00						
2001	2.13 ± 1.88	0.94 ± 0.58	2.55 ± 1.40	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00						
2002	1.00 ± 1.00	0.07 ± 0.07	0.13 ± 0.13	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00						
2003	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00						
Phenacomys intermedius	**A**	**A**	**A**	**A**	**B**	**B**	5.04	0.01	0.81	0.52	0.21	1.00
1999	0.45 ± 0.28	0.34 ± 0.17	0.39 ± 0.39	0.33 ± 0.19	0.00 ± 0.00	0.00 ± 0.00						
2000	0.28 ± 0.28	0.39 ± 0.15	0.33 ± 0.10	0.33 ± 0.19	0.00 ± 0.00	0.00 ± 0.00						
2001	0.06 ± 0.06	0.22 ± 0.15	0.22 ± 0.05	0.11 ± 0.06	0.00 ± 0.00	0.00 ± 0.00						
2002	0.27 ± 0.27	0.47 ± 0.13	0.33 ± 0.07	0.40 ± 0.31	0.00 ± 0.00	0.00 ± 0.00						
2003	0.17 ± 0.17	0.00 ± 0.00	0.00 ± 0.00	0.33 ± 0.33	0.00 ± 0.00	0.00 ± 0.00						
Sorex monticolus	**AB**	**ABC**	**A**	**BC**	**C**	**C**	4.77	0.02	12.66	<0.01	0.59	0.90
1999	1.61 ± 0.58	0.56 ± 0.06	1.72 ± 0.29	0.28 ± 0.15	0.33 ± 0.25	0.00 ± 0.00						
2000	2.83 ± 0.70	2.67 ± 0.44	4.28 ± 1.24	2.39 ± 0.98	0.78 ± 0.46	1.67 ± 1.01						
2001	2.33 ± 0.48	1.00 ± 0.33	2.83 ± 0.73	1.00 ± 0.59	0.50 ± 0.29	1.11 ± 0.31						
2002	1.60 ± 0.50	1.07 ± 0.27	2.53 ± 1.28	1.80 ± 0.83	0.33 ± 0.18	0.40 ± 0.12						
2003	0.00 ± 0.00	0.17 ± 0.17	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00						
Sorex cinereus							3.06	0.06	3.79	<0.01	0.43	0.98
1999	0.06 ± 0.06	0.72 ± 0.43	0.89 ± 0.53	0.84 ± 0.44	0.50 ± 0.42	0.33 ± 0.00						
2000	0.06 ± 0.06	0.28 ± 0.15	1.55 ± 1.16	0.55 ± 0.15	0.78 ± 0.31	1.22 ± 0.49						
2001	0.00 ± 0.00	0.34 ± 0.17	1.39 ± 0.81	0.44 ± 0.24	0.50 ± 0.19	0.83 ± 0.19						
2002	0.00 ± 0.00	0.13 ± 0.07	0.67 ± 0.41	0.40 ± 0.23	0.00 ± 0.00	0.07 ± 0.07						
2003	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00						
Mustela erminea							0.80	0.57	3.09	0.02	0.56	0.92
1999	0.17 ± 0.10	0.06 ± 0.06	0.00 ± 0.00	0.06 ± 0.06	0.11 ± 0.06	0.17 ± 0.00						
2000	0.22 ± 0.15	0.11 ± 0.06	0.00 ± 0.00	0.11 ± 0.06	0.11 ± 0.06	0.17 ± 0.10						
2001	0.06 ± 0.06	0.11 ± 0.06	0.17 ± 0.10	0.00 ± 0.00	0.00 ± 0.00	0.06 ± 0.06						
2002	0.20 ± 0.12	0.13 ± 0.07	0.13 ± 0.07	0.20 ± 0.12	0.13 ± 0.07	0.07 ± 0.07						
2003	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00						

YP, young plantation; Th, thinned; Th + F, thinned and fertilized; UnTh, unthinned; MF, mature forest; OG, old-growth.

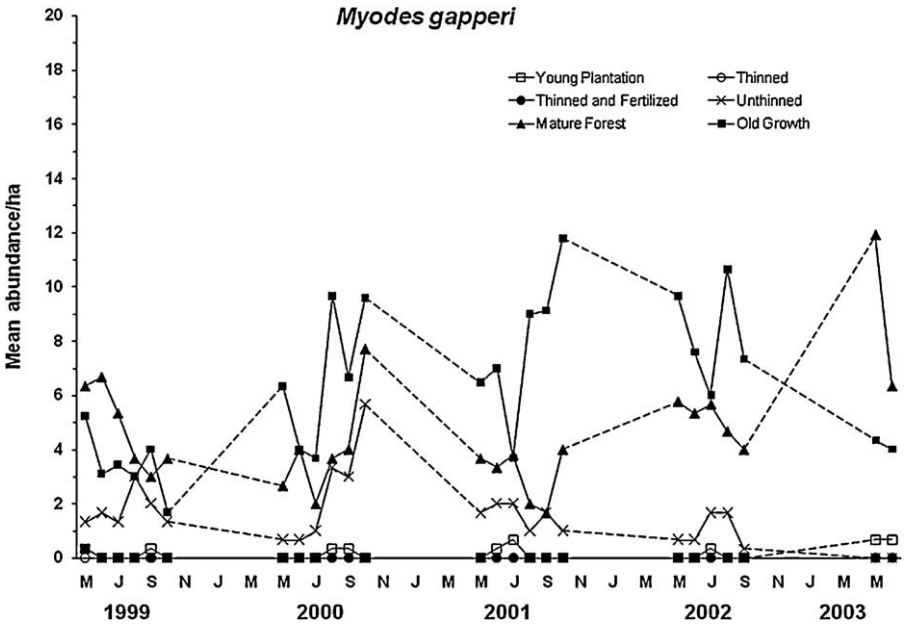

Fig. 6. Mean ($n = 3$) abundance per ha of *Myodes gapperi* in the six treatment stands from 1999 to 2003.

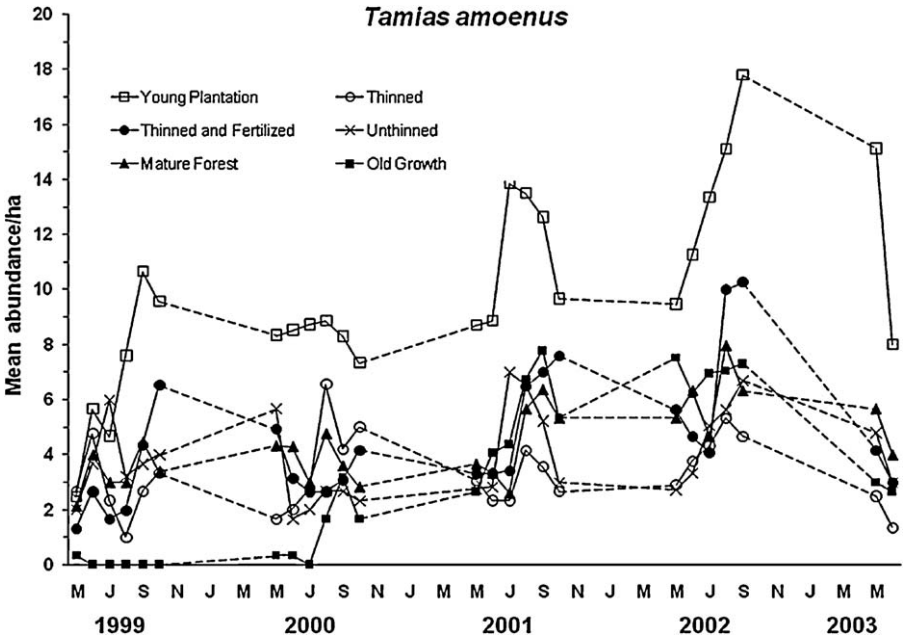

Fig. 7. Mean ($n = 3$) abundance per ha of *Tamias amoenus* in the six treatment stands from 1999 to 2003.

managed forests with comparison to unmanaged stands of the same age and mature and old-growth forests. Characteristics of old-growth forests in the PNW of North America include large old trees, a multi-layered canopy, canopy gaps with patches of understory herbs and shrubs, diverse tree community, numerous large logs and snags, and abundant coarse woody debris (Franklin et al., 1981; Kneeshaw and Burton, 1998). Clearly, the smaller tree sizes (diameter, height, BA) in the young lodgepole pine stands did not support H1, that tree size, abundance, species diversity, and structural diversity would be enhanced by PCT and fertilization treatments to levels found in mature and old-growth forests. However, the similar abundance (stems/ha) of overstory and total conifers did support the abundance part of H1. The mean densities/ha of overstory trees were reasonably similar for the thinned and thinned–fertilized stands (1078–1082) compared with the mature forest (2217) and old-growth (830) stands. In another study at 15 years after heavy PCT ($\leq$1000 stems/ha) of similar pole-sized lodgepole pine stands, overstory densities of old-growth stands ranged from 1370 to 1870 stems/ha with the pine component at 230–730 stems/ha (Sullivan et al., 2006). Marcos et al. (2007) reported similar results for stand density pattern and tree dimensions across a range of plantation ages (2–80 years) and natural forests of Scots pine (*Pinus sylvestris*).

The diversity component of H1 was supported by the similarity in species and structural diversity of total conifers among the various stand treatments. Species diversity of overstory conifers also followed this pattern. The significant CV of tree diameter, but not height, suggested a wider range of tree sizes in the young pine and mature stands than old-growth stands. These layers of conifers, and hence tree-size diversity were similar among stands,

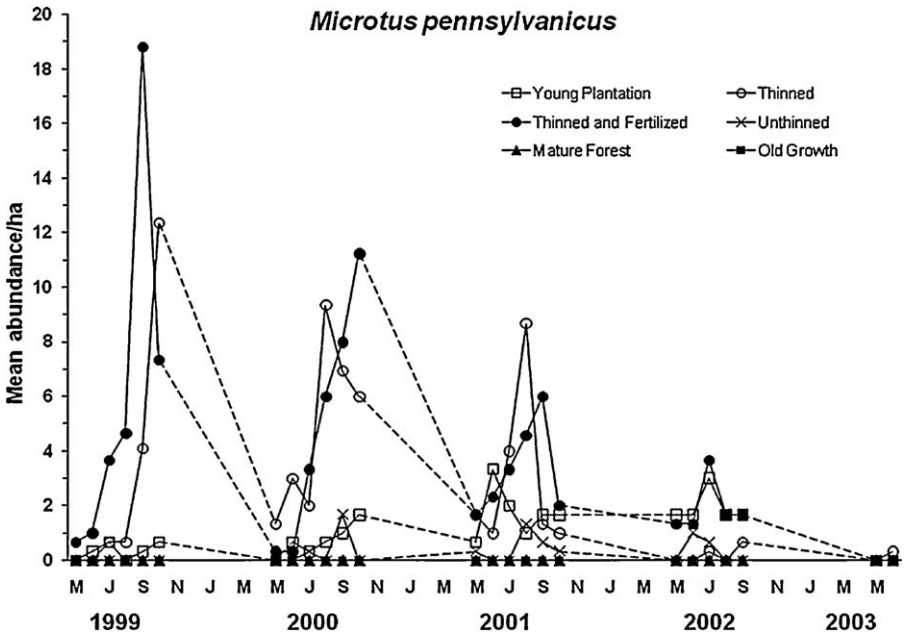

Fig. 8. Mean ($n = 3$) abundance per ha of *Microtus pennsylvanicus* in the six treatment stands from 1999 to 2003.

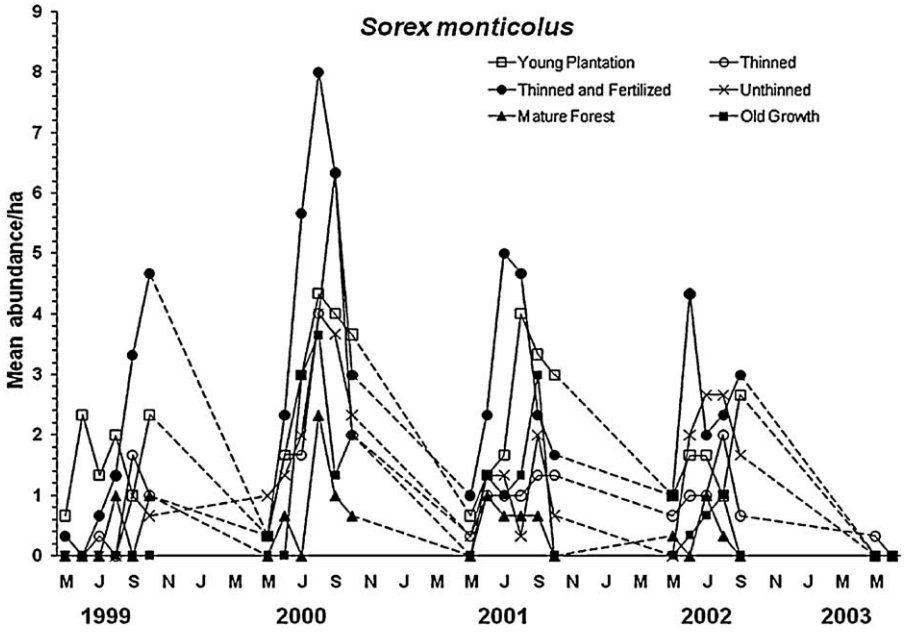

Fig. 9. Mean ($n = 3$) abundance per ha of *Sorex monticolus* in the six treatment stands from 1999 to 2003.

despite the relative differences in tree dimensions. Mean crown volumes of crop trees in the thinned and thinned–fertilized stands (Lindgren et al., 2007) were likely larger than those of the unthinned pine and potentially similar to the mature and old-growth stands as described for other managed and unmanaged stand comparisons (Sullivan et al., 2001, 2006).

4.2. Vegetation communities

Response of understory vegetation to the stand treatments was dominated by the abundance of herbs in the thinned–fertilized stands. Mean volume of herbs in these stands ranged from 2.1 times higher than the unthinned stands to 178.1 times higher than the mature stands. The lack of difference in shrub abundance among stands was similar to the results in older (32–42 years) lodgepole pine stands at 12–15 years post-thinning (Lindgren et al., 2006), and in young (40-year old) Douglas-fir at 20 years post-thinning (Lindh and Muir, 2004). The similar abundance of herbs and shrubs in the thinned and old-growth stands suggested that thinning to 1000 stems/ha may approximate the overstory–understory light and nutrient conditions of the older unmanaged stands. Similar results were reported for understory herbaceous cover in thinned Douglas-fir forests of western Oregon (Bailey et al., 1998). PCT that prescribes a single target density to an entire stand has generally increased the biomass of understory vegetation (Crouch, 1986; Thomas et al., 1999).

The composite abundance of mosses and terrestrial lichens was lower in the young managed stands, particularly the thinned–fertilized, perhaps due to shade and competition by the herb layer. Abundance of mosses in the young stands was best developed in

the thinned stands, reaching 46% of the biomass recorded in the old-growth stands. Similar results were reported in Sullivan et al. (2001) and for mosses, but not for terrestrial lichens, in Lindgren et al. (2006). Because bryophyte diversity in forested ecosystems is related to the number and type of microhabitats (Newmaster et al., 2003), our young stands likely need several decades to develop these attributes (Ramovs and Roberts, 2005). Coniferous plantations generally have fewer bryophytes than natural forests (Newmaster et al., 2006).

The greater total species richness of herbs, shrubs, and trees in the young managed stands than natural mature stands, and similar totals with the old-growth stands suggested that PCT and fertilization did not simplify stand floristics. The similarity in total species diversity of vascular plants, and also of total conifers, supported this conclusion. This pattern was also reported by Lindh and Muir (2004) in young PCT Douglas-fir stands and Bailey et al. (1998) for older commercially thinned Douglas-fir stands. In addition, our managed stands did not encourage establishment of exotic plant species nor contribute to a loss of native species, a result also recorded for older pine stands 12–14 years post-thinning (Lindgren et al., 2006). Although some authors have suggested a connection between exotic species and intensive forest management (Bailey et al., 1998; Newmaster et al., 2006), our stands were remote from source populations of invasive species.

In summary, our results supported the abundance part of H2, that PCT and repeated fertilization of young lodgepole pine stands would enhance abundance and species diversity of vegetation to levels found in mature and old-growth forests, at least for herbs and shrubs, but not for the non-vascular mosses and terrestrial lichens. Species richness and diversity were similar in managed and old-growth forests, and richness was lowest in the mature stands.

4.3. Small mammal communities

The higher total abundance of small mammals in the 4–8-year-old plantations and old-growth stands fits the pattern of changes in mammal abundance with post-harvest succession (Fisher and Wilkinson, 2005). Surprisingly, total abundance was lower in the thinned stands, which contrasted with the higher numbers of small mammals in heavily thinned and old-growth stands than other stands at 10 years after PCT (Sullivan et al., 2001). Similarly, total abundance of individuals was higher in conventionally thinned stands than those with variable-density thinning at 4–5 years post-treatment (Carey and Wilson, 2001) or legacy retention (Wilson and Carey, 2000). In a retrospective study, Suzuki and Hayes (2003) reported more small mammals in thinned than unthinned stands.

Species richness and Shannon–Wiener diversity did not differ among stands in contrast with Sullivan et al. (2001) who reported highest richness and diversity of small mammals in heavily thinned stands of lodgepole pine at 10 years after PCT. Ecke et al. (2002) reported a higher species richness of small mammals in 1–5-year-old stands compared with mature forest in northern Sweden. Although dominated by habitat generalists, species richness of small mammal communities was also highest on recent clearcuts (up to 9–10 years old) in south-central BC (Sullivan et al., 1999; Sullivan and Sullivan, 2001). These results contrast with the high species richness generally reported for old-growth forests, perhaps due to species-specific responses as detailed below.

M. gapperi is an indicator of late successional or old-growth forest conditions in western North America (Merritt, 1981; Nordyke and Buskirk, 1991). Thus, if stand characteristics in the intensively managed juvenile stands begin to converge with those of mature and old-growth forests, *M. gapperi* should appear in comparable abundance. We did not observe this result in our 20–25-year-old stands, at 6–10 years after initiation of treatments. In contrast, Sullivan et al. (2005) reported that in lodgepole pine stands 29–39 years old, and at 12–14 years after PCT, abundance and demographic attributes of *M. gapperi* were similar to old-growth except in years of high numbers. *M. gapperi* appeared to respond to the large-diameter trees, large crowns, diverse coniferous stand structure, and diverse understory vegetation in these heavily thinned stands (Lindgren et al., 2006; Sullivan et al., 2006).

Volume of herbaceous vegetation was enhanced in the thinned and thinned–fertilized stands and likely contributed to the high abundance of *M. pennsylvanicus*, and secondarily *M. longicaudus*. These microtines prefer early successional stages after disturbance with an abundance of herbs and grasses (Reich, 1981; Getz, 1985). *M. longicaudus* also occupies habitats with some open areas and shrub-sapling cover after forest harvesting (Smolen and Keller, 1987). Thus, the abundant plant growth in the thinned and fertilized juvenile lodgepole pine stands appeared to provide ideal habitats for these *Microtus* spp., comparable to that in the young plantations. The presence of *Microtus* in these stands may have competitively displaced *M. gapperi* because the red-backed vole does not compete well with *M. pennsylvanicus*, at least according to experimental studies (Iverson and Turner, 1972; Morris and Grant, 1972). Interestingly, *M. pennsylvanicus* was at very low abundance in all study sites where *M. gapperi* reached levels of abundance and productivity comparable to old-growth forest (Sullivan et al., 2001, 2005).

P. intermedius also occurred in all four young stands, but at low (<1 animal/ha) abundance, typical of this species (McAllister and Hoffman, 1988). Heather voles occupy dry, open coniferous forests with an understory of low shrubs and also moist, mossy meadows (Banfield, 1974). We did not capture this species in the mature or old-growth forests as was also recorded in closed pine and spruce-fir forests in Alberta (Millar et al., 1985). Our observed densities were at the lower end of a range of 0.5–4.3 animals/ha reported in montane forest in southwestern Alberta (Innes and Millar, 1982).

The substantial herb layer in the thinned–fertilized stands provided a suitable microclimate for *S. monticolus* and *S. cinereus*. Although we did not measure relative humidity or soil moisture levels, the heavy cover of fireweed and grasses seemed to maintain relatively moist conditions during summer periods. Invertebrate prey may be associated with a moist microclimate as well as the breakdown of woody debris (Wrigley et al., 1979). *S. monticolus* occurs most often in early successional stages after disturbance, with 85–90% herbaceous ground cover, and also commonly occurred in riparian zones (Gunther et al., 1983; Smith and Belk, 1996). This shrew was reported at densities of 5–12/ha in coastal coniferous forest (Hawes, 1977) and ranged up to 9/ha in seed-tree stands in montane spruce forests (Sullivan et al., 2000) in BC. Our highest mean densities were 8 shrews/ha, with a maximum of 19 shrews/ha in one replicate in 2000. *S. cinereus* also preferred moist habitats in our study and that of Homyack et al. (2005), and utilizes a wide range of vegetation types (Nagorsen, 1996; Whitaker, 2004). In other similar studies, these insectivores were found at comparable numbers across stand treatments (Carey and Wilson, 2001; Sullivan et al., 2001, 2005), although montane shrews were at greater abundance in thinned than legacy stands (Wilson and Carey, 2000).

The moist conditions in the thinned–fertilized stands would seemingly have provided habitat for *M. gapperi* which depends on mesic habitats in coniferous, deciduous, and mixed forests with an abundance of coarse woody debris and consequent moist microclimate and hypogeous fungi as a food source (Merritt, 1981; Ure and Maser, 1982). Understory shrubs and conifers also appear important for this microclimatic condition (Carey and Johnson, 1995; Moses and Boutin, 2001). Presumably, decomposition of woody material and fungal development have not reached levels found in older closed canopy forests.

The habitat generalists, *P. maniculatus* (Banfield, 1974; Carey and Johnson, 1995), and *T. amoenus* (Sutton, 1992), seemed to readily occupy all habitats.

Thus, our H3, that PCT and repeated fertilization of young lodgepole pine stands would enhance abundance and diversity of forest-floor small mammals to levels found in mature and old-growth forests, was supported for total abundance, species richness, and diversity. However, on a species-specific basis, this hypothesis was not supported for *M. gapperi*, but was for the generalist species *P. maniculatus* and *T. amoenus*. The two insectivores were at comparable or higher abundance than in the older unmanaged forests. The three other microtines were early successional vegetation specialists, and hence did not fit the prediction of H3.

5. Conclusions

We investigated the role of PCT and repeated fertilization in enhancing tree growth, vegetative succession, and overall stand structure in young even-aged stands of lodgepole pine. The major question is when do these structural attributes start to converge with those of mature and old-growth forests? Is it in decades or centuries? A summary of the 30 response variables, measured as an inference to biodiversity across the six treatment stands, indicated that 13 variables did not differ among stands. Of the other 17 variables compared between the intensively managed stands and the old-growth stands, the thinned stands were the same or higher in 9/17 cases, and the thinned–fertilized were the same or higher in 11/17 cases.

Compositional differences in coniferous structure between our intensively managed young stands and unmanaged older stands were primarily quantitative rather than qualitative. The managed stands likely will require decades for tree sizes to converge with those in the mature and old-growth forests. Repeated thinning with variable-density prescriptions (Carey and Wilson, 2001) for canopy gaps and spatial heterogeneity, combined with continued fertilization, may accelerate this convergence. Thus, recovery of old-growth composition, both stand structure and aspects of understory vegetation, may be accelerated by stand thinning treatments (see Lindh and Muir, 2004). We further suggest that fertilization, particularly multiple applications, may hasten this structural development.

Our results with *M. gapperi* suggested that considerable further habitat development will be required before the intensively managed stands reach levels of abundance comparable to those in older natural forests. However, in older (31–42 years) PCT lodgepole pine forests, *M. gapperi* populations seemed to be maintained at levels comparable to old-growth. Similarly, in these same older PCT stands, abundance of the northern flying squirrel (*Glaucomys sabrinus*) was the same or higher in thinned (2000 stems/ha) stands than in old-growth (Ransome et al., 2004).

Thus, we conclude that despite quantitative differences in stand structure and species-specific variability between the intensively managed and older natural stands, old-growth attributes seem to be developing at an accelerated rate in response to the PCT and fertilization treatments.

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