SILVA FENNICA
Silva Fennica 44(5) research articles
www.metla.fi/silvafennica · ISSN 0037-5330
The Finnish Society of Forest Science · The Finnish Forest Research Institute

Green-Tree Retention and Life after the Beetle: Stand Structure and Small Mammals 30 Years after Salvage Harvesting

Thomas P. Sullivan, Druscilla S. Sullivan, Pontus M.F. Lindgren and Douglas B. Ransome

Sullivan, T.P., Sullivan, D.S., Lindgren, P.M.F & Ransome, D.B. 2010. Green-tree retention and life after the beetle: Stand structure and small mammals 30 years after salvage harvesting. Silva Fennica 44(5): 749–774.

We report on a retrospective investigation of the impacts of salvage harvesting of lodgepole pine (*Pinus contorta* var. *latifolia* Engelm. ex S. Wats.), killed by an outbreak of mountain pine beetle (*Dendroctonus ponderosae* Hopk.) in the 1970s, with variable retention of Douglas-fir (*Pseudotsuga menziesii* (Mirbel) Franco). Our inference to biodiversity was coniferous stand structure and four mammal species: the southern red-backed vole (*Myodes gapperi* Vigors), common shrew (*Sorex cinereus* Kerr), red squirrel (*Tamiasciurus hudsonicus* Erxleben) and northern flying squirrel (*Glaucomys sabrinus* Shaw). We tested hypotheses that, at 30 years after salvage harvest of beetle-killed lodgepole pine trees, (1) abundance and diversity of stand structure, and (2) abundance of mammal species, will increase with higher levels of green-tree retention (GTR). Stand structure attributes and small mammals were sampled during 2005–2008 in young pine stands, with a range of GTR seed-trees (none, dispersed, and aggregated Douglas-fir), and uncut forest in south-central British Columbia, Canada. Diameters and heights of Douglas-fir and lodgepole pine and basal area of total conifers supported hypothesis (1). Mean abundance of the red-backed vole was consistently higher (2.3 to 6.4 times) in the uncut forest than other stands. Overall mean patterns of abundance for common shrews, red squirrels, and northern flying squirrels were similar among treatment stands. Mean abundance of the red-backed vole supported hypothesis (2), but numbers of the other three species did not. There is "life after the beetle" at 30 years after salvage harvesting, and this was enhanced by GTR.

Keywords biodiversity, ecological indicators, green-tree retention, small mammals, mountain pine beetle, *Pinus contorta, Pseudotsuga menziesii,* salvage harvest, stand structure
Addresses *Sullivan* and *Sullivan*, Department of Forest Sciences, Faculty of Forestry, University of BC, 2424 Main Mall, Vancouver, BC, Canada V6T 1Z4; *Lindgren* and *Ransome*, Applied Mammal Research Institute, 11010 Mitchell Avenue, Summerland, BC, Canada V0H 1Z8
E-mail tom.sullivan@ubc.ca
Received 29 June 2010 **Revised** 2 December 2010 **Accepted** 8 December 2010
Available at http://www.metla.fi/silvafennica/full/sf44/sf445749.pdf

1 Introduction

A massive epidemic of mountain pine beetle (MPB) (*Dendroctonus ponderosae* Hopk.) is currently (2003–present) spreading throughout the range of lodgepole pine (*Pinus contorta* var. *latifolia* Engelm. ex S. Wats.) in British Columbia (B.C.) and extending into Alberta, Canada (Safranayik 2004, Nelson et al. 2006, Shore et al. 2006). Nearly one-half of merchantable pine volume (nearly 600 million m^3) over some 13 million ha had been killed by 2007 (B.C. MoFR 2008). Up to 80% of pine volume is predicted to be lost to MPB by 2015 (B.C. MoFR 2008). To capture some of the economic value affected by this outbreak, substantial salvage logging operations have been, and continue to be, active across large (>1000s ha) landscape units. Salvage logging is essentially very large-scale clearcutting and may result in openings covering 1000s of ha. The potential ecological consequences of salvage logging of forest stands that have been killed by natural disturbances such as beetle outbreaks, wildfire, or windthrow include alteration of populations of organisms, stand structure, and ecological processes and functions (Bunnell et al. 2004, Lindenmayer and Noss 2006, Lindenmayer et al. 2008). In B.C. and other parts of the Pacific Northwest (PNW), there is much controversy as to whether beetle-killed stands should be harvested or left as part of the consequences of natural disturbances.

In this age of concern for conservation of mature and old-growth forests in temperate and boreal vegetation zones, an array of variable retention harvest systems is available to counter the historical practice of clearcutting (Franklin et al. 1997). Variable retention harvests include long-term (at least one rotation) reserves of trees as individuals or in groups within the chosen silvicultural system. These alternative silvicultural systems are more aligned with natural processes by retaining large live trees, snags, and downed logs (coarse woody debris; CWD) after harvest (Franklin et al. 1997, 2002, Bunnell and Dunsworth 2009). Residual live trees increase structural diversity of the regenerating stand and provide attributes of mature forest habitat that develop sooner than in typical even-aged management by clearcutting (McComb et al. 1993, Franklin et al. 2000). In many disturbance events, some pockets of residual live trees are often left, depending on the severity of the disturbance and tree species composition. This pattern of patchy natural disturbance that leaves live trees as individuals and in clumps forms the basis for green-tree retention (GTR). Although GTR has been practiced for the last 15–20 years in the PNW and Europe, we do not know if the long-term goals of developing mature forest habitat and its inherent biodiversity will be achieved within these managed stands (Rosenvald and Lohmus 2008, Aubry et al. 2009).

Large-scale harvest studies in mature, late successional forests and over long periods are lacking (Aubry et al. 1999). However, some retrospective studies in the PNW, investigating potential long-term consequences of GTR in two-tiered (two-aged) stands have been conducted. The effects of GTR on biodiversity include impacts on growth and tree species composition of future forests where past wildfire was used as an analogue for timber harvest (Rose and Muir 1997), canopy lichen communities (Peck and McCune 1997), understory vegetation, and small mammals (North et al. 1996, Sullivan et al. 2000), and stand structural complexity (Zenner 2000). Canopy tree retention and diversity of birds has been reported by Hansen and Hounihan (1996), and others. However, to our knowledge, there are no studies investigating stand structure attributes and responses of a range of small mammal species to a variety of retention levels for residual green trees over the long term (i.e., decades). In a comprehensive review, Rosenvald and Lohmus (2008) concluded that long-term (including retrospective) studies were much needed to further our understanding of the biodiversity aspects of GTR.

A MPB outbreak in the mid-1970's in the southern interior of B.C. resulted in salvage logging of lodgepole pine from mixed pine – Douglas-fir (*Pseudotsuga menziesii* (Mirbel) Franco) stands and mixed pine – western larch (*Larix occidentalis* Nutt.) stands. In pine-leading stands, fir or larch were left as residual standing trees. This seed-tree silvicultural system leaves a variable number of wind-firm seed trees standing singly (dispersed retention), or in groups (aggregated retention), to provide a source of fir or larch regeneration as secondary species to lodgepole pine, which regenerates naturally from abundant cone slash (Smith 1986). This is a relatively widespread practice that has been in place since the early to mid-1970's when lodgepole pine became an important commercial timber species. Because of this relatively long history, it is possible to do a retrospective investigation of the influence of harvesting lodgepole pine on stand structure and biodiversity 30 years after salvage harvesting of beetle-killed timber. Stands with residual green trees, composed of dispersed to aggregated Douglas-fir with understory lodgepole pine, cover several landscapes throughout B.C.'s southern interior, having arisen from harvesting over the past 30 years. Thus, a major question is: how do these stands compare to those uncut in terms of stand structure and development of late seral forest conditions? This question has direct relevance to sustainable forest management for wildlife habitat and biodiversity.

Selecting bio-indicator or management indicator species (MIS) (Smith et al. 2005) that are particularly associated with mature late succession forest types may help determine the effect of structural changes resulting from management practices (Pearce and Venier 2005). The criteria for selection of MIS are usually those species whose populations appear to reflect the "health" of an ecosystem (Landres et al. 1988, Simberloff 1998). Ecosystem health encompasses many habitat features and processes that may be difficult, if not impossible, to measure in field studies. As discussed by Aubry et al. (1991) and Carey (2000), certain forest-floor and arboreal small mammals have relatively complex life histories among terrestrial vertebrates and are good MIS candidates to provide a measure of ecosystem function in temperate coniferous forests. If stable ("healthy") populations of these species occur, then it is likely that several aspects of ecosystem structure and function are intact.

There are several ecological roles associated with small mammals such as consumption of invertebrates (Buckner 1966), distribution of beneficial mycorrhizal fungi (Maser et al. 1978), consumption of plants and plant products (Carey et al. 1999), and serving as prey for a wide variety of avian, reptilian, and mammalian predators (Martin 1994). Examples of species that seem to require late-seral forests, at least for part of their life cycle, are the southern red-backed vole (*Myodes gapperi* Vigors) and common shrew (*Sorex cinereus* Kerr) on the forest-floor (Nordyke and Buskirk 1991, Hallett et al. 2003), and the northern flying squirrel (*Glaucomys sabrinus* Shaw) and red squirrel (*Tamiasciurus hudsonicus* Erxleben) in the arboreal mammals (Smith et al. 2003). The red-backed vole commonly inhabits late successional coniferous and deciduous forests across temperate North America and is an important indicator species of "old forest conditions" (Merritt 1981, Nordyke and Buskirk 1991). The common shrew is sometimes the numerically dominant shrew in closed-canopy forests in at least parts of the inland PNW (Hallett and O'Connell 1997, Sullivan et al. 2008, Oaten and Larsen 2008). Northern flying squirrels and red squirrels play an important role in dispersing spores of ectomycorrhizal fungi when they defecate (Maser et al. 1986, Maser and Maser 1988). This process forms new mycorrhizal colonies enhancing growth and health of trees, and this dispersal is especially important for young tree growth in early seral stages (Cazares et al. 1999, Molina et al. 1999). Both tree squirrels are primary prey of a variety of carnivores and predatory birds (Carey 2000). Consequently, red-backed voles and tree squirrels might prove to be vital links ("keystone species") between critical belowground processes and higher trophic levels, especially in late-seral forests.

Our study was designed to determine the ecological impacts of salvage harvesting lodgepole pine, after an MPB outbreak, with variable retention of Douglas-fir as major stand-level structures to maintain biodiversity over time. This 30-year vision into the future is a unique opportunity to quantify these impacts and provide an inference to biodiversity by using ecological indicators of coniferous stand structure and an array of mammal species (Carey and Harrington 2001, Pearce and Venier 2005). Variable retention in these mixed stands is currently a major method of harvesting throughout the southern interior of B.C. and other inland (Sullivan et al. 2000) and coastal (Aubry et al. 2009, Bunnell and Dunsworth 2009) areas of the PNW as well. What functions will these retained structures provide in future decades? Will stand-level biodiversity be maintained? Can we look 30 years into the future?

Thus, we tested the hypotheses that, at 30 years after salvage harvest of beetle-killed lodgepole pine trees, (1) abundance (e.g., basal area and density of coniferous trees and amount of vegetation) and diversity (species diversity and structural diversity of the herb, shrub, and coniferous tree layers) of various aspects of stand structure, and (2) abundance of several mammalian indicator species, will increase with higher levels of Douglas-fir tree retention. In these hypotheses, response variables should be greater in sites with GTR (variable retention harvest) than in those without GTR (clearcut "salvage" harvest).

2 Materials and Methods

2.1 Study Area

This study was conducted in the Bald Range 25 km west of Summerland in south-central B.C., Canada (49°40'N; 119°53'W). This area is within the Montane Spruce (MS_{dm}) biogeoclimatic zone (Meidinger and Pojar 1991). Topography is rolling hills at 1400 to 1520 m elevation. This zone has 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. The MS landscape has extensive, young and maturing seral stages of lodgepole pine, which have regenerated after wildfire and clearcut harvesting. Hybrid interior spruce (*Picea glauca* (Moench) Voss × *P. engelmannii* Parry) and subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.) 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* Michx.) and black cottonwood (*Populus trichocarpa* T. & G.) are common seral species (Meidinger and Pojar 1991).

Clearcut harvesting of lodgepole pine with dispersed (single or uniform) and aggregated (group) seed-tree reserves of Douglas-fir began in this area in 1977 in response to an outbreak of MPB. The seed-tree silvicultural system was designed to maintain, and perhaps increase, the proportion of Douglas-fir in the regenerated forest. The dominant tree species in these stands is lodgepole pine having regenerated naturally from cone slash after harvesting. Depending on the original composition of the harvested stands and the degree of windthrow damage after harvesting, the number of residual Douglas-fir range from a few trees per ha up to a maximum of approximately 100 trees/ha.

Stands were categorized as: "young pine" (no seed-trees), "dispersed retention" (single seed-trees of fir), "aggregated retention" (group seed-trees of fir) (Fig. 1), and old-growth stands were termed "uncut forest". At the start of our study in 2005, the young pine stands were 28 years old, seed-tree stands had an understory of 28-year-old pine with a Douglas-fir overstory ranging in average age from 116 to 159 years. Uncut forest stands ranged in average age from 80 to 143 years. Area of stands ranged from 16.9 to 22.9 ha in young pine, 16.5 to 24.0 ha in seed-tree, and 10 to 100^+ ha for the old-growth stands. The pine within the young pine and seed-tree stands were pre-commercially thinned to a range of 1371 to 1674 stems/ha in 1985 or 1987.

2.2 Experimental Design

The experimental design was completely randomized with 3 replicates each of (a) young pine (no residual trees), (b) single seed-tree (dispersed retention), (c) group seed-tree (aggregated retention), and (d) uncut stands. These 12 stands were selected on the basis of operational scale, proximity, and reasonable randomization based on location and elevation. Because of the retrospective nature of our study, we could not intersperse the treatment units randomly within the study area. However, there would appear to be little, if any, bias in assignment of treatment units based on past cutting history, subsequent successional development, and availability of particular experimental units with which to test our hypotheses. Because none of these factors was under our control, it could be argued that the treatment units were essentially randomized and spatially segregated to enhance statistical independence (Hurlbert 1984). Stands were separated by a range of 0.2–3.1 km.

Fig. 1. Photograph of site that was clearcut harvested (1978) with seed-tree reserves (aggregated retention) and the same site 30 years later (2008) with regenerated lodgepole pine in the understory and retained Douglas-fir in the overstory.

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) at 20 points randomly located at trap stations on the 9-ha live-trapping grid (for tree squirrels) in each stand in August 2007. For all trees in a given plot, species, dbh (diameter at breast height, 1.3 m above soil surface), and total height were tallied. A fifth class for seed-trees (retained trees at the time of harvesting) was added for the single seed-tree and group seed-tree stands; and for veteran (≥24 cm dbh) trees for the uncut forest stands. Tree layers were defined as "understory" (<3 m height), "overstory" or "dominant layer" (>3 m height), and "seed-tree" (harvested stands) or "veteran layer" (uncut stands). These veteran or "emergent" trees have survived previous wildfire disturbance (old-growth stands) or been retained as seed-trees. Number of snags and decay class were also recorded where present.

Down wood was recorded along two transect lines of 20 m each at five randomly selected points in each stand. As each piece was encountered the following attributes were recorded: (a) species, (b) diameter where line crosses wood (cm), and (c) hardness (5 decay classes). These five decay classes describe a range of decomposition with 1 being a recently fallen log and 5 being a well decomposed log (Maser et al. 1979) Volume of down wood (m^3/ha) was calculated by the method of Van Wagner (1968).

2.4 Understory Vegetation

Understory vegetation was sampled on three 25-m transects, each consisting of five 5-m × 5-m plots, in each of the 12 experimental units. 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 terrestrial 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 cover of the ground was made for each species height class combination within the appropriate nested subplot. Total percentage cover for each layer was also estimated for each subplot. These data were then used to calculate crown volume index (m^3/0.01 ha) for each plant species (Stickney, 1985). 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 a tabular value given for each species and layer. Sampling was done in July–August 2005. Mosses and lichens were not identified to species. Plant species were identified in accordance with Parish et al. (1996) and Hitchcock and Cronquist (1973). Species richness, species diversity and structural diversity were calculated for these data.

2.5 Forest-Floor Small Mammals

Forest-floor small mammals were sampled six times at 4-week intervals from May to October 2005 and 2006, and four times during 2007. Each treatment stand had a trapping grid (1 ha) with 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, with 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 southern red-backed vole, deer mouse (*Peromyscus maniculatus* Wagner), northwestern chipmunk (*Tamias amoenus* Allen), meadow vole (*Microtus pennsylvanicus* Ord), long-tailed vole (*M. longicaudus* Merriam), heather vole (*Phenacomys intermedius* Merriam), western jumping mouse (*Zapus princeps* Allen), montane shrew (*Sorex monticolus* Merriam), common shrew, and short-tailed weasel (*Mustela erminea* L.).

2.6 Tree Squirrels

The red squirrel and northern flying squirrel were sampled at 4- to 6-week intervals in early winter (October–November) and early spring (March–April) in 2006–2008. Each treatment stand had a 9-ha trapping grid with 100 (10 × 10 or 6 × 16 + 4) stations at 30-m intervals with one Tomahawk live-trap (Model 201, Tomahawk Live trap Company, Tomahawk, Wisconsin) equipped with a nest box (1-L plastic jar with coarse brown cotton) at every other station, resulting in ~5 traps/ha. Traps were baited with sunflower seeds (*Helianthus annuus* L.) and set in the evening on day 1 and checked in the morning and afternoon of day 2 and morning of day 3. Monitoring of these mammals commenced in the fall of 2006.

All captured small mammals (except shrews and weasels) were ear-tagged with individually numbered tags (Monel no.1, National Band and Tag Co.) and immediately released at the point of capture (Krebs et al. 1969). Unfortunately, there was a high mortality rate for shrews because of the overnight trapping technique, but this was unavoidable in practice. Shrews that died in traps 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.

2.7 Abundance Estimates

To determine the effects of stand treatments on abundance of the major species, we measured trappability and population density. Jolly trappability was calculated according to the trappability estimate discussed by Krebs and Boonstra (1984).

Population estimates of the southern red-backed vole, red squirrel, northern flying squirrel, deer mouse, and northwestern chipmunk were derived from the Jolly-Seber (J-S) model (Seber 1982, Krebs 1999) with small sample size corrections (Krebs 1991). Number of animals captured was used as the population estimate for the first and last sampling weeks when the J-S estimate was not calculated. The reliability of the J-S model declines when population sizes are very low and no marked animals are captured. In these cases, the total number of individuals captured was used to compare populations of the common shrew, heather vole, and two *Microtus* species.

The two sciurid species occupy home ranges that are considerably larger than those of the forest-floor mammal species, at least in relation to area of treatment stands. Therefore, we calculated effective trapping area (ETA) for each sciurid species in each of the 12 treatment stands. An estimate of ETA was calculated by adding a buffer of one-half the mean maximum distance moved (MMDM) around the area encompassed by the perimeter traps on the 9-ha trapping grid (Wilson and Anderson 1985). Estimates of population size for each species were calculated by dividing the J-S estimates from the respective trapping grids by the ETA. For forest-floor small mammals, ETA was similar among all treatment grids for *M. gapperi* in another study (Sullivan et al. 1999), and hence we used the 1-ha units in this study.

2.8 Diversity Measures

Diversity of vascular plant and forest-floor small mammal communities was measured by species richness and species 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 (S-W) 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 was calculated using the crown volume index for each plant species averaged across the three transects in a given site. Species diversity of understory and overstory coniferous trees was also calculated using the density of trees (stems/ha) for each species within the appropriate height classes averaged across the 20 plots in a given stand. 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.

Diversity of coniferous stand structure (e.g., foliar height diversity) also used the S-W index with coniferous tree species represented by height classes and relative abundance represented by density of trees (stems/ha) in the five height classes. In addition, we used the coefficient of variation (CV) of tree size, based on mean diameter and mean height of the four coniferous tree species, as a measure of tree-size diversity in each stand (Edgar and Burke 2001, Staudhammer and LeMay 2001).

2.9 Statistical Analyses

A one-way analysis of variance (ANOVA) (Zar 1999) was used to determine the effect of harvest treatments on mean crown volume index of herbs, shrubs, mosses, and terrestrial lichens, mean total species richness, and mean total species diversity of the entire plant community (herbs, shrubs, and trees). This ANOVA was also used to evaluate differences in mean abundance, mean species diversity, and mean structural diversity of coniferous tree layers, as well as to compare mean diameter, mean height, mean basal area (BA), mean volume of CWD, and mean CVs of tree size (based on mean diameter and mean height) of the four overstory coniferous tree species.

A repeated measures (RM) ANOVA (SPSS Institute Inc. 2007) was conducted to determine the effects of treatment and time (2005–2008) on mean values of abundance of each small mammal species, total abundance, species richness, and species diversity. 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). Linear regression analysis was used to determine relationships between forest-floor small mammals (mean total abundance, mean species richness, and mean abundances of red-backed voles and common shrews) and habitat structure parameters (structural diversity of total vegetation, down wood, species diversity of conifers, and BA of overstory conifers).

Overall mean ($n=9$; 3 replicates × 3 years) values and 95% confidence intervals (CI) were calculated for abundance of red-backed voles, common shrews, red squirrels, and northern flying squirrels. 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 BA of overstory trees was significantly ($F_{3,8}=8.69$; $P<0.01$) higher in the uncut forest (DMRT; $P=0.05$) than in all three harvested sites, which were similar (Table 1). However, mean density of overstory trees was similar ($F_{3,8}=1.09$; $P=0.41$) among stands ranging from 1402 to 2303 stems/ha (Table 1). The various height classes of understory trees and total conifers also followed this pattern (Table 1). In terms of relative species composition of the four conifers, mean abundance of lodgepole pine was significantly ($F_{3,8}=14.86$; $P<0.01$) different among stands with similar densities (DMRT; $P=0.05$) in the single seed-tree and young pine stands, the single greater than the group seed-tree stands, followed by the uncut forest stands. The other three conifers had similar mean abundances among stands, but with the

Table 1. Mean ($n=3$ replicate sites) ± SE basal area and stand density of overstory (>3 m height) coniferous trees, and abundance of understory (<3 m height) conifers, and abundance and species composition of total conifers, with results of analyses at the Summerland study area, British Columbia. Within a row, values followed by different letters are significantly different.

Parameter	Young pine	Single seed-tree	Group seed-tree	Uncut forest	Analysis	
					$F_{3,8}$	P
Overstory conifers						
Basal area (m^2/ha)	31.44^{b}	30.43^{b}	40.00^{b}	71.34^{a}	8.69	**<0.01**
Density (stems/ha)	1965.0 ± 208.2	2303.3 ± 238.1	1941.7 ± 531.0	1401.7 ± 361.3	1.09	0.41
Species diversity	0.81 ± 0.16	0.77 ± 0.05	0.84 ± 0.13	1.36 ± 0.32	2.14	0.17
Understory conifers (stems/ha)						
0–1 m height class	203.3 ± 97.7	256.7 ± 71.0	488.3 ± 343.4	410.0 ± 121.0	0.48	0.71
1–2 m height class	250.0 ± 135.0	286.7 ± 92.5	276.7 ± 49.1	185.0 ± 74.9	0.24	0.87
2–3 m height class	260.0 ± 35.5	383.3 ± 119.6	206.7 ± 19.2	95.0 ± 35.0	3.34	0.08
Total conifers (stems/ha)	2678.3 ± 134.2	3230.0 ± 164.8	2913.3 ± 243.4	2091.7 ± 498.0	2.62	0.12
Lodgepole pine	1973.3^{ab} ± 73.7	2783.3^{a} ± 86.2	1878.3^{b} ± 64.4	380.0^{c} ± 18.2	14.86	**<0.01**
Douglas-fir	258.3 ± 9.6	213.3 ± 6.6	761.7 ± 26.2	655.0 ± 31.3	1.08	0.41
Subalpine fir	145.0 ± 5.4	143.3 ± 4.4	141.7 ± 4.9	1015.0 ± 48.5	2.01	0.19
Interior Spruce	301.7 ± 11.3	90.0 ± 2.8	131.7 ± 4.5	41.7 ± 2.0	2.47	0.14
Species diversity	1.14 ± 0.20	0.81 ± 0.06	1.18 ± 0.04	1.30 ± 0.22	1.94	0.20
Structural diversity	1.17 ± 0.25	1.42 ± 0.21	1.43 ± 0.24	1.59 ± 0.03	0.73	0.57

Table 2. Mean ($n = 3$ replicate sites) ± SE diameter (cm), height (m), and basal area (BA) (m^2/ha) for the four coniferous species in the >3 m height class (dominant layer) and seed-tree class (veteran layer, Douglas-fir diameter ≥24 cm)) in the four treatment stands and results of analyses at the Summerland study area, British Columbia. Within a row, values followed by different letters are significantly different.

Parameter and species [1]	Young pine	Single seed-tree	Group seed-tree	Uncut forest	Analysis	
					$F_{3,8}$	P
Mean diameter						
Pl	$14.54^{b} \pm 0.24$	$12.75^{b} \pm 0.86$	$13.80^{b} \pm 0.90$	$20.50^{a} \pm 1.94$	9.06	<**0.01**
DF	$11.40^{b} \pm 0.90$	$7.44^{b} \pm 1.98$	$9.68^{b} \pm 3.60$	$36.34^{a} \pm 1.54$	36.44	<**0.01**
SubAl	10.50 ± 5.59	5.77 ± 1.31	6.29 ± 3.15	11.69 ± 6.43	0.42	0.74
Sp	10.15 ± 1.56	4.23 ± 2.24	1.93 ± 1.93	13.00 ± 6.88	1.80	0.23
DF (vet)	-	45.07 ± 13.19	59.24 ± 3.44	42.43 ± 4.07	1.21[2]	0.36
Mean height						
Pl	$9.15^{b} \pm 0.62$	$7.82^{b} \pm 0.54$	$9.31^{b} \pm 0.44$	$18.10^{a} \pm 1.38$	32.29	<**0.01**
DF	$7.70^{b} \pm 0.26$	$5.77^{b} \pm 1.07$	$6.98^{b} \pm 1.54$	$19.44^{a} \pm 2.26$	18.66	<**0.01**
SubAl	6.08 ± 3.04	4.40 ± 0.58	4.24 ± 2.13	11.31 ± 6.04	0.87	0.50
Sp	7.13 ± 0.96	3.47 ± 1.77	1.79 ± 1.79	10.75 ± 5.93	1.50	0.29
DF (vet)	-	22.02 ± 4.35	24.80 ± 1.01	21.83 ± 1.98	0.35[2]	0.72
Mean BA						
Pl	28.65 ± 4.52	27.21 ± 3.68	27.34 ± 10.28	11.58 ± 1.42	1.85	0.22
DF	$1.10^{b} \pm 0.34$	$2.96^{b} \pm 0.30$	$10.84^{b} \pm 6.44$	$49.35^{a} \pm 14.87$	7.77	<**0.01**
SubAl	0.68 ± 0.35	0.20 ± 0.15	0.56 ± 0.40	8.66 ± 4.65	3.05	0.09
Sp	1.01 ± 0.40	0.05 ± 0.04	1.26 ± 1.26	1.75 ± 1.70	0.44	0.73
DF (vet)	-	1.96 ± 0.97	4.33 ± 1.22	6.89 ± 2.47	2.14[2]	0.20

[1] Pl lodgepole pine; DF Douglas-fir; SubAl subalpine fir; Sp spruce

[2] $F_{2,6}$

group seed-tree and uncut forest having 2.5–3.6 times as many Douglas-fir as the young pine and single seed-tree stands (Table 1).

Mean diameters of lodgepole pine ($F_{3,8} = 9.06$; $P < 0.01$) and Douglas-fir ($F_{3,8} = 36.44$; $P < 0.01$) were significantly higher (DMRT; $P = 0.05$) in the uncut forest than the other treatment stands, which were all similar (Table 2). Mean height also followed this species-specific pattern with significantly ($P < 0.01$) higher values of 18.10 m for lodgepole pine and 19.44 m for Douglas-fir in the uncut forest than in the other stands (Table 2). Subalpine fir and spruce had similar mean diameters and mean heights among stands. Mean BA of Douglas-fir was significantly ($F_{3,8} = 7.77$; $P < 0.01$) higher in the uncut forest (DMRT; $P = 0.05$) than the other treatment stands.

Mean density of dead standing trees (snags) was five snags/ha in two of three group seed-tree stands and 337/ha in the uncut stands. There were no snags in the young pine or single seed-tree stands. Mean volume (m^3/ha) of down wood was similar ($F_{2,6} = 1.72$; $P = 0.26$) among treatment stands ranging from 83 in the seed-tree to 114 in the young pine, to 120 in the uncut stands. The young pine stands had a significantly ($F_{2,6} = 5.84$; $P = 0.04$) greater number (DMRT; $P = 0.05$) of pieces in the 5–25 cm diameter class than the seed tree or uncut stands. Conversely, the uncut stands had significantly ($F_{2,6} = 7.43$; $P = 0.02$) more large (>25 cm) diameter pieces (DMRT; $P = 0.05$) than the other stands in these down wood samples. The young pine and seed-tree stands had significantly ($F_{2,6} = 5.57$; $P = 0.04$) more pieces (DMRT; $P = 0.05$) in decay classes 3 and 4 than the uncut stands, possibly owing to an accumulation of woody debris from the harvesting operations.

Mean species diversity of those conifers >3 m ($F_{3,8} = 2.14$; $P = 0.17$) and for total conifers ($F_{3,8} = 1.94$; $P = 0.20$) were similar among stands (Table 1). Mean structural diversity of the five height classes was also similar ($F_{3,8} = 0.73$; $P = 0.57$) among stands (Table 1). Another measure of structural diversity is variation in tree sizes by species for each stand, based on the CV of diameter and height. The mean CV for diameters

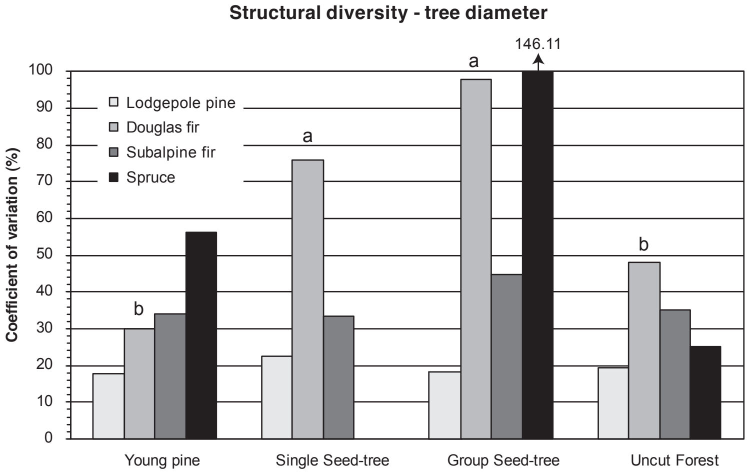


Fig. 2. Mean ($n=3$ replicate sites) structural diversity based on the coefficient of variation of tree diameter within the combined dominant and seed-tree or veteran layers (all trees >3 m in height) for the four tree species in the four treatment stands. Within a species, histograms with different letters are significantly different.

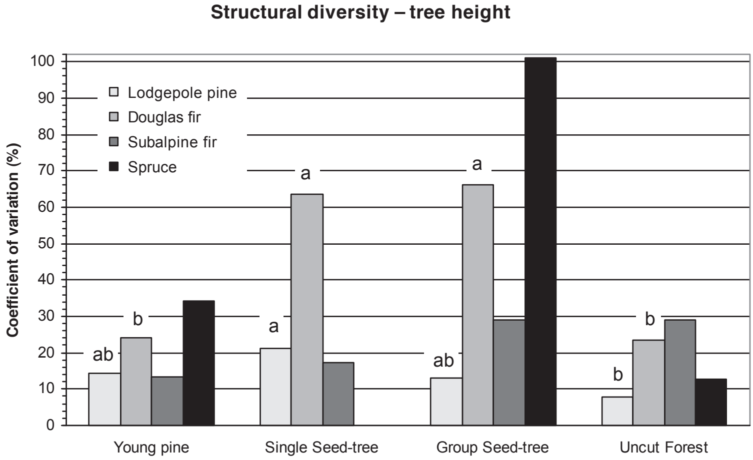


Fig. 3. Mean ($n=3$ replicate sites) structural diversity based on the coefficient of variation of tree height within the combined dominant and seed-tree or veteran layers (all trees >3 m in height) for the four tree species in the four treatment stands. Within a species, histograms with different letters are significantly different.

Table 3. Mean ($n=3$ replicate sites) ± SE crown volume index (m^3/0.01 ha) of herbs, shrubs, mosses, and terrestrial lichens and total species richness and total species diversity of vascular plants in the four treatment stands and results of analyses at the Summerland study area, British Columbia. Within a row, values followed by different letters are significantly different.

Vegetation parameter	Young pine	Single seed-tree	Group seed-tree	Uncut forest	Analysis	
					$F_{3,8}$	P
Volume						
Herbs	6.95 ± 1.84	13.01 ± 5.05	6.81 ± 1.35	8.88 ± 4.43	0.66	0.60
Shrubs	64.75^a ± 3.06	9.73^b ± 4.99	74.65^a ± 28.42	2.08^b ± 1.06	6.56	**0.02**
Mosses	2.99 ± 1.28	0.83 ± 0.20	0.90 ± 0.34	2.68 ± 2.08	0.86	0.50
Terrestrial lichens	0.36 ± 0.07	0.39 ± 0.08	0.33 ± 0.04	0.28 ± 0.03	0.63	0.62
Total species richness	24.4 ± 4.3	20.1 ± 0.3	19.8 ± 2.1	15.1 ± 3.1	1.79	0.23
Total species diversity	1.27 ± 0.08	0.88 ± 0.08	1.05 ± 0.13	1.29 ± 0.17	2.60	0.12

of Douglas-fir was significantly ($F_{3,8}=22.21$; $P<0.01$) different among stands with the seed-tree stands having a greater (DMRT; $P=0.05$) range of diameters than the other stands (Fig. 2). This same pattern was also recorded for mean CV for diameters of spruce ($F_{3,8}=10.25$; $P=0.02$), at least for the group seed-tree stands (Fig. 2). Mean CVs of lodgepole pine and subalpine fir diameters were similar among stands.

Mean CV for tree heights of Douglas-fir was significantly ($F_{3,8}=18.23$; $P<0.01$) different among stands with the same pattern of variation as in tree diameters for this species (Fig. 3). The mean CV for tree heights for lodgepole pine was also significantly ($F_{3,8}=4.97$; $P=0.03$) different among stands with a gradation (DMRT; $P=0.05$) in structural height diversity from the single-seed tree to uncut forest (Fig. 3). Mean CV of spruce heights followed the same significant ($F_{3,8}=22.28$; $P<0.01$) pattern as for diameters in this species. Again, mean CVs of heights were similar among stands for subalpine fir.

3.2 Understory Vegetation

Mean crown volume index of herbs was similar ($F_{3,8}=0.66$; $P=0.60$) among treatments (Table 3). However, mean volume of shrubs was significantly ($F_{3,8}=6.56$; $P=0.02$) different among stands with the young pine and group seed-tree stands having higher (DMRT; $P=0.05$) amounts of shrub biomass than the single-seed tree and uncut forest stands (Table 3). Mean crown volume index of mosses ($F_{3,8}=0.86$; $P=0.50$) and terrestrial lichens ($F_{3,8}=0.63$; $P=0.62$) was similar among stands, with considerable variability of moss volume in the young pine and uncut forest stands (Table 3). There was a total of 40 species of herbs, 23 species of shrubs, and 5 species of trees in our treatment stands. Mean total species richness ($F_{3,8}=1.79$; $P=0.23$) and mean total species diversity ($F_{3,8}=2.60$; $P=0.12$) were both similar among stands (Table 3).

Prominent herb species in these stands included pine grass (*Calamagrostis rubescens* Buckl.), fireweed (*Epilobium angustifolium* L.), white-flowered hawkweed (*Hieracium albiflorum* Hook.), heart-leaved arnica (*Arnica cordifolia* Hook.), Arctic lupine (*Lupinus arcticus* S. Wats.), racemose pussytoes (*Antennaria racemosa* Hook.), and one-sided wintergreen (*Orthilia secunda* L.). Prominent shrubs included Sitka alder (*Alnus sitchensis* (Regel) Sarg.), kinnikinnick (*Arctostaphylos uva-ursi* (L.) Sprengel.), twinflower (*Linnaea borealis* L.), Utah honeysuckle (*Lonicera utahensis* L.), falsebox (*Pachistima myrsinites* Nutt.), birch-leaved spiraea (*Spiraea betulifolia* Pall.), and grouseberry (*Vaccinium scoparium* Leib. ex Coville).

3.3 Forest-Floor Small Mammals

P. maniculatus was the most abundant of 10 species with a total of 806 individuals captured (42.4% of a total of 1900 forest floor mammals) over the

3-year study. The next most abundant species, in terms of individuals, were *M. gapperi* (618, 32.5% of total), *T. amoenus* (145), *S. monticolus* (112), *P. intermedius* (90), and *S. cinereus* (78). Numbers of individuals for the less common species were 24 for *M. pennsylvanicus,* 18 for *M. longicaudus*, 2 for *Z. princeps* and 7 for *M. erminea.* Susceptibility to capture was measured by Jolly trappability estimates with a mean value of 85.1% (range 57.1–100.0%) for *M. gapperi* and 84.5% (range 70.8–98.7%) for *P. maniculatus.*

Population changes of the red-backed vole during 2005–2007 indicated that this microtine was consistently higher ($F_{3,8}=3.65$; $P=0.06$) in mean abundance per ha in the uncut forest than other stands (Fig. 4a, Table 4). On average, populations of red-backed voles were 2.3 to 6.4 times higher in the uncut than harvested sites (Fig. 5a). Population changes of the common shrew ($F_{3,8}=0.97$; $P=0.45$) (Fig. 4b) were similar among treatment stands with respect to mean abundance, with numbers declining from 2005 to 2007 (Table 4). Overall mean numbers of red-backed voles (Fig. 5a) and common shrews (Fig. 5b) also followed this pattern.

Mean total abundance of small mammals was similar ($F_{3,8}=1.66$; $P=0.25$) among stands, as were numbers ($P>0.05$) of the deer mouse, northwestern chipmunk, two species of *Microtus*, and the montane shrew (Table 4). Mean abundance of the heather vole was significantly ($F_{3,8}=6.58$; $P=0.02$) different among stands with overall numbers higher (DMRT; $P=0.05$) in the young pine and single seed-tree stands than uncut forest stands (Table 4).

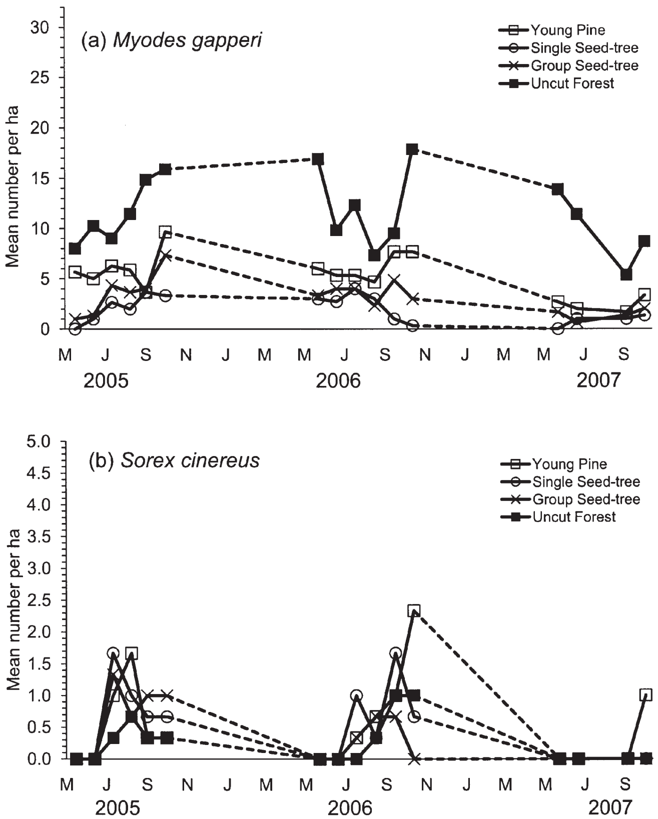
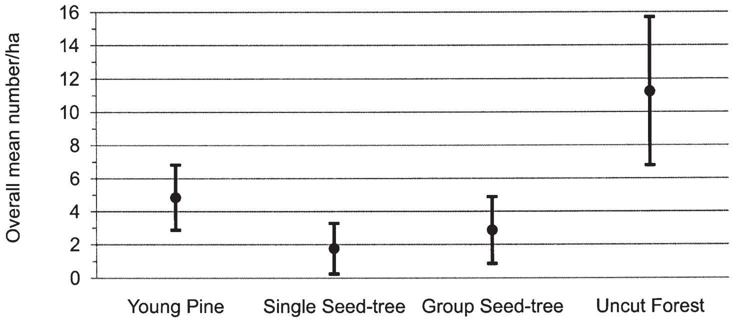


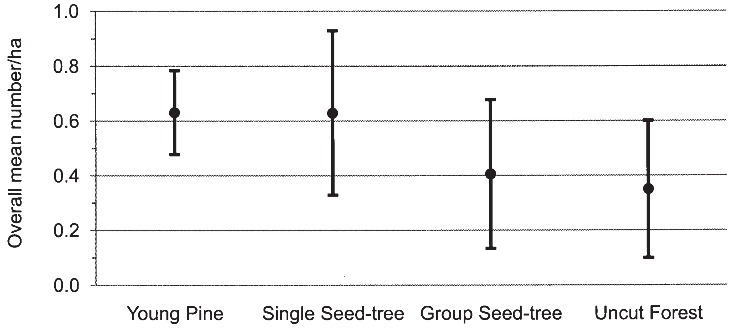
Fig. 4. Mean ($n=3$ replicate sites) total abundance per ha of (a) red-backed voles (*Myodes gapperi*) and (b) common shrews (*Sorex cinereus*) in the young pine, single-seed-tree, group seed-tree, and uncut forest stands in 2005–2007 at the Summerland study area.

Table 4. Mean ($n = 3$ replicate sites) ± SE abundance per ha of forest-floor small mammals each year and results of repeated measures analysis of variance (RM-ANOVA). 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. Columns of mean values with different letters are significantly different by Duncan's multiple range test (DMRT), adjusted for multiple contrasts. Superscript letters are used to indicate the location of significant differences resulting from univariate ANOVAs.

Species and year	Young pine	Single seed-tree	Group seed-tree	Uncut forest	RM-ANOVA results					
					Site		Time		Site × time	
					$F_{3,8}$	P	$F_{2,16}$	P	$F_{6,16}$	P
Total					1.66	0.25	23.00	<**0.01**	1.27	0.32
2005	21.39 ± 3.34	17.26 ± 1.05	20.43 ± 2.50	24.99 ± 6.95						
2006	23.56 ± 3.28	19.17 ± 3.27	20.30 ± 1.16	28.08 ± 8.78						
2007	15.29 ± 2.13	10.55 ± 0.98	10.60 ± 1.65	20.93 ± 4.23						
M .gapperi					3.65	0.06	6.99	<**0.01**	0.68	0.67
2005	6.02 ± 1.66	2.11 ± 1.06	3.61 ± 1.83	11.59 ± 4.18						
2006	6.11 ± 0.64	2.35 ± 1.79	3.59 ± 1.95	12.30 ± 3.81						
2007	2.42 ± 1.08	0.83 ± 0.44	1.42 ± 0.65	9.82 ± 3.34						
P. maniculatus					1.30	0.34	5.72	**0.01**	1.29	0.32
2005	12.07 ± 2.76	8.86 ± 1.80	11.80 ± 1.92	9.54 ± 3.43						
2006	12.61 ± 2.88	6.63 ± 2.04	10.74 ± 2.22	12.54 ± 5.29						
2007	10.54 ± 0.79	4.63 ± 0.83	5.36 ± 0.31	8.79 ± 2.64						
P. intermedius	**A**	**A**	**AB**	**B**	6.58	**0.02**	8.83	<**0.01**	2.71	**0.05**
2005	0.33^{ab} ± 0.10	1.00^{a} ± 0.42	0.56^{a} ± 0.31	0.00^{b} ± 0.00						
2006	1.33^{a} ± 0.10	2.17^{a} ± 1.50	0.39^{ab} ± 0.11	0.00^{b} ± 0.00						
2007	0.58^{a} ± 0.22	0.33^{a} ± 0.08	0.00^{b} ± 0.00	0.00^{b} ± 0.00						
T. amoenus					0.30	0.83	0.77	0.48	1.69	0.19
2005	2.13 ± 0.98	2.79 ± 1.47	2.97 ± 1.71	3.20 ± 1.91						
2006	2.06 ± 1.22	4.19 ± 1.76	4.42 ± 2.15	2.46 ± 1.40						
2007	1.25 ± 0.72	4.26 ± 0.68	3.49 ± 2.19	2.23 ± 1.62						
M. pennsylvanicus					0.94	0.47	1.31*	0.29	0.94*	0.48
2005	0.00 ± 0.00	0.61 ± 0.61	0.00 ± 0.00	0.00 ± 0.00						
2006	0.00 ± 0.00	1.06 ± 1.06	0.11 ± 0.06	0.00 ± 0.00						
2007	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00						
M. longicaudus					1.91	0.21	1.01*	0.38	1.28*	0.33
2005	0.00 ± 0.00	0.00 ± 0.00	0.11 ± 0.06	0.00 ± 0.00						
2006	0.00 ± 0.00	0.56 ± 0.47	0.06 ± 0.06	0.00 ± 0.00						
2007	0.00 ± 0.00	0.17 ± 0.08	0.00 ± 0.00	0.00 ± 0.00						
S. monticolus					1.28	0.35	7.25*	<**0.01**	0.67*	0.67
2005	0.28 ± 0.15	1.22 ± 0.73	0.72 ± 0.22	0.39 ± 0.39						
2006	0.72 ± 0.05	1.22 ± 0.55	0.72 ± 0.31	0.39 ± 0.15						
2007	0.25 ± 0.25	0.17 ± 0.08	0.33 ± 0.22	0.08 ± 0.08						
S. cinereus					0.97	0.45	14.34	<**0.01**	0.63	0.71
2005	0.45 ± 0.15	0.67 ± 0.35	0.66 ± 0.33	0.28 ± 0.15						
2006	0.72 ± 0.05	0.61 ± 0.20	0.28 ± 0.05	0.39 ± 0.24						
2007	0.17 ± 0.17	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00						



(a) *Myodes gapperi*



(b) *Sorex cinereus*

Fig. 5. Overall mean abundance/ha ($n=9$; 3 replicates × 3 years) ± 95% C.I. of (a) red-backed voles (*Myodes gapperi*) and (b) common shrews (*Sorex cinereus*) in the young pine, single-seed-tree, group seed-tree, and uncut forest stands in 2005–2007 at the Summerland study area.

Mean species richness appeared similar ($F_{3,8}=2.06$; $P=0.19$) among stands but the significant ($F_{6,16}=4.57$; $P<0.01$) site × time interaction indicated that the number of small mammal species was higher (DMRT; $P=0.05$) in the single seed-tree than group seed-tree or uncut forest stands in 2006 (Table 5). Mean species richness was similar in the young pine, group seed-tree, and uncut stands in 2006. Mean S-W ($F_{3,8}=1.48$; $P=0.29$) and log-series ($F_{3,8}=3.21$; $P=0.08$) measures of species diversity were similar among stands (Table 5). Mean species richness and S-W species diversity declined significantly ($P<0.01$) with time in a similar pattern to total abundance (Table 5).

There were positive relationships between mean total abundance of small mammals (r values =0.58 to 0.81; $P\leq0.05$), and mean abundance of red-backed voles (r values=0.70 to 0.80; $P\leq0.01$), with mean values for total structural diversity of vegetation, volume of down wood, and mean BA and species diversity of overstory conifers. Mean species richness of small mammals showed an inverse relationship with BA of overstory conifers ($r=0.61$; $P=0.04$). Mean log-series diversity of small mammals showed an inverse relationship with mean structural diversity of vegetation ($r=0.66$; $P=0.02$) and species diversity of total coniferous trees ($r=0.59$; $P=0.05$). Interestingly, mean abundance of common shrews was also inversely related to these latter two parameters (r values=0.58 to 0.60; $P\leq0.05$).

Table 5. Mean ($n=3$ replicate sites) ± SE small mammal diversity within each sample period and results of repeated measures analysis of variance (RM-ANOVA). No correlation among repeated measures was detected. Superscript letters are used to indicate the location of significant differences resulting from univariate ANOVAs.

Parameter and year	Young pine	Single seed-tree	Group seed-tree	Uncut forest	RM-ANOVA results					
					Site		Time		Site × time	
					$F_{3,8}$	P	$F_{2,16}$	P	$F_{6,16}$	P
Species richness					2.06	0.19	59.99	<**0.01**	4.57	<**0.01**
2005	3.50 ± 0.19	3.83 ± 0.51	3.83 ± 0.10	3.11 ± 0.11						
2006	4.28^{ab} ± 0.40	5.00^{a} ± 0.54	3.72^{b} ± 0.20	3.22^{b} ± 0.22						
2007	3.08 ± 0.44	3.25 ± 0.29	2.58 ± 0.08	2.67 ± 0.30						
S-W Species diversity					1.48	0.29	15.78	<**0.01**	1.90	0.14
2005	1.23 ± 0.16	1.59 ± 0.25	1.37 ± 0.08	1.33 ± 0.09						
2006	1.58 ± 0.10	1.90 ± 0.20	1.41 ± 0.15	1.29 ± 0.11						
2007	1.11 ± 0.28	1.43 ± 0.14	1.11 ± 0.05	1.16 ± 0.18						
Log diversity					3.21	0.08	2.27	0.14	1.42	0.27
2005	1.24 ± 0.10	1.91 ± 0.39	1.78 ± 0.05	1.08 ± 0.16						
2006	1.65 ± 0.29	2.67 ± 0.76	1.42 ± 0.04	1.04 ± 0.16						
2007	1.26 ± 0.16	2.09 ± 0.43	1.31 ± 0.24	0.90 ± 0.19						

Table 6. Mean ($n=3$ replicate sites) ± SE abundance per ha of *T. hudsonicus* and *G. sabrinus* each season and results of repeated measures analysis of variance (RM-ANOVA). No correlation among repeated measures was detected. Superscript letters are used to indicate the location of significant differences resulting from univariate ANOVAs.

Species and period	Young pine	Single seed-tree	Group seed-tree	Uncut forest	RM-ANOVA results					
					Site		Time		Site × time	
					$F_{3,8}$	P	$F_{4,32}$	P	$F_{12,32}$	P
Tamiasciurus hudsonicus					1.51	0.28	6.66	<**0.01**	2.21	**0.04**
Fall 2006	2.07^{a} ± 0.29	2.23^{a} ± 0.08	2.15^{a} ± 0.15	1.09^{b} ± 0.18						
Spring 2007	1.81 ± 0.26	1.86 ± 0.25	2.09 ± 0.24	1.40 ± 0.12						
June 2007	1.78 ± 0.17	1.99 ± 0.41	2.43 ± 0.48	1.44 ± 0.35						
Fall 2007	1.87 ± 0.45	1.96 ± 0.38	1.99 ± 0.15	1.88 ± 0.14						
Spring 2008	1.11 ± 0.10	1.45 ± 0.17	1.27 ± 0.20	1.50 ± 0.16						
Glaucomys sabrinus					0.26	0.85	7.47	<**0.01**	1.11	0.39
Fall 2006	0.24 ± 0.12	0.50 ± 0.14	0.40 ± 0.04	0.51 ± 0.33						
Spring 2007	0.14 ± 0.07	0.35 ± 0.10	0.31 ± 0.05	0.38 ± 0.29						
June 2007	0.13 ± 0.07	0.25 ± 0.13	0.16 ± 0.06	0.33 ± 0.29						
Fall 2007	0.23 ± 0.09	0.43 ± 0.08	0.35 ± 0.11	0.39 ± 0.34						
Spring 2008	0.21 ± 0.07	0.30 ± 0.12	0.25 ± 0.08	0.13 ± 0.13						

3.4. Tree Squirrels

T. hudsonicus was the more abundant arboreal sciurid, with a total of 568 individuals captured (77.8% of a total of 730), compared with *G. sabrinus* at 162 individuals. Mean values of Jolly trappability were 70.1% (range 53.3–81.0%) for red squirrels and 58.5% (range 45.3–72.3%) for northern flying squirrels. Mean abundance of red squirrels was similar ($F_{3,8}=1.51$; $P=0.28$) among stands, but with a significant site × time interaction ($F_{12,32}=2.21$; $P=0.04$) where there were more (DMRT; $P=0.05$) red squirrels in the three harvested stands than uncut stands in fall 2006 (Table 6), ranging between 0.9 and 2.4 animals per ha (Fig. 6a). The pattern of overall mean abun-

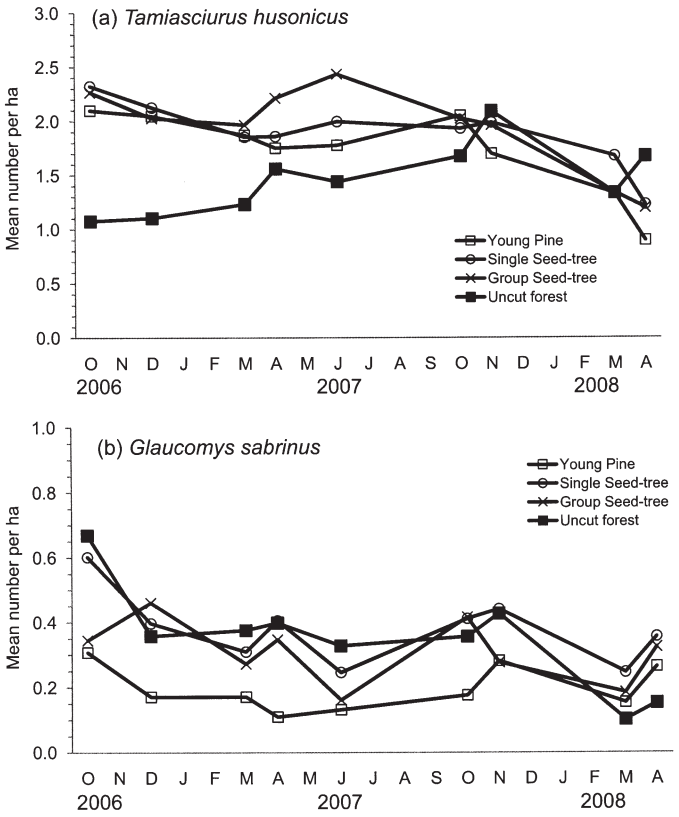


Fig. 6. Mean ($n=3$ replicate sites) total abundance/ha of (a) red squirrels (*Tamiasciurus hudsonicus*) and (b) northern flying squirrels (*Glaucomys sabrinus*) in the young pine, single-seed-tree, group seed-tree, and uncut forest stands in 2006–2008 at the Summerland study area.

dance of red squirrels was similar among the four treatment stands (Fig. 7a). Mean abundance of northern flying squirrels also followed this trend for similar ($F_{3,8}=0.26$; $P=0.85$) numbers through time (range 0.1–0.7/ha) (Table 6, Fig. 6b). The pattern of overall mean abundance of flying squirrels was also similar among the four treatment stands (Fig. 7b).

4 Discussion

4.1 Salvage Logging and GTR

The MPB is native to western North America and may attack most pine species, with lodgepole pine as the primary host (Aukema et al. 2006). Thus, this beetle is a major factor controlling the dynamics, and hence natural disturbance regimes in lodgepole pine forests, in addition to fire (Barclay et al. 2005). Because of the extent (13 million ha) of the current MPB epidemic in B.C., salvage logging is being conducted at an unprecedented scale, reaching 20% of the provincial harvest (BC MoFR 2007, Lindenmayer et al. 2008). According to Lindenmayer et al. (2008), salvage logging alters: (1) populations of organisms, (2) stand structure, and (3) ecosystem processes and functions. However, what are the long-term consequences of this practice, particularly where GTR occurs at the time of harvest?

Our study is the first investigation of the long-

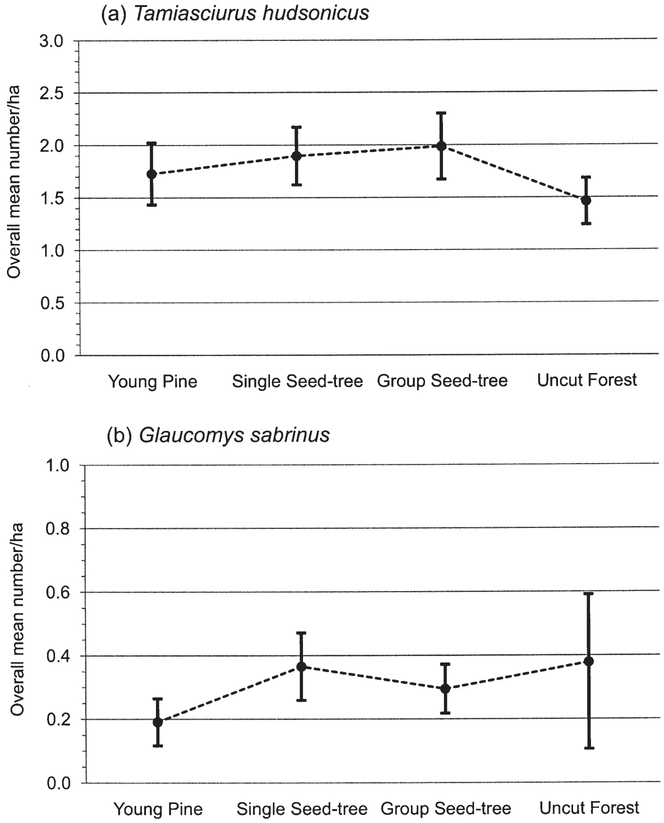


Fig. 7. Overall mean abundance/ha ($n=21$; 3 replicates × 7 trapping periods) ± 95% C.I. of (a) red squirrels (*Tamiasciurus hudsonicus*) and (b) northern flying squirrels (*Glaucomys sabrinus*) in the young pine, single-seed-tree, group seed-tree, and uncut forest stands in 2006–2008 at the Summerland study area.

term (3 decades) effects of salvage logging of beetle-killed timber, and the subsequent influence of GTR, on biodiversity via inferences from ecological indicators of stand structure and mammals. As discussed by Franklin et al. (1997), retention of green trees can (1) maintain some species and ecological processes from the original forest, (2) provide structure in the regenerating forest stand, and (3) provide some connectivity in the commercial forest landscape. These attributes are particularly enhanced by retention of aggregated or group seed-tree patterns of residual trees (Aubry et al. 2009). The structural components of variable retention, regardless of pattern, include large live Douglas-fir trees, understory vascular plants, fallen wood over a range of decay classes, some snags (5–10/ha), and relatively undisturbed layers of forest floor (Franklin et al. 1997, 2002).

Our seed-tree stands (both dispersed and aggregated) included some of these attributes except for the absence of snags and understory thickets in the young pine and single seed-tree stands. This snag deficiency may soon be rectified as the MPB moves south through the interior of B.C., with at least some attack of lodgepole pine forecast for our geographical area. Because harvesting was completed 28–30 years ago, the forest floors were essentially undisturbed in all stands, but not at the time of harvest. The original silvicultural goal in the 1970s was regeneration from residual Douglas-fir seed-trees, and hence our study was not a direct test of structural retention as advocated by Franklin (1997, 2002) or Lindenmayer et al. (2006). However, the study does provide a 30-year temporal perspective on the effects of retention harvest as advocated by Rosenvald and Lohmus (2008).

Our study was retrospective based on the assumption that past disturbances (either natural or harvesting) provide experimental units that have undergone successional change, often over decades, but still allow reasonably rigorous comparisons to be made among treatments. Our young pine and seed-tree stands were 28 years old at the start of the study. We have assumed that the original forest composition on these sites prior to harvesting in the mid 1970s, and their subsequent successional development were reasonably similar among stands. It would have been ideal to follow changes in stand structure and mammals from pre-harvest to 30 years of post-harvest successional change. Successional dynamics in boreal and temperate forests are initiated and driven by natural disturbances such as wildfire and insect outbreaks. Thus, it could be argued that a "natural" control for this study might be stands at the beginning of forest succession after disturbance, rather than those (mature/old-growth forest) in the end-phase of succession. The study design had true replicates of experimental units (Hurlbert 1984), and all units were of a size typical of commercial forestry operations.

4.2 Stand Structure Attributes

In terms of hypothesis (1) that abundance and diversity of various aspects of stand structure would increase with higher levels of Douglas-fir tree retention, BA of overstory conifers was higher in the uncut than the other stands. In addition, mean diameters and heights of lodgepole pine and Douglas-fir were also highest in the uncut stands. However, density of overstory, understory, and all height classes of conifers were similar among stands. Abundance of understory vascular (herbs and shrubs) and non-vascular plants (mosses and terrestrial lichens) also followed the tree density pattern, and hence did not support hypothesis (1). In terms of diversity, hypothesis (1) was not supported by species richness and diversity measurements of herbs, shrubs, and coniferous trees. Lodgepole pine did dominate the coniferous species composition of the managed stands compared with the uncut forest, but the other three conifers were similar among stands. Indices of structural diversity based on coniferous stand density and CV of various tree sizes also failed to support hypothesis (1).

Our seed-tree study sites seemed to have incorporated most of the structural components of variable retention: at least some (10–20/ha) large live Douglas-fir trees with comparable diameters and heights to those in the uncut mature/old-growth stands. In addition, the range of "legacy trees" (Franklin et al. 2000) on our seed-tree sites was similar to the size classes, number, and distribution of Douglas-fir in the original pre-salvage logged stands. The trend for higher numbers overall of Douglas-fir trees in the group seed-tree and uncut stands than young pine or single seed-tree stands also suggested a large component of this species in the future forest composition, particularly with aggregated GTR.

The importance of residual Douglas-fir to structural diversity in the seed-tree stands was indicated by the significant pattern of tree sizes (based on CVs). Three components of structural diversity of forests were suggested by Pommerening (2002): spatial distribution, species diversity, and variations in tree dimensions (e.g., our CVs of tree sizes). A fourth component would be our measure of structural diversity (e.g., foliage height diversity). Our CVs of tree diameters and heights reached a maximum in the two-storied seed-tree stands as the standard deviation measured the differences of individual trees to their mean (Varga et al. 2005). Diversity calculations using the S-W index increase with increasing richness of classes (e.g., species for species diversity and height classes for structural diversity) and reach a maximum when proportions are equal for all classes (Magurran 2004). This measure found similarity among stands for both species and structural diversity of conifers. Thus, the similarity in variety of canopy layers and conifer species in the seed-tree and uncut stands suggested that structural complexity and diversity were maintained. Several authors have reported a similar relationship between multiple tree species and sizes and high diversity or complexity (Buongiorno et al. 1994, Önal 1997, Zenner 2000).

There are few long-term investigations comparing understory vegetation in uncut and GTR stands. The similarity in species richness of vascular plants among our treatment stands was similar to long-term (12–96 years) results reported by Deal (2001) for partially cut and uncut western hemlock (*Tsuga heterophylla* Sarg.) – Sitka spruce (*Picea sitchensis* (Bong.) Carr.) forests in southeast Alaska. An 8-year post-harvest study by Sullivan et al. (2001, 2008) reported that retention of live Douglas-fir trees had no effect on total species richness of vascular plants, but did provide suitable conditions for some forest interior species. Similar results were reported for 7 years post-harvest for the DEMO study (Aubry et al. 2009). Several other studies reported only short-term (1–3 years) changes in vegetation attributes, to date. However, development of understory vegetation seemed to be related to structural and compositional redevelopment of overstory trees (Nagaike et al. 1999, Deal 2001, Roberts and Zhu 2002).

4.3 Forest-Floor Small Mammals

Our hypothesis (2) that abundance of several mammalian indicator species will increase with higher levels of Douglas-fir tree retention was partially supported for red-backed voles when the young pine and seed-tree stands were compared to uncut forest. The important result was that the uncut forest supported 2.3 to 6.4 times as many red-backed voles as the young pine and seed-tree stands. The positive relationships of mean abundance of red-backed voles and total small mammals to habitat structural features were similar to those reported for similar species in forests of northern Sweden (Ecke et al. 2001, 2002). However, we did not find any positive relationships for either mean species richness or diversity of small mammals with habitat features. *M. gapperi* is readily found in mesic to moist habitats in mature deciduous, coniferous, and mixed forests with sufficient amounts of CWD (downed logs), understory vegetation, and dense cover of trees (Merritt 1981, Yahner 1986, Moses and Boutin 2001); but also at relatively high abundance in dry Douglas-fir forests (Klenner and Sullivan 2009). These ecological conditions provide berry production (e.g., *Vaccinium* spp.), seed-fall from overstory trees, and hypogeous fungi as food sources for *M. gapperi*.

Suitable habitat conditions for red-backed voles have been maintained in partially cut forests with GTR levels of > 15 m^2/ha BA or 30% uncut forest across a variety of forest ecosystems (several studies reviewed by Sullivan et al. 2008). Thus, although our young pine and seed-tree stands had a range of BA of total conifers from 30–40 m^2/ha, these levels were presumably insufficient to maintain abundance of *M. gapperi* at levels recorded in uncut forest (71 m^2/ha BA). The seed-tree stands had only 6.4–10.8% of their total BA as Douglas-fir vets; thus large diameter trees may be required for seed sources and fungal substrates. Relative amounts and decay of CWD were generally similar among stands as was abundance of understory herbs, but not shrubs. The low volume of shrubs may have contributed to relatively fewer red-backed voles in the single seed-tree stands. Alternatively, *M. gapperi* appear to require > 15 m^2/ha BA of mature coniferous trees to provide sufficient cover and food resources to maintain populations at levels found in mature/old-growth forest.

S. cinereus has been reported as a cosmopolitan insectivore, occupying many different habitats (Whitaker 2004). However, like the variable habitat preferences of *M. gapperi* in eastern and western parts of North America (Kirkland 1990), *S. cinereus* may occupy mature/old-growth forests as its preferred habitat in certain forests and regions (Hallett and O'Connell 1997, Ford and Rodrigue 2001). It appears to be the numerically dominant shrew species in closed-canopy forests of some inland parts of the PNW, including our study area (Sullivan et al. 2008). This insectivore was found at comparable abundance in all treatment stands in this study, thereby suggesting that ecological conditions were suitable on the forest floor for this insectivorous small mammal.

Gitzen et al. (2007) concluded that much variability in the responses of closed-canopy species to GTR may relate to short-term results immediately after harvest, flexibility in habitat occupancy, favourable changes in forest-floor conditions, and regional variation in composition of small mammal communities and climatic gradients. The retrospective nature of our study makes it difficult to comment on immediate post-harvest conditions from 30 years ago.

4.4 Tree Squirrels

Our study is the first investigation of the influence of relatively long-term GTR on abundance of tree squirrels. Populations of *T. hudsonicus* and *G. sabrinus* were maintained in all treatment stands, and hence hypothesis (2) was not supported for these indicator species. An exception was higher mean abundance of red squirrels in the group seed-tree than uncut stands in fall 2006. Tree squirrels and other arboreal rodents are an important group because of their close association with forest canopies and responses to potential impacts from management, particularly harvesting (Smith et al. 2003). These sciurids function as indicators of ecological productivity via their foraging on, and dissemination of ectomycorrhizal fungi as well as serve as prey for raptors and mammalian carnivores (Carey 2000, Carey and Harrington 2001, Ransome et al. 2004). Our seed-tree and young pine stands provided high structural diversity and overstory cover, at least of the dominant tree layer, for decreased predation risk for tree squirrels (Vahle and Patton 1983, Carey 2000). These habitat attributes for tree squirrels were related to higher numbers of both sciurids in relatively intact coniferous and deciduous forests in Ontario (Holloway and Malcolm 2006). Relative to old-growth forests, shelterwood harvesting seemed to lower habitat quality for both species in Ontario (Holloway and Malcolm 2006) and for northern flying squirrels in California (Waters and Zabel 1995). Comparable densities of *T. hudsonicus* and *G. sabrinus* were reported for 30- to 40-year old managed (pre-commercially thinned 15 years previously) lodgepole pine forests and old-growth stands in the interior of B.C. (Ransome et al. 2004). Numbers of red squirrels were similar in thinned, unthinned, and old-growth stands, and those of flying squirrels were the same or significantly higher in thinned (1000–2000 stems/ha) stands than in old-growth stands (Ransome et al. 2004). There is much variability in responses of these sciurids to managed and old-growth forests in the PNW (Smith 2003). However, wherever late successional (legacy) features such as large live Douglas-fir, spruce, or other coniferous trees, snags, and abundant CWD are present within managed stands, both species seem to be maintained (Carey 2000, Smith 2003).

4.5 Is There Life after the Beetle?

This study provided a way of inferring biodiversity and sustainability by comparing forest structural attributes and MIS as ecological indicators across various stand types. At 30 years after salvage harvesting, we have an indication of how close we are to managing forests sustainably by comparing wildlife habitat and biodiversity, in young forests with and without residual fir trees, to those in uncut mature/old-growth forests. The study has advanced existing knowledge on stand-level structures and biodiversity by examining past disturbance to provide a picture of forest conditions 3 decades into the future. An overall summary of response variables indicated that the seed-tree stands had the same or higher value than the uncut forest in 19 of 25 cases (Table 7). The 6 of 25 cases where the uncut forest was higher than the seed tree stands included the mean diameters and heights of the major conifers (Douglas-fir and lodgepole pine), BA of total conifers, and mean abundance of red-back voles.

Stand-replacement fires and insect attacks that kill trees over large areas, without subsequent salvage harvesting, are also natural disturbance regimes in boreal and temperate forests. It would be most interesting to compare our young pine and seed-tree stands to same-age and structurally similar stands arising from these disturbances. Such comparisons would be of a so-called “true” ecological nature. Depending on the intensity of wildfire, amounts of CWD and plant community recovery would likely be greater in salvage-harvested stands than those arising from wildfire. Such responses in insect-killed standing timber would likely be intermediate. These latter studies and measurements have yet to be conducted except for the short-term work of Stone (1995) in Utah and McDonough and Rexstad (2005) in Alaska. Our MPB outbreak in B.C. provides a plethora of study opportunities in this regard.

In a comprehensive review of habitat heterogeneity (structural diversity) and animal species diversity, Tews et al. (2004) concluded that “keystone structures” of a given vegetation complex had profound implications for biodiversity management. Mazurek and Zielinski (2004) reported that individual legacy trees provided important habitat for wildlife in managed stands. Several

Table 7. Summary of response variables measured during 2005–2008. Columns with different letters are significantly different by ANOVA and Duncan's multiple range test (DMRT).

	Young pine	Single seed-tree	Group seed-tree	Uncut forest
Coniferous stand structure				
Tree measurements				
Abundance of total conifers	a	a	a	a
BA of total conifers	b	b	b	a
Douglas-fir diameter	b	b	b	a
Douglas-fir height	b	b	b	a
Lodgepole pine diameter	b	b	b	a
Lodgepole pine height	b	b	b	a
Douglas-fir vets diameter	a	a	a	a
Douglas-fir vets height	a	a	a	a
BA Douglas-fir vets	a	a	a	a
Diversity				
Species diversity of total conifers	a	a	a	a
Structural diversity of total conifers	a	a	a	a
CV Douglas-fir diameter	b	a	a	b
CV Douglas-fir height	b	a	a	b
CV Lodgepole pine diameter	a	a	a	a
CV Lodgepole pine height	ab	a	ab	b
Understory vegetation				
Herb volume	a	a	a	a
Shrub volume	a	b	a	b
Moss volume	a	a	a	a
Terrestrial lichen volume	a	a	a	a
Total species richness	a	a	a	a
Total species diversity	a	a	a	a
Forest floor small mammals				
Red-backed vole	a	a	a	a
Common shrew	a	a	a	a
Arboreal mammals				
Red squirrels	a	a	a	a
Northern flying squirrels	a	a	a	a

authors have noted the importance of GTR for maintenance of mycorrhizal fungal networks for tree nutrition and sporocarp food sources for a variety of species such as red-backed voles, red squirrels, and flying squirrels (Cazares et al. 1999, Hagerman et al. 2001, Lazaruk et al. 2005).

Thus, assuming that our selection of stand structure attributes and MIS accurately reflected the "health" of this forest ecosystem, at 30 years after salvage harvesting, there is "life after the beetle". This "life" is enhanced by GTR at the time of harvest since the mature forest habitat provides structural diversity for the regenerating stand and appears to contribute considerably to maintaining some degree of ecological function in these stands. With respect to our MIS, the density of GTR was insufficient to maintain populations of red-backed voles, but common shrews persisted on the forest floor, as did the two arboreal sciurids, at least at comparable population levels to those in uncut mature/old-growth forest.

Acknowledgements

We thank the Forest Science Program (Forest Investment Account), BC Ministry of Forests and Range, Okanagan Innovative Forestry Society (Innovative Forest Practices Association), and Gorman Bros. Lumber Ltd. for financial and logistical support. We thank T. Lindgren, T. Seebacher, H. Sullivan, and B. Tilling for assistance with the fieldwork.

References

Aubry, K.B., Crites, M.J. & West, S.D. 1991. Regional patterns in small mammal abundance and community composition in Oregon and Washington. In: Ruggiero, L.F., Aubry, K.B., Carey, A.B., Huff, M.H. (tech. coord.). Wildlife and Vegetation of Unmanaged Douglas-fir Forests. U.S. Forest Service General Technical Report PNW-285. Pacific Northwest Research Station, Portland, Oregon p. 285–294.

— , Amaranthus, M.P., Halpern, C.B., White, J.D., Woodward, B.L., Peterson, C.E., Lagoudakis, C.A. & Horton, A.J. 1999. Evaluating the effects of varying levels and patterns of green-tree retention: experimental design of the DEMO study. Northwest Science 73: 12–26.

— , Halpern, C.B. & Peterson, C.E. 2009. Variable-retention harvests in the Pacific Northwest: A review of short-term findings from the DEMO study. Forest Ecology and Management 258: 398–408.

Aukema, B.H., Carroll, A.L., Zhu, J., Raffa, K.F., Sickley, T.A. & Taylor, S.W. 2006. Landscape level analysis of mountain pine beetle in British Columbia, Canada: spatiotemporal development and spatial synchrony within the present outbreak. Ecography 29: 427–441.

Barclay, L., Chao, H.J., Benson, L., Taylor, S. & Shore, T. 2005. Effects of fire return intervals on traversability of lodgepole pine forests for mountain pine beetle (Coleoptera: Scolytidae) and the use of patch metrics to estimate traversability. Canadian Entomologist 137: 566–583.

British Columbia Ministry of Forests and Range. 2007. Mountain pine beetle in British Columbia: Beetle facts infestation information. Online. Research Branch, British Columbia Ministry of Forests and Range, Victoria BC. Available from http://www.for.gov.bc.ca/hfp/mountain_pine_beetle/facts.htm.

— 2008. Provincial-level projection of the current mountain pine beetle outbreak: Update of the infestation projection based on the 2007 provincial aerial overview of forest health and revisions to the “Model” (BCMPB.v5).

Buckner, C.H. 1966. The role of vertebrate predations in the biological control of forest insects. Annual Review of Entomology 11: 449–470.

Bunnell, F.L. & Dunsworth, G.B. 2009. Forestry and biodiversity: learning how to sustain biodiversity in managed forests. UBC Press, Vancouver, BC. 374 p.

— , Squires, K.A. & Houde, I. 2004. Evaluating effects of large-scale salvage logging for mountain pine beetle on terrestrial and aquatic vertebrates. Mountain pine beetle initiative working paper 2004-2. Natural Resources Canada, Canadian Forest Service, Victoria, BC.

Burton, P.J., Balisky, A.C., Coward, L.P., Cumming, S.G. & Kneeshaw, D.D. 1992. The value of managing for biodiversity. Forestry Chronicle 68: 225–237.

Buongiorno, J., Dahir, S., Lu, H.C. & Lin, C.R. 1994. Tree size diversity and economic returns in uneven-aged forest stands. Forest Science 40: 83–103.

Carey, A.B. 2000. Effects of new forest management strategies on squirrel populations. Ecological Applications 10: 248–257.

— & Harrington, C.A. 2001. Small mammals in young forests: Implications for management for sustainability. Forest Ecology and Management 154: 289–309.

— , Kershner, J., Biswell, B. & DeToledo, L.D. 1999. Ecological scale and forest development: squirrels, dietary fungi, and vascular plants in managed and unmanaged forests. Wildlife Monographs 142: 1–71.

Cazares, E., Luoma, D.L., Amaranthus, M.P., Chambers, C.L. & Lehmkuhl, J.F. 1999. Interaction of fungal sporocarp production with small mammal abundance and diet in Douglas-fir stands of the southern Cascade range. Northwest Science 73: 64–76.

Deal, R.L. 2001. The effects of partial cutting on forest plant communities of western hemlock-Sitka spruce stands in southeast Alaska. Canadian Journal of Forest Research 31: 2067–2079.

Ecke, F., Löfgren, O., Hörnfeldt, B., Eklund, U., Ericsson, P. & Sörlin, D. 2001. Abundance and diversity of small mammals in relation to structural habitat factors. Ecological Bulletins 49: 165–171.

— , Löfgren, O. & Sörlin, D. 2002. Population dynamics of small mammals in relation to forest age and structural habitat factors in northern Sweden. Journal of Applied Ecology 39: 781–792.

Edgar, C.B. & Burk, T.E. 2001. Productivity of aspen forests in northeastern Minnesota, U.S.A., as related to stand composition and canopy structure. Canadian Journal of Forest Research 31: 1019–1029.

Ford, W.M. &, Rodrigue, J.L. 2001. Soricid abundance in partial overstory removal harvests and riparian areas in an industrial forest landscape of the central Appalachians. Forest Ecology and Management. 152: 159–168.

Franklin, J.F., Berg, D.R., Thornburgh, D.A. & Tappeiner, J.C. 1997. Alternative silvicultural approaches to timber harvesting: variable retention harvest systems. In: Kohm, K.A. & Franklin, J.F. (eds.). Creating a Forestry for the 21st Century: The Science of Ecosystem Management. Island Press, Washington, DC. p. 111–139.

— , Lindenmayer, D., MacMahon, J.A., McKee, A., Magnuson, J., Perry, D.A., Waide, R. & Foster, D. 2000. Threads of continuity: ecosystem disturbances, biological legacies and ecosystem recovery. Conservation Biology in Practice 1: 8–16.

— , Spies, T.A., Van Pelt, R., Carey, A.B., Thornburgh, D.A., Berg, D.R., Lindenmayer, D.B., Harmon, M.E., Keeton, W.S., Shaw, D.C., Bible, K. & Chen, J. 2002. Disturbances and structural development of natural forest ecosystems with silvicultural implications, using Douglas-fir forests as an example. Forest Ecology and Management 155: 399–423.

Gitzen, R.A., West, S.D., Maguire, C.C., Manning, T. & Halpern, C.B. 2007. Response of terrestrial small mammals to varying amounts and patterns of green-tree retention in Pacific Northwest forests. Forest Ecology and Management 251: 142–155.

Hagerman, S.M., Sakakibara, S.M. & Durall, D.M. 2001. The potential for woody understory plants to provide refuge for ectomycorrhizal inoculums at an interior Douglas-fir forest after clear-cut logging. Canadian Journal of Forest Research 31: 711–721.

Hallett, J.G. & O'Connell, M.A. 1997. Habitat occupancy and population patterns of small mammals in managed forests. In: Hallett, J.G. & O'Connell, M.A. (eds.). East-side Studies: Research Results. Volume 3 of Wildlife use of managed forests: a landscape perspective. Final report to the Timber, Fish, and Wildlife Cooperative Monitoring, Evaluation, and Research Committee. TFW-WL$_{4\text{-}98\text{-}003}$, Washington Department of Natural Resources, Olympia, WA. p. 2.1–2.16.

— , O'Connell, M.A. & Maguire, C.C. 2003. Ecological relationships of terrestrial small mammals in western coniferous forests. In: Zabel, C.J. & Anthony, R.G. (eds.). Mammal community dynamics. Management and conservation in forests of western North America. Cambridge University Press, Cambridge, UK. p. 120–156.

Hansen, A.J. & Hounihan, P. 1996. Canopy tree retention and avian diversity in the Oregon Cascades. In: Szaro, R.C. & Johnston, D.W. (eds.). Biodiversity in managed landscapes. Theory and practice. Oxford University Press. New York. p. 402–421.

Hitchcock, C.L. & Cronquist, A. 1973. Flora of the Pacific Northwest. University of Washington Press, Seattle, WA.

Holloway, G.L. & Malcolm, J.R. 2006. Sciurid habitat relationships in forests managed under selection and shelterwood silviculture in Ontario. Journal of Wildlife Management 70: 1735–1745.

Hurlbert, S.H. 1984. Pseudoreplication and the design of ecological field experiments. Ecological Monographs 54: 187–211.

Kirkland, G.L. 1990. Patterns of initial small mammal community change after clearcutting of North American forests. Oikos 59: 313–320.

Klenner, W. & Sullivan, T.P. 2009. Partial and clearcut harvesting of dry Douglas-fir forests: Implications for small mammal communities. Forest Ecology and Management 257: 1078–1086.

Krebs, C.J. 1991. Small mammal programs for mark-recapture analysis. Dept. of Zoology, University of B.C., Vancouver, Canada. 35 p.

— 1999. Ecological methodology. Addison Wesley Longman, Inc. 624 p.

— & Boonstra, R. 1984. Trappability estimates for mark-recapture data. Canadian Journal of Zoology 62: 2440–2444.

— , Keller, B.L. & Tamarin, R.H. 1969. Microtus population biology: demographic changes in fluctuating populations of Microtus ochrogaster and M. pennsylvanicus in southern Indiana. Ecology 50: 587–607.

Kuehl, R.O. 1994. Repeated measures designs. In: Statistical principles of research design and analysis. Duxbury Press, Belmont, CA. p. 499–528.

Landres, P.B., Verner, J. & Thomas, J.W. 1988. Ecological uses of vertebrate indicator species: a critique. Conservation Biology 2: 316–328.

Lazaruk, L.W., Kernaghan, G., Macdonald, S.E. & Khasa, D. 2005. Effects of partial cutting on the ectomycorrhizae of Picea glauca forests in north-western Alberta. Canadian Journal of Forest Research 35: 1442–1454.

Lindenmayer, D.B. & Noss, R.F. 2006. Salvage logging, ecosystem processes, and biodiversity conservation. Conservation Biology 20: 949–958.

— , Burton, P.J. & Franklin, J.F. 2008. Salvage logging and its ecological consequences. Island press, Washington, DC. 227 p.

Littel, R.C. 1989. Statistical analysis of experiments with repeated measures. HortScience 24: 36–40.

Magurran, A.E. 2004. Measuring biological diversity. Blackwell Publishing, Oxford, UK.

Martin, S.K. 1994. Feeding ecology of American martens and fishers. In: Buskirk, S.W., Harestad, A.S., Raphael, M.G. & Powell, R.A. (eds.). Martens, Sables, and Fishers. Biology and Conservation. Pages 297–315 Comstock Publishing Associates, Cornell University Press, Ithaca and London.

Maser, C. & Maser, Z. 1988. Interactions among squirrels, mycorrhizal fungi, and coniferous forests in Oregon. Great Basin Naturalist 48: 358–369.

— , Trappe, J.M. & Nussbaum, R.A. 1978. Fungal-small mammal interrelationships with emphasis on Oregon coniferous forests. Ecology 59: 799–809.

— , Anderson, R.G., Cromack, K. Jr., Williams, J.T. & Martin, R.E. 1979. Dead and down woody material. In: Thomas, J.W. (Tech. ed.). Wildlife habitats in managed forests: the Blue Mountains of Oregon and Washington. USDA Forest Service Agricultural Handbook No. 553. p.78–95.

— , Maser, Z., Witt, J.W. & Hunt, G. 1986. The northern flying squirrel: a mycophagist in southwestern Oregon. Canadian Journal of Zoology 64: 2086–2089.

Mazurek, M.J. & Zielinski, W.J. 2004. Individual legacy trees influence vertebrate wildlife diversity in commercial forests. Forest Ecology and Management 193: 321–334.

McComb, W.C., Spies, T.A. & Emmingham, W.H. 1993. Douglas-fir forests. Managing for timber and mature-forest habitat. Journal of Forestry 91: 31–42.

McDonough, T.J. & Rexstad, E. 2005. Short-term demographic response of the red-backed vole to spruce beetle infestations in Alaska. Journal of Wildlife Management 69: 246–254.

Meidinger, D. & Pojar, J. 1991. Ecosystems of British Columbia. Research Branch, Ministry of Forests, Victoria, British Columbia, Canada. Special Report Series Number 6.

Merritt, J.F. 1981. Clethrionomys gapperi. Mammalian species. No. 146. Amer. Soc. Mammal., Provo, Utah, USA.

Molina, R., O'Dell, T., Dunham, S. & Pilz, D. 1999. Biological diversity and ecosystem functions of forest soil fungi: management implications. In: Meurisse, R., Ypsilantis, W.G. & Seybold, C. (eds.). Proceedings: Pacific Northwest Forest & Rangeland Soil Organism Symposium, March 17–19, 1998, Oregon State University, Corvallis Oregon. USDA, Forest Service, Pacific Northwest Research Station, Portland Oregon, General Technical Report PNW-GTR-461.

Moses, R.A. & Boutin, S. 2001. The influence of clearcut logging and residual leave material on small mammal populations in aspen-dominated boreal mixedwoods. Canadian Journal of Forest Research 31: 483–495.

Nagaike, T., Kamitani, T. & Nakashizuka, T. 1999. The effect of shelterwood logging on the diversity of plant species in a beech (Fagus crenata) forest in Japan. Forest Ecology and Management 118: 161–171.

Nagorsen, D.W. 1996. Opossums, shrews, and moles of British Columbia. Volume 2. The mammals of British Columbia. UBC Press, Vancouver, BC, Canada.

Nelson, T., Boots, B., Wulder, M.A., Shore, T., Safanyik, L. & Ebata, T. 2006. Rating the susceptibility of forests to mountain pine beetle infestations: the impact of data. Canadian Journal of Forest Research 36: 2815–2825.

Nordyke, K.A. & Buskirk, S.W. 1991. Southern red-backed vole, Clethrionomys gapperi, populations in relation to stand succession and old-growth character in the central Rocky mountains. Canadian Field-Naturalist 105: 330–334.

North, M., Chen, J., Smith, G., Krakowiak, L. & Franklin, J. 1996. Initial response of understory plant diversity and overstory tree diameter growth to a green tree retention harvest. Northwest Science 70: 24–35.

Oaten, D.K. & Larsen, K.W. 2008. Aspen stands as small mammal "hotspots" within dry forest ecosystems of British Columbia. Northwest Science 82: 276–285.

Önal, H. 1997. Trade-off between structural diversity and economic objectives in forest management. American Journal of Agricultural Economics 79: 1001–1012.

Parish, R., Coupé, R. & Lloyd, D. 1996. Plants of Southern Interior British Columbia. Lone Pine Publishing, Vancouver, BC, Canada. 464 p.

Pearce, J. & Venier, L. 2005. Small mammals as bioindicators of sustainable boreal forest management.

Forest Ecology and Management 208: 153–175.

Peck, J.E. & McCune, B. 1997. Remnant trees and canopy lichen communities in western Oregon: a retrospective approach. Ecological Applications 7: 1181–1187.

Pommerening, A. 2002. Approaches to quantifying forest structures. Forestry 75: 305–324.

Ransome, D.B., Lindgren, P.M.F., Sullivan, D.S. & Sullivan, T.P. 2004. Long-term responses of ecosystem components to stand thinning in young lodgepole pine forest: I. Population dynamics of northern flying squirrels and red squirrels. Forest Ecology and Management 202: 355–367.

Roberts, M.R. & Zhu, L. 2002. Early response of the herbaceous layer to harvesting in a mixed coniferous-deciduous forest in New Brunswick, Canada. Forest Ecology and Management 155: 17–31.

Rose, C.R. & Muir, P.S. 1997. Green-tree retention: consequences for timber production in forests of the western Cascades, Oregon. Ecological Applications 7: 209–217.

Rosenvald, R. & Lohmus, A. 2008. For what, when, and where is green-tree retention better than clearcutting? A review of biodiversity aspects. Forest Ecology and Management 255: 1–15.

Safranyik, L. 2004. Mountain pine beetle epidemiology in lodgepole pine. In: Shore, T.L., Brooks, J.E. & Stone, J.E. (eds.). Challenges and Solutions: Proceedings of the mountain pine beetle symposium. Kelowna, BC, Canada. Oct. 30–31, 2003. Natural Resources Canada, Canadian Forest Service, Pacific Forestry Centre, Information report BC-X-399. p. 33–40.

Seber, G.A.F. 1982. The Estimation of Animal Abundance and Related Parameters. 2nd Edition. Charles Griffin, London, UK.

Shore, T.L., Safranyik, L., Hawkes, B.C. & Taylor, S.W. 2006. Effects of the mountain pine beetle on lodgepole pine stand structure and dynamics. In: Safranyik, L. & Wilson, B. (eds.). The Mountain Pine Beetle A Synthesis of Biology, Management, and Impacts on Lodgepole Pine. Natural Resources Canada, Canadian Forest Service, Victoria, BC. p. 95–114.

Simberloff, D. 1998. Flagships, umbrellas, and keystones: is single species management passé in the landscape era? Biological Conservation 83: 247–257.

Smith, D.M. 1986. The Practice of Silviculture. John Wiley and Sons, NY.

Smith, W.P., Anthony, R.G., Waters, J.R., Dodd, N.L. & Zabel, C.J. 2003. Ecology and conservation of arboreal rodents of western coniferous forests. In: Zabel, C.J. & Anthony, R.G. (eds.). Mammal community dynamics. Management and conservation in forests of western North America. Cambridge University Press, Cambridge, UK. p. 157–206.

— , Gende, S.M. & Nichols, J.V. 2005. The northern flying squirrel as an indicator species of temperate rain forest: test of an hypothesis. Ecological Applications 15: 689–700.

SPSS Institute Inc. 2007. Statistical Programs of the Social Sciences. Chicago, Illinois.

Staudhammer, C.L. & LeMay, V.M. 2001. Introduction and evaluation of possible indices of stand structural diversity. Canadian Journal of Forest Research 31: 1105–1115.

Stickney, P.F. 1985. Data base for early postfire succession on the sundance burn, northern Idaho. US Forest Service General Technical Report INT-189, Intermountain Research Station, Ogden, Utah, USA.

Stone, W.E. 1995. The impact of a mountain pine beetle epidemic on wildlife habitat and communities in post-epidemic stands of a lodgepole pine forest in northern Utah. Dissertation, Utah State University, Logan, USA.

Sullivan, T.P., Sullivan, D.S. & Kurta, C. 1999. Relations of small mammal populations to even-aged shelterwood systems: A reply. Journal of Wildlife Management 63: 1381–1389.

— , Sullivan, D.S. & Lindgren, P.M.F. 2000. Small mammals and stand structure in young pine, seed-tree, and old-growth forest, southwest Canada. Ecological Applications 10: 1367–1383.

— , Sullivan, D.S. & Lindgren P.M.F. 2001. Influence of variable retention harvests on forest ecosystems. I. Diversity of stand structure. Journal of Applied Ecology 38: 1221–1233.

— , Sullivan, D.S. & Lindgren, P.M.F. 2008. Influence of variable retention harvests on forest ecosystems: Plant and mammal responses up to 8 years post-harvest. Forest Ecology and Management 254: 239–254.

Tews, J., Brose, U., Grimm, V., Tielbörger, K., Wichmann, M.C., Schwager, M. & Jeltsch, F. 2004. Animal species diversity driven by habitat heterogeneity/diversity: the importance of keystone structures. Journal of Biogeography 31: 79–92.

Vahle, J.R. & Patton, D.R. 1983. Red squirrel cover requirements in Arizona mixed conifer forests. Journal of Forestry 81: 14–15, 22.

Van Wagner, C.E. 1968. The line intersect method in forest fuel sampling. Forest Science 14: 20–26.

Varga, P., Chen, H.Y.H. & Klinka, K. 2005. Tree-size diversity between single- and mixed-species stands in three forest types in western Canada. Canadian Journal of Forest Research 35: 593–601.

Waters, J.R. & Zabel, C.J. 1995. Northern flying squirrel densities in fir forests of northeastern California. Journal of Wildlife Management 59: 858–866.

Whitaker, J.O. 2004. Sorex cinereus. Mammalian Species 743: 1–9.

Wilson, K.R. & Anderson, D.R. 1985. Evaluation of two density estimators of small mammal population size. Journal of Mammalogy 66: 13–21.

Yahner, R.H. 1986. Microhabitat use by small mammals in even-aged forest stands. American Midland Naturalist 115: 174–180.

Zar, J.H. 1999. Biostatistical analysis. Prentice-Hall, Englewood Cliffs, NJ, USA.

Zenner, E.K. 2000. Do residual trees increase structural complexity in Pacific Northwest coniferous forests? Ecological Applications 10: 800–810.

Total of 97 references