

Article

Acceleration of Forest Structural Development for Large Trees and Mammals: Restoration in Decades or Centuries?

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Abstract: There is a demand for more progressive restoration directives to regenerate forest ecosystems impacted by harvesting, wildfire, insect outbreaks, and mineral resource extraction. Forest restoration may take many decades and even centuries without active silvicultural intervention to grow large trees that provide suitable habitat for various wildlife species. We tested the hypotheses (H) that, compared with unmanaged (unthinned and old-growth) stands, large-scale precommercial thinning (heavy thinning to <500 stems/ha) of young lodgepole pine (*Pinus contorta* var. *latifolia*), at 20–25 years post-treatment, would enhance: (H₁) the architecture of large overstory trees (e.g., diameter, height, and crown dimensions); (H₂) mean (i) total abundance and species diversity of forest-floor small mammals, (ii) abundance of tree squirrels; and (H₃) relative habitat use by mule deer (*Odocoileus hemionus*). There were three levels of thinning with mean densities of crop trees/ha: 353 (low), 712 (medium) and 1288 (high), an unthinned, and old-growth stand replicated at three areas in south-central British Columbia, Canada. Mammal abundance and habitat use were measured during the period 2013 to 2015. Mean diameter of crop trees was significantly different among stands with the low-density, medium-density, and old-growth stands having diameters larger than the high-density and unthinned stands. Mean height of crop trees was highest in the old-growth stands. Mean crown volume of crop trees was significantly different among stands with the low-density stands 2.1 to 5.8 times higher than the high-density, unthinned, and old-growth stands, and hence partial support for H₁. Mean total abundance of forest-floor small mammals was significantly different among stands with the low-density and old-growth stands 1.9 to 2.4 times higher than the other three treatment stands. Mean abundances per stand of the red squirrel (*Tamiasciurus hudsonicus*) (range of 4.8 to 12.0) and the northern flying squirrel (*Glaucomys sabrinus*) (range of 3.2 to 4.3) were similar among stands. Mean relative habitat use by mule deer was similar among stands, but variable with counts of pellet-groups/ha in the thinned stands were 3.8 to 4.2 and 2.1 to 2.3 times higher than the unthinned and old-growth stands, respectively. Thus, mean total abundance of forest-floor small mammals of H₂ was supported, but species diversity and abundance of tree squirrels was not. Enhanced relative habitat use by mule deer (H₃) was not supported. To our knowledge, this is the first concurrent measurement of several mammal species in heavily thinned, unthinned, and old-growth forest across three replicate study areas at 20–25 years post-treatment. Although not all mammal responses were significant, there was a strong indication that restored forests via heavy thinning (<500 trees/ha) produced large overstory trees (at least for diameter and crown dimensions) in stands 33 to 42 years old. Comparable old-growth stands, albeit with crop trees of greater height and merchantable volume, ranged from 120 to 167 years of age. Restored forests with large trees capable of supporting at least these mammal species may be achieved in decades rather than centuries.

Keywords: crown architecture; forest-floor small mammals; forest restoration; lodgepole pine; mule deer; large overstory trees; silviculture; stand thinning; tree squirrels



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1. Introduction

Forest restoration is heralded as a crucial endeavour for future economic and environmental sustainability in temperate and boreal coniferous forests of North America and Eurasia in the 21st century [1,2]. The current loss of forest cover from ongoing harvesting and unpredictable outbreaks of wildfire, insects, windthrow, and drought seems to be unprecedented in modern industrial times [3–6]. Paradoxically, there are growing demands to increase biomass production for timber and forest cover for conventional wood products, wood fibre for bioenergy production, and carbon sequestration to help mitigate climate change [7,8]. Despite the increased production imperative, there are new conservation strategies that seek to maintain intact habitat as well as increase the size of protected areas to conserve forest biodiversity and species at risk [9,10]. Concurrent with these conservation efforts is the concern for loss of old-growth forests, particularly in some jurisdictions in the Pacific Northwest (PNW) of North America where as little as 14–30% or less remain or is of poor quality [11,12]. All of these factors suggest strongly that a timber supply crisis is imminent or, in fact, has been affecting the forest industry for some time, at least in many parts of North America and Europe [7,13].

Further to this quandary is the demand for very large-scale restoration of lands disturbed by forest and mineral resource industries with respect to conservation of boreal and woodland caribou (*Rangifer tarandus*) populations [14]. In addition, “more progressive restoration directives that exceed the need to merely revegetate the land must be developed” to provide regenerated forest ecosystems and economic activities for both indigenous and rural communities [14]. Restoration of boreal and temperate forest ecosystems is a laudable goal for both economic and environmental reasons. However, forest regeneration and eventual restoration may take many decades and even centuries depending on tree species, ecosystem, temperate vs. boreal latitude, and adaptation to changing climatic conditions. Therefore, we seek to determine if there are ways to significantly accelerate restoration activities that grow new forests in reduced lengths of time (e.g., decades) that will provide both economic (e.g., timber and non-timber products) and environmental (e.g., wildlife habitat and biodiversity) benefits such as reduction in the need to harvest old-growth forests? There is a dearth of actual silvicultural treatments designed to grow timber rapidly while simultaneously enhancing other forest values such as conservation of biodiversity and wildlife habitats [15]. This conundrum is particularly clear when examining silvicultural treatment of young lodgepole pine (*Pinus contorta* var. *latifolia*) stands where pre-commercial thinning (PCT) may enhance diameter growth of crop trees [16]. However, the range of PCT density levels in young pine forests is quite narrow with a major focus on wood production (merchantable stand volume) from an economic perspective. Young lodgepole pine stands have historically been thinned operationally to within a very narrow range of stand densities, for example: 2000–3000 stems/ha in Alberta [17] and 2000–2900 stems/ha in British Columbia (BC), Canada [18–20], with very few stands <1000 stems/ha. Although PCT is geared to enhance merchantable volume of stands, the time-line for reaching operability in many of these high-density PCT stands is a rotation age of 80–100 years [20]. It is not clear how this range of rotation ages would ever fit into a much-needed mid-term timber supply [21] in any jurisdiction of which we are aware, nor to the forest restoration targets advocated by environmentalists.

In general, biomass production in boreal and temperate forests may be enhanced by silvicultural treatments such as stand thinning and fertilization [22–25]. Silvicultural interventions in young forests represent “active” rather than “passive” restoration [26–28] and ideally will help develop complex stand structure and late-seral structural features [29,30]. Thus, what is a realistic range of ages, or structural stages, of forest regeneration when the “restored forest” actually provides habitat attributes for wildlife, biodiversity, and potentially wood products? Clearly, this desirable goal needs to be in decades, not centuries, and most importantly, how do we get there? This question is particularly germane as we enter 2021–2030 which the United Nations General Assembly has declared as the “Decade on Ecosystem Restoration” [31]. There is much controversy over the relative successes

of “active” vs. “passive” restoration, but few studies have focused on animals and their responses to forest recovery [32].

2. Forest Restoration Structures and Mammals

Our premise in forest restoration rests on the assumption that if accelerated development of mature/old-growth forest attributes that include large diameters and crowns of crop trees, understory conifers, vegetation, and ingress are a goal, then stands need to be thinned to <1000 stems/ha, and likely to <500 stems/ha [29,33,34]. Fertilization may also be added either as a single or repeated application. Although there is some concern that these intensive practices may reduce biodiversity [35,36], the actual impacts of such practices have received little research attention [25,37]. In addition, there seems to be an increased understanding of the presumed relationship between a diversity of forest habitat conditions, wood production, and biodiversity [24,38,39]. To this end, structural attributes may constitute adequate surrogates of forest biodiversity and presumably wildlife habitats [40,41]. A major assumption is that the presence of wildlife species occupying restored forests should be linked to specific structural (ecological) features, such as large overstory trees, rather than just age of the forest [42]. To evaluate this assumption of how various mammal species might inhabit restored forests requires relatively long-term (i.e., decades) investigations as advocated by [10,15,25]. In addition, we need concurrent comparisons of the responses of mammal species in restored and mature/old-growth forests that have similar overstory coniferous stand structure composed of large trees with mean diameters ≥ 15 cm and mean heights ≥ 10 m, for example.

Forest-floor small mammals as a group and the arboreal American red squirrel (*Tamiasciurus hudsonicus*) and northern flying squirrel (*Glaucomys sabrinus*) may be considered candidate ecological indicators of mature successional coniferous forests across temperate and boreal North America [43]. The abundance and diversity of forest-floor small mammals may serve as ecological indicators of the effect of structural changes resulting from forest restoration via silvicultural practices [44,45]. This group is usually composed of specialist and generalist species that change in abundance as forest succession proceeds from the time of harvest (e.g., clearcutting) to mature and old forest conditions. The southern red-backed vole (*Myodes gapperi*) is a good candidate for evaluation of the development of “old forest” structural attributes in young stands [45,46]. Other specialist species include several species of field voles (*Microtus* spp.), the heather vole (*Phenacomys intermedius*), and *Sorex* shrews that may be found in “open” stand conditions dominated by forbs, grasses, and shrubs for up to 5–10 years after disturbance [46,47]. The generalist deer mouse (*Peromyscus maniculatus*) and northwestern chipmunk (*Neotamias amoenus*) occupy a variety of habitats after forest disturbance [46]. The early successional forest-floor species typically decline in abundance as canopy closure occurs in coniferous stands. The red squirrel and northern flying squirrel occupy older forests with tall trees, complex stand structure, snags, and large-diameter woody debris [48]. However, both sciurids seem to persist in a relatively broad range of young managed forest habitats, as well as in old-growth stands [43]. Functions of these small mammals include prey for many furbearers and raptors [49,50], distribution of beneficial mycorrhizal fungi [51], and consumers of invertebrates, plants and plant products [52].

Mule deer (*Odocoileus hemionus*) are another candidate indicator species in the Pacific Northwest of North America and a prominent mammal in many interior forest ecosystems, particularly Douglas-fir (*Pseudotsuga menziesii*). During winter months in areas of relatively high snowpacks, mule deer seem to require mature and old-growth forest stands with high levels of canopy closure [53]. These old forests have snow-interception cover, security cover, and availability of forage such as herbs, shrubs, arboreal lichen, and Douglas-fir litterfall [54].

Thus, we tested the hypotheses (H) that, compared with unmanaged (unthinned and old-growth) stands, large-scale PCT (heavy thinning to <500 stems/ha), of young lodgepole pine at 20–25 years post-treatment, would enhance: (H₁) the architecture of large overstory

trees (e.g., diameter, height, and crown dimensions); (H₂) mean (i) total abundance and species diversity of forest-floor small mammals, (ii) abundance and body mass of tree squirrels; and (H₃) relative habitat use by mule deer. We predict that the above response variables in heavily thinned stands will be comparable to or higher than those in uncut mature/old growth forest.

3. Materials and Methods

3.1. Study Areas and Experimental Design

Three study areas each containing several lodgepole pine stands were originally established in 1988 (Penticton) and 1993 (Summerland and Kelowna). The Penticton Creek area was located 15 km northeast of Penticton, British Columbia (BC) Canada (49°34' N; 119°27' W) with all stands located in the dry and cool Interior Douglas-fir (IDF_{dk}; d,k = dry precipitation regime, cool temperature regime) biogeoclimatic zone [55]. Stands were 0.2–2.3 km apart, ranged in area from 20 ha (each of the thinned pine stands) to 100+ ha (unthinned and old-growth stands), and were 17 years old in 1988 at the time of pre-commercial thinning (PCT). The Summerland study area was located in the Bald Range, 25 km west of Summerland in south-central BC (49°40' N; 119°53' W). The Kelowna study area was located 37 km northwest of Kelowna, BC (50°04' N; 119°34' W). Both areas are in the Montane Spruce (MS_{dm}; d,m = dry precipitation regime, mild temperature regime) biogeoclimatic zone [55]. Area of stands ranged from 8.9 to 11.3 ha (thinned and unthinned pine stands) to 100+ ha (old-growth stands), and all stands were 13 years old in 1993 at the time of PCT.

Dominant tree species in these stands included lodgepole pine with a minor component of Douglas-fir, interior spruce (*Picea engelmannii* × *P. glauca*), subalpine fir (*Abies lasiocarpa*), western larch, trembling aspen (*Populus tremuloides*), and black cottonwood (*P. trichocarpa*). Dominant understory vegetation included willow (*Salix* spp.), Sitka alder (*Alnus sinuata*), twinflower (*Linnaea borealis*), grouseberry (*Vaccinium scoparium*), fireweed (*Epilobium angustifolium*), pine grass (*Calamagrostis rubescens*), and Arctic lupine (*Lupinus arcticus*). Further descriptions of these study areas are provided in [42,56].

The study was a randomized complete block design based on geographic location and PCT with three replicate blocks each with five treatments: three thinning densities, an unthinned stand, and an old-growth stand. The key feature of this design was that some of the thinned stands had comparable sizes of overstory trees as those occurring in the old-growth stands. Comparisons of stand architecture, tree squirrels, and mule deer in this design had three replicates: Penticton, Summerland-1 and Summerland-2 blocks. Comparison of forest-floor small mammals among treatment stands had three replicates: Summerland-1, Summerland-2, and Kelowna blocks. This design reflected where mammal sampling had been possible in the various treatment stands and blocks.

In 2013, at 20- (Summerland and Kelowna replicates) and 25-years (Penticton replicate) post-thinning, each treatment block had three levels of PCT densities (mean ± SE) for lodgepole pine crop trees: (1) low-density (353 ± 102; range 210–550 stems/ha), (2) medium-density (712 ± 239; range 460–1190 stems/ha), and (3) high-density (1288 ± 192; range 1074–1670 stems/ha). An unthinned stand and an old-growth stand (age range 120–167 years) completed the design for each replicate block. Treatments were assigned to stands in a randomized complete block design. Pruning (3-m lift) was done in the low-density stand at Penticton in 1992 and in the low- and medium-density stands in 1998 at Summerland and Kelowna. Due to partial disturbance from mountain pine beetle (MPB) (*Dendroctonus ponderosae*) and a ground fire in 2008–2009, a low-density PCT stand was unavailable at Kelowna. The Penticton and Summerland study areas had little or no disturbance from MPB or fire. Characteristics of the stands at each area at 20–25 years after PCT are listed in Table 1.

Table 1. Experimental design and characteristics for crop trees in the three replicate blocks of lodgepole pine stands in 2013 at 20–25 years after pre-commercial thinning at Penticton and Summerland.

Replicate Block and Stand	Density (stems/ha)	Lodgepole Pine Crop Trees ¹ (Mean ± SE)		Total Understory Conifers/ha	DBH (cm)	Height (m)	Total Canopy Closure (%)
		Tree Crown Volume (m ³)	Basal Area (m ² /ha)				
Penticton							
Low	550	88.4 ± 7.4	21.2 ± 1.2	2040 ± 283	21.8 ± 0.3	13.9 ± 0.1	87.4 ± 1.3
Medium	1190	27.2 ± 4.1	33.5 ± 1.7	1475 ± 206	18.7 ± 0.2	15.4 ± 0.1	89.8 ± 0.7
High	1670	30.9 ± 3.4	39.3 ± 2.4	960 ± 186	16.9 ± 0.2	14.7 ± 0.1	92.3 ± 0.5
Unthinned	4462	7.7 ± 2.0	44.4 ± 7.2	3050 ± 603	10.6 ± 0.3	11.7 ± 0.2	88.9 ± 1.4
Old-growth	790 + 360 ²	8.1 ± 0.7	46.8 ± 3.9 ³	2390 ± 372	19.3 ± 0.5	21.0 ± 0.3	87.3 ± 1.7
Summerland-1							
Low	210	44.3 ± 4.0	5.5 ± 0.2	4845 ± 681	19.4 ± 0.4	10.2 ± 0.2	70.4 ± 2.9
Medium	460	45.7 ± 3.7	11.0 ± 0.5	4290 ± 593	16.8 ± 0.4	9.6 ± 0.2	76.5 ± 3.5
High	1119	23.0 ± 1.2	21.6 ± 1.0	2041 ± 206	15.0 ± 0.2	9.3 ± 0.1	86.7 ± 1.2
Unthinned	3617	7.8 ± 1.4	25.5 ± 2.6	6413 ± 167	9.0 ± 0.4	9.9 ± 0.1	91.9 ± 0.7
Old-growth	330 + 440 ²	-	31.3 ± 2.2 ³	2720 ± 530	17.4 ± 3.4	15.3 ± 2.6	82.4 ± 4.4
Summerland-2							
Low	300	41.3 ± 3.4	6.8 ± 0.2	1370 ± 285	19.4 ± 0.3	9.2 ± 0.1	73.3 ± 4.2
Medium	485	41.8 ± 2.6	13.5 ± 0.5	2060 ± 342	18.3 ± 0.3	9.2 ± 0.1	86.1 ± 1.7
High	1074	27.6 ± 3.2	27.5 ± 0.9	779 ± 95	16.5 ± 0.3	9.7 ± 0.1	88.8 ± 2.4
Unthinned	1675	19.1 ± 2.4	28.5 ± 1.7	4095 ± 430	14.4 ± 0.4	9.5 ± 0.1	87.1 ± 0.8
Old-growth	760 + 240 ²	11.9 ± 1.1	39.8 ± 2.5 ³	2920 ± 445	18.6 ± 0.6	17.9 ± 0.7	88.8 ± 1.4

¹ Crop trees of lodgepole pine were those trees retained during the PCT treatment. ² Total crop trees in old-growth stands included lodgepole pine + other coniferous species. ³ Basal area for old-growth stands included all crop tree species.

3.2. Size and Crown Dimensions of Crop Trees

Diameter, height, and crown dimensions of crop trees in all stands were measured to determine relative tree size at 20- to 25-years after PCT. Merchantable volume of stands was estimated to determine the potential economic impact of these treatments. Sampling of lodgepole pine crop trees was done with permanent variable-radius plots, systematically located in each of the three (PCT) young pine stands. Plot density was 20 per managed stand at Penticton and ranged from 11 to 29 at Summerland depending on stand area. The 10 crop trees closest to each plot center were permanently tagged in all stands immediately after thinning to represent the “original” crop trees. In the unthinned stands, crop trees (dominant or co-dominant stems of good form) were chosen on the basis that those trees would be left as the future crop if the stand was thinned. Measurements of dbh (diameter at breast height, 1.3 m above soil surface) (cm) and total height (m) were done after the growing season in 2013 to provide 20- and 25-year responses to PCT. Measurement of tree heights were to the nearest 0.1 m using a digital hypsometer (Forester Vertex).

Tree volume (VT) and merchantable tree volume (VM) were calculated using the equations of [57]:

$$VT (dm^3) = ((Dbhob^2)/(A + (B/Ht))) * 1000 \quad (1)$$

where A = 158.12 and B = 23881.7 and

$$VM (dm^3) = VT(dm^3) * ((A + (B * X)) + (C * (X^2))) \quad (2)$$

where A = 0.9604, B = −0.1660, and C = −0.7868

$$\text{and } X = ((\text{top dib} / \text{dbhob})^2) * (1.0 + (\text{stump ht} / \text{total ht}))$$

where top dib = 7.5 cm and stump ht = 0.15 m.

Merchantable volume is total volume minus the volume of the stem below stump height (30 cm) and above the point where the stem has a diameter of 10 cm. At the stand level, total and merchantable volume/ha were estimated by multiplying the mean tree values by an estimate of density (stems/ha) for each stand.

Height (m) and width (m) of tree crowns were measured for all sample crop trees in every other plot in the thinned stands, and in every plot in the unthinned and old-growth

stands, at each study area. Crown volume (CRVOL) was represented by a cone shape and was calculated by:

$$\text{CRVOL (m}^3\text{)} = 1/3 ((h) (\pi r^2)) \quad (3)$$

where h = height of crown (m), $\pi = 3.14$, and r = one-half diameter of crown at the widest point (m).

In each of the three old-growth stands, ten temporary plots were located every 50 or 100 m in a grid pattern throughout the stand to provide measurements of mean dbh, total top height, and crowns for comparison of tree size dimensions with the young pine stands.

In the interval between the central plot tree and its nearest neighbour, percent canopy closure (CC) was estimated by four spherical densiometer measurements, one in each of the four cardinal directions [58]. This resulted in 80 densiometer measurements for each of the thinned and unthinned stands and 40 measurements in each of the old-growth stands.

3.3. Understory Coniferous Stand Structure

Sampling of understory 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 m²) located in the center of each crop tree plot in fall 2013. Understory trees were seedlings (0–1 m), small saplings (1–2 m), or large saplings (2–3 and >3 m). Total abundance of conifers per ha was calculated for all four classes.

3.4. Forest-Floor Small Mammals and Tree Squirrels

Forest-floor small mammal populations were sampled in the two Summerland and one Kelowna replicate blocks at 4-week intervals from May to October 2013 and 2014. One live-trapping grid (1 ha) was located in each of the 15 sites and had 49 (7 × 7) trap stations at 14.3-m intervals with one Longworth live-trap at each station. Traps were supplied with whole oats and carrot, with cotton as bedding. Each trap had a 30-cm × 30-cm plywood cover for protection from sunlight (heat) and precipitation. Traps were set on the afternoon of day 1, checked on the mornings of days 2 and day 3, and then locked open between trapping periods. All small mammals captured were ear-tagged with serially numbered tags and point of capture recorded. Animals were released on the grids immediately after processing. Unfortunately, there was a high mortality rate for shrews in the traps overnight, but this was unavoidable in practice. Therefore, shrews were collected, frozen, and later identified according to [59].

Squirrel populations were sampled in September and November 2014 and in November 2015 at each of the three replicate blocks. Each of the 15 sites had a grid of two (2 × 15) or three (3 × 10) lines with trap 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 each station. The 2 × 15 and 3 × 10 grid lines were each separated by 90 m; both grid shapes were designed to represent the configuration of a 9-ha rectangle or square as per [60]. Traps were baited with sunflower seeds (*Helianthus annuus*) and a slice of apple; and covered with a sheet of tar paper for insulation and protection from precipitation. 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 closed between trapping periods. All squirrels captured were ear-tagged with serially numbered tags, weighed on Pesola spring balances, and point of capture recorded [60]. Squirrels were released on the grids immediately after processing.

All handling of animals followed guidelines approved by the American Society of Mammalogists [61] and the Animal Care Committee, University of British Columbia.

3.5. Demographic Analysis

Abundance estimates of the red-backed vole, deer mouse, and northwestern chipmunk were derived from the Jolly-Seber (J-S) stochastic model for open populations with small sample size corrections [62,63]. Minimum number alive was used to estimate populations of the long-tailed vole (*Microtus longicaudus*), meadow vole (*M. pennsylvanicus*) and heather

vole; number of individuals was used for the montane shrew (*S. monticolus*) and common shrew (*S. cinereus*). These estimates are a density index [64]. Species richness was the total number of species sampled for the mammal communities in each site [63]. Species diversity was based on the Shannon-Wiener index which is well represented in the ecological literature [65]. Mean annual measurements of abundance, species richness, and species diversity of small mammals were calculated using the estimated parameter for each species or community for a given sampling period and then averaged over the number of sampling periods for each year.

Minimum number alive was used to estimate abundance of *T. hudsonicus* and *G. sabrinus* as an index of population size [64]. To provide an index of body condition [66], mean body mass was derived from the sample of animals captured in each trapping session and then summed for each trapping period. Comparisons of body mass between treatments were based on a mean value for each adult in the non-breeding period (e.g., autumn) which were then averaged for each year of the study. Mass (g) at sexual maturity was used to determine age classes: *T. hudsonicus*, juvenile < 180; adult $\geq$ 180; *G. sabrinus*, juvenile < 100; adult $\geq$ 100. Movements of squirrels among stands between trapping periods were recorded for each species.

3.6. Relative Habitat Use by Mule Deer

Sampling of fecal pellet-groups was used to measure relative habitat use by mule deer in May 2013 in all treatment sites. This sampling time represented an accumulation of pellet-groups over the period since the last sampling and clearing of plots in 2008. All new and recent pellet-groups (minimum of 20 pellets per group) were counted on permanent 5-m² ($r = 1.26$ m) circular plots [67]. Sample plots were located systematically, in 5-plot arrays installed at stations every 50 m, for a total of 100 plots in each stand at Penticton and 55 to 145 at Summerland. Plots were permanently marked with a flagged aluminum “pig-tail” stake and a small painted rock was located in the plot center to counter disruption by cattle (*Bos taurus*) or other large mammals. Counts of pellet-groups used a rope of 1.26-m radius attached to the center stake and rotated around the plot. Pellet-groups located on the edge of a sample plot had to have 50% or more of the group within the plot to be counted. This technique, consistency of sampling personnel, and the relatively small edge to area ratio of our plots likely minimized potential inclusion bias. Pellet-group degradation was not likely an issue as only new pellets deposited during the 5-year period since the fall of 2008 were counted. Although decomposition rates of pellets may be variable in different habitats and periods [68], we have assumed that such conditions were consistent in our treatment sites in relatively dry ecosystems. Density of pellet-groups was estimated per 5 m² plot and then converted to a per ha value.

3.7. Statistical Analysis

A randomized block one-way analysis of variance (ANOVA) model III [69] was conducted to determine the effect of stand treatment (3 levels of PCT: low, medium, and high, plus unthinned and old-growth) on mean values for stand density, diameter, height, crown volume, basal area, and merchantable volume of crop trees, abundance of understory conifers, and canopy closure. This same analysis was conducted to detect differences among treatment sites for relative habitat use (cumulative number of pellet-groups/ha) by mule deer. A repeated-measures analysis of variance (RM-ANOVA) [69] was used to determine the effect of the five treatments on mean values for total abundance, species richness, and species diversity of the forest-floor small mammal community, as well as time and treatment $\times$ time interactions. This same analysis was also conducted to compare mean abundance of *M. gapperi*, *P. maniculatus*, *N. amoenus*, *T. hudsonicus*, *G. sabrinus*, and the less common species that had sufficient sample size for analysis, as well as mean body mass of each tree squirrel species. Homogeneity of variance was assessed with Levene’s test of equality of error variances. Sphericity (independence of data among repeated measures) was not an issue with just two years of data. Proportional data were transformed by arcsin

square root [70]. Duncan's multiple range test (DMRT), with multiple contrasts, was used to compare mean values whenever a significant difference was found based on ANOVA results [71]. In all analyses, the level of significance was at least $p = 0.05$ [72].

4. Results

4.1. Architecture of Large Trees

Mean density of lodgepole pine crop trees was significantly ($F_{4,8} = 11.37$; $p < 0.01$) different among stands with the thinned and old-growth stands having fewer (DMRT; $p = 0.05$) trees (range of 353 to 1288 trees/ha) than the unthinned stands (Table 2). Mean diameter of crop trees was significantly ($F_{4,8} = 21.71$; $p < 0.01$) different among stands with the low-density, medium-density, and old-growth stands having diameters larger (DMRT; $p = 0.05$) than the high-density and unthinned stands (Table 2; Figure 1a). Mean height of crop trees was also significantly ($F_{4,8} = 24.25$; $p < 0.01$) different among stands with the old-growth stands (mean = 18.1 m) having taller (DMRT; $p = 0.05$) trees than any of the other four treatments which were all similar in height ranging from 10.4 to 11.4 m (Table 2; Figure 1b).

Table 2. Mean ($n = 3$ replicate sites) $\pm$ SE 20- to 25-year responses of overstory crop trees and understory conifer attributes for lodgepole pine stands with three post-thinning (PCT) densities, unthinned, and old-growth treatments. Results of analysis of variance (ANOVA) are also provided. Within a row, mean values with different letters (a, b, or c) are significantly different by Duncan's multiple range test. Significant values in bold text.

Stand Attribute	Treatment					ANOVA	
	Low	Medium	High	Unthinned	Old-Growth	$F_{4,8}$	p
Density pine crop trees/ha	353.3 $\pm$ 101.7b	711.7 $\pm$ 239.3b	1287.7 $\pm$ 191.6b	3251.3 $\pm$ 825.1a	973.3 $\pm$ 110.5b	11.37	<0.01
DBH (cm)	20.2 $\pm$ 0.8a	17.9 $\pm$ 0.6ab	16.1 $\pm$ 0.6b	11.3 $\pm$ 1.6c	18.4 $\pm$ 0.6ab	21.71	<0.01
Height (m)	11.1 $\pm$ 1.4b	11.4 $\pm$ 2.0b	11.2 $\pm$ 1.7b	10.4 $\pm$ 0.7b	18.1 $\pm$ 1.6a	24.25	<0.01
Basal area (m ² /ha)	11.2 $\pm$ 5.0c	19.3 $\pm$ 7.1bc	29.5 $\pm$ 5.2abc	32.8 $\pm$ 5.9ab	39.3 $\pm$ 4.5a	56.03	<0.01
Merchantable volume (m ³ /ha)	68.6 $\pm$ 34.4	112.9 $\pm$ 59.1	155.8 $\pm$ 51.3	128.6 $\pm$ 29.7	246.1 $\pm$ 27.8	3.09 ¹	0.09
Crown volume (m ³ /tree)	58.0 $\pm$ 15.2a	38.2 $\pm$ 5.6ab	27.2 $\pm$ 2.3b	11.5 $\pm$ 3.8b	10.0 $\pm$ 1.9b	4.93 ¹	0.03
Canopy closure (%)	77.0 $\pm$ 5.3	84.1 $\pm$ 4.0	89.3 $\pm$ 1.6	89.3 $\pm$ 1.4	86.2 $\pm$ 1.9	3.59	0.06
Total understory conifers (trees/ha)	2752 $\pm$ 1064ab	2608 $\pm$ 858ab	1260 $\pm$ 394b	4519 $\pm$ 994a	2677 $\pm$ 154ab	5.98	0.02
Mule deer (pellet-groups/ha)	694.0 $\pm$ 87.7	700.0 $\pm$ 399.5	758.0 $\pm$ 113.8	180.7 $\pm$ 42.3	332.0 $\pm$ 28.0	1.93	0.20

¹ $F_{4,7}$.

Mean basal area was significantly ($F_{4,8} = 56.03$; $p < 0.01$) different among stands with the medium-density, high-density, and old-growth stands having the highest (DMRT; $p = 0.05$) and similar coverage of tree stems. The medium-density, high-density, and unthinned stands had similar mean basal areas as did the three thinned stands (Table 2). Mean merchantable volume (m³/ha) was similar ($p = 0.09$) among stands but with considerable variability ranging from 68.6 to 155.8 m³/ha in the young pine stands and up to 246.1 in the old-growth stands (Table 2; Figure 1c).

Mean crown volume of lodgepole pine crop trees was significantly ($F_{4,7} = 4.93$; $p = 0.03$) different among stands with the low-density stands 2.1 to 5.8 times higher (DMRT; $p = 0.05$) than the high-density, unthinned, and old-growth stands, but similar to the medium-density stands (Table 2; Figure 1b). Mean canopy closure was similar ($p = 0.06$) statistically among stands but did range from 77% (low-density) to 89% (medium-density and unthinned) (Table 2). Mean density of understory conifers was significantly ($F_{4,8} = 6.00$; $p = 0.02$) different among stands but with similar numbers in the low-, medium-density, and old-growth stands ranging from 2608 to 2752 trees/ha (Table 2).

4.2. Forest-Floor Small Mammals

A total of 1012 individual forest-floor small mammals representing eight species were captured in the 2-year study. The red-backed vole was most common with 480 individuals followed by the deer mouse (216), northwestern chipmunk (107), montane shrew (81), masked shrew (73), heather vole (38), long-tailed vole (11), and meadow vole (6). Mean total abundance (as a density index) was significantly ($F_{4,7} = 7.79$; $p = 0.01$) different among stands with the low-density and old-growth stands 1.9 to 2.4 times higher (DMRT; $p = 0.05$).

than the other three treatment stands (Table 3). The pattern of population changes over the two years clearly illustrated this difference with peak annual mean numbers in low-density and old-growth stands reaching 31 and 25 in 2013 and 22 and 19 in 2014, respectively (Figure 2). Mean numbers in the other three stands were consistently similar throughout the two years. Mean species richness and diversity approached statistical significance ($p \leq 0.10$) and increased significantly ($p < 0.01$) from 2013 to 2014 (Table 3). Both measures tended to be higher in the low-density, high-density, and old-growth stands.

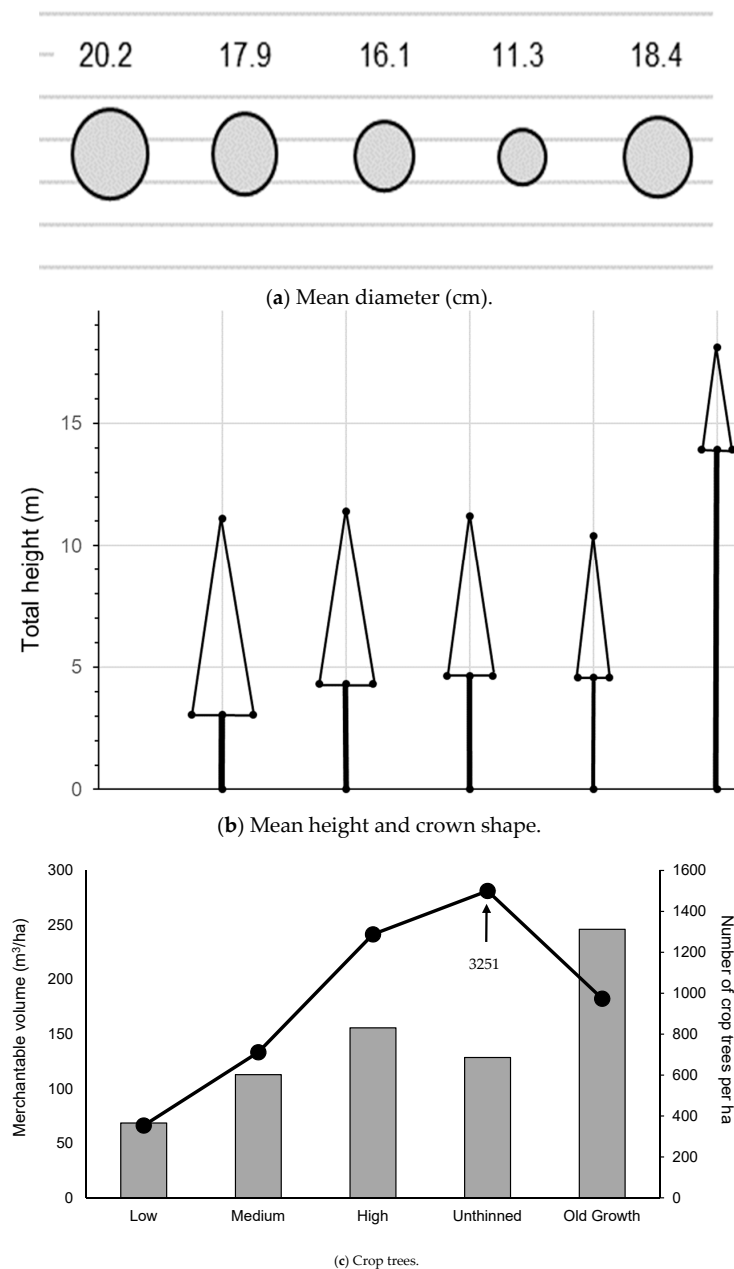


Figure 1. Profiles of lodgepole pine crop trees (large overstory trees) with three densities of thinned stands, an unthinned stand, and an old-growth stand in 2013 at 20–25 years after precommercial thinning: (a) mean diameter (cm), (b) mean total height (m) and crown shape, and (c) mean merchantable volume (m^3/ha) and number of trees/ha.

Table 3. Overall mean ($n = 6$; 3 replicate sites $\times$ 2 years) $\pm$ SE abundance (density index) of each species, total abundance, species richness, and species diversity of the forest-floor small mammal community (2013–2014), and abundance and body mass of tree squirrels (2014–2015) in the five treatments, and results of RM-ANOVA. Within a row mean values with different letters (a, b, or c) are significantly different by Duncan’s multiple range test. Significant values in bold text.

Species and Parameter	Low ¹	Medium	Treatment High	Unthinned	Old-Growth	RM-ANOVA Treatment		Time		Treatment $\times$ Time	
						$F_{4,7}$	p	$F_{1,9}$	p	$F_{4,9}$	p
<i>M. gapperi</i>	10.4 $\pm$ 2.7a	0.7 $\pm$ 0.5bc	3.5 $\pm$ 0.8bc	4.8 $\pm$ 1.1abc	8.6 $\pm$ 2.7ab	3.97	0.05	1.61	0.24	0.13	0.97
<i>P. maniculatus</i>	1.9 $\pm$ 1.0	2.7 $\pm$ 1.0	2.0 $\pm$ 0.7	1.5 $\pm$ 0.7	2.1 $\pm$ 0.4	0.76	0.58	15.59	<0.01	0.44	0.78
<i>N. amoenus</i>	2.7 $\pm$ 0.4ab	2.1 $\pm$ 0.5ab	0.7 $\pm$ 0.3b	0.5 $\pm$ 0.2b	3.1 $\pm$ 0.4a	4.19	0.05	0.01	0.92	0.21	0.93
<i>P. intermedius</i>	0.2 $\pm$ 0.1	0.5 $\pm$ 0.3	0.3 $\pm$ 0.1	0.03 $\pm$ 0.03	0.03 $\pm$ 0.03	2.51	0.14	0.27	0.62	0.16	0.95
<i>S. monticolus</i>	0.7 $\pm$ 0.3	0.3 $\pm$ 0.2	0.6 $\pm$ 0.2	0.5 $\pm$ 0.4	0.6 $\pm$ 0.2	1.17	0.40	3.84	0.08	0.06	0.99
<i>S. cinereus</i>	0.6 $\pm$ 0.2	0.4 $\pm$ 0.1	0.7 $\pm$ 0.2	0.4 $\pm$ 0.1	0.3 $\pm$ 0.3	2.82	0.11	1.22	0.07	0.06	0.99
<i>M. longicaudus</i>	0.0	0.2 $\pm$ 0.1	0.0	0.0	0.1 $\pm$ 0.1	-	-	-	-	-	-
<i>M. pennsylvanicus</i>	0.04 $\pm$ 0.04	0.03 $\pm$ 0.03	0.05 $\pm$ 0.03	0.06 $\pm$ 0.06	0.0	-	-	-	-	-	-
Total abundance	16.5 $\pm$ 2.5a	7.0 $\pm$ 0.9b	7.8 $\pm$ 0.8b	7.7 $\pm$ 0.8b	14.8 $\pm$ 2.2a	7.13	0.01	0.33	0.58	0.21	0.93
Species richness	3.31 $\pm$ 0.35	2.44 $\pm$ 0.22	3.10 $\pm$ 0.36	2.33 $\pm$ 0.25	3.07 $\pm$ 0.23	3.24	0.08	15.60	<0.01	0.25	0.90
Species diversity	1.18 $\pm$ 0.13	0.94 $\pm$ 0.11	1.20 $\pm$ 0.19	0.78 $\pm$ 0.18	1.24 $\pm$ 0.18	3.00	0.10	17.33	<0.01	0.98	0.46
	Low	Medium	High	Unthinned	Old-growth	$F_{4,8}$	p	$F_{1,10}$	p	$F_{4,10}$	p
<i>T. hudsonicus</i>	6.3 $\pm$ 1.8	6.2 $\pm$ 1.2	7.2 $\pm$ 0.7	4.8 $\pm$ 1.1	12.0 $\pm$ 2.4	3.25	0.07	2.38	0.15	0.26	0.90
<i>G. sabrinus</i>	3.3 $\pm$ 0.8	4.3 $\pm$ 0.8	3.2 $\pm$ 0.3	4.0 $\pm$ 1.6	3.3 $\pm$ 1.7	0.17	0.95	0.66	0.44	0.17	0.95
Mean body mass											
<i>T. hudsonicus</i>	221.6 $\pm$ 1.1a	214.8 $\pm$ 3.3ab	208.9 $\pm$ 2.6b	210.3 $\pm$ 3.4b	218.4 $\pm$ 4.7a	6.50	0.01	0.13	0.73	0.35	0.84
<i>G. sabrinus</i>	136.7 $\pm$ 3.8	129.3 $\pm$ 4.5	133.5 $\pm$ 2.5	128.5 $\pm$ 3.7	130.9 $\pm$ 6.0	0.50 ²	0.74	0.03	0.87	0.12	0.97

¹ Two replicate sites. ² $F_{4,7}$.

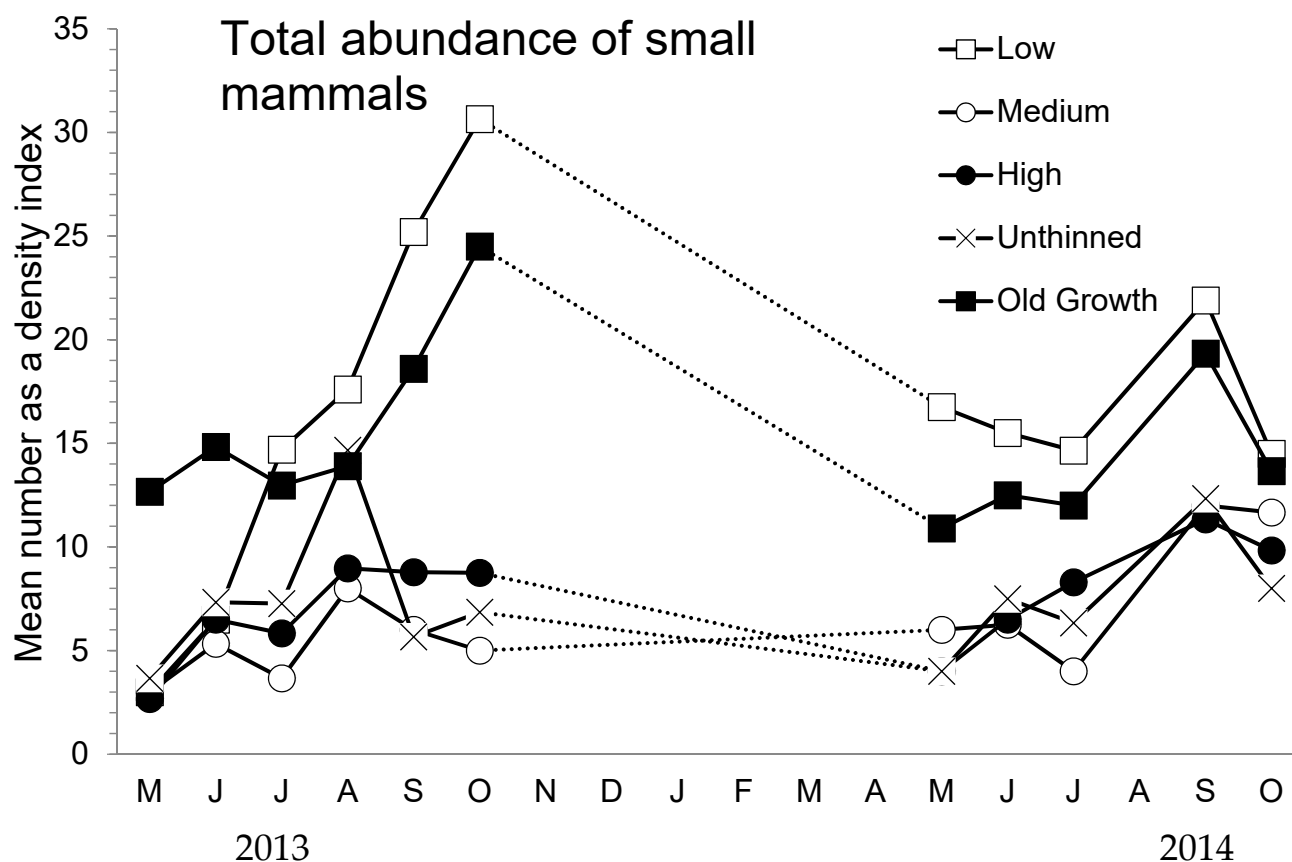


Figure 2. Mean ($n = 3$ replicate sites) total abundance of forest-floor small mammals as an index based on Jolly-Seber population estimates 2013 to 2014 in three thinned, unthinned, and old-growth stands in south-central British Columbia, Canada. Datapoints indicate individual trapping weeks each summer (May to October) and dots indicate the winter period when we did not sample populations.

Mean abundance of the dominant species, *M. gapperi*, was significantly ($F_{4,8} = 3.97$; $p = 0.05$) different among stands being 2.2 to 17.4 times higher in the low-density and old-growth stands than other stands (Table 3). Mean abundance of *N. amoenus* was significantly ($F_{4,7} = 4.19$; $p = 0.05$) different among stands with higher (DMRT; $p = 0.05$) numbers (3.5 to 5.2 times) in the two lower-density and old-growth stands than the high-density and unthinned stands. Mean abundance of *P. maniculatus* and the less common *P. intermedius* and two *Sorex* species were similar ($p \geq 0.11$) among stands.

4.3. Tree Squirrels

We captured 214 individuals of *T. hudsonicus* in 309 captures and 112 individuals of *G. sabrinus* in 140 captures during the autumn trapping periods in 2014–2015. Mean abundance (as an index) of *T. hudsonicus* was similar ($p = 0.07$) among stands ranging from 4.8 (unthinned stands) to 12.0 (old-growth stands) squirrels per stand (Table 3; Figure 3a). Mean abundance of *G. sabrinus* was also similar ($p = 0.95$) among stands ranging from 3.2 to 4.3 squirrels per stand (Table 3; Figure 3b). Mean numbers of red squirrels in the old-growth stands and flying squirrels in the unthinned and old-growth stands showed the most variability with a significant block effect for *G. sabrinus* at the second Summerland replicate. Mean body mass of adult red squirrels was significantly ($F_{4,8} = 6.50$; $p = 0.01$) different among stands with the low-density and old-growth stands having heavier (DMRT; $p = 0.05$) animals than the high-density and unthinned stands (Table 3). Mean body mass of

adult flying squirrels was similar among stands. There were few movements of individual squirrels among stands: five *T. hudsonicus* and two *G. sabrinus*.

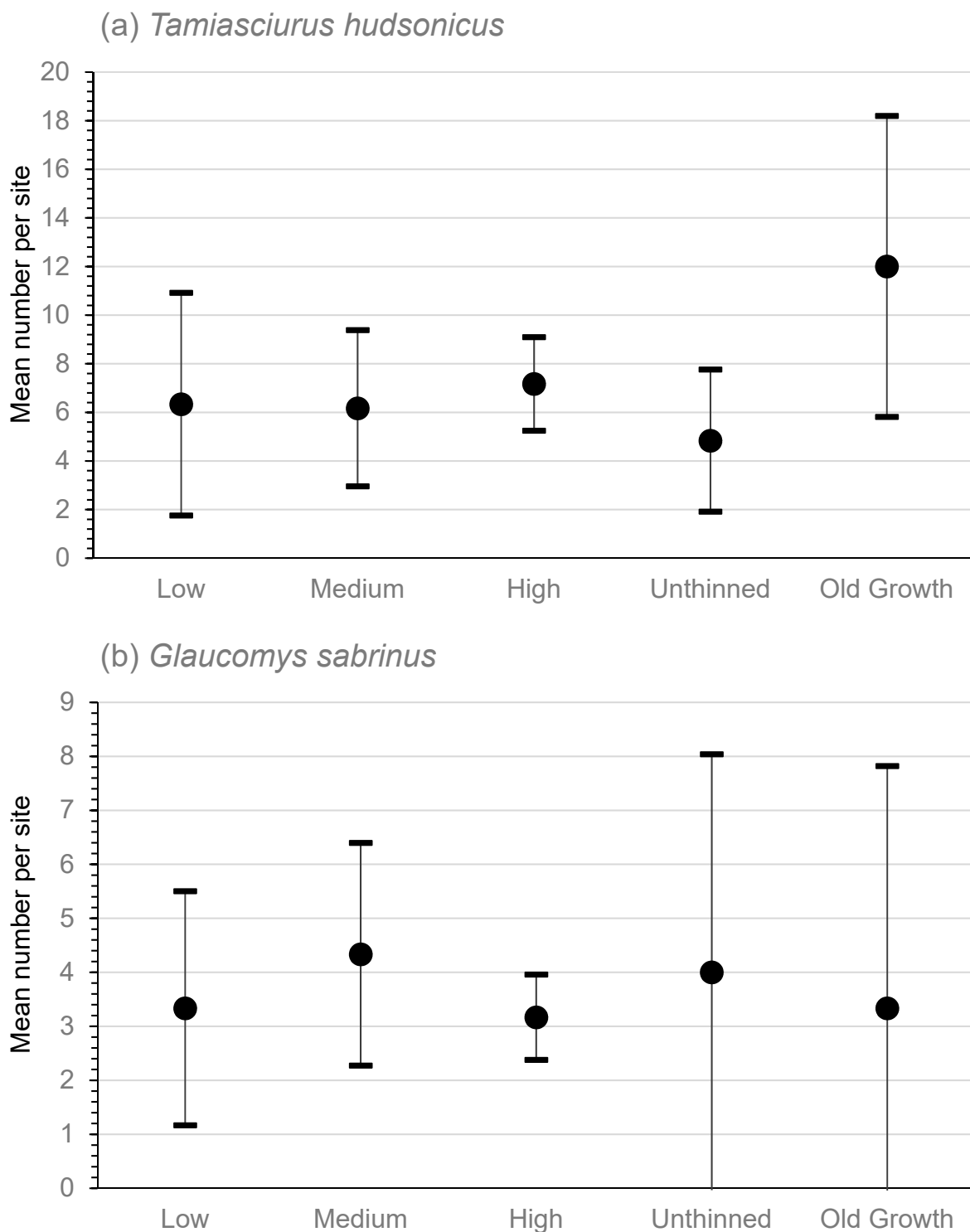


Figure 3. Mean ($n = 6$; 3 replicate sites $\times$ 2 years) $\pm$ 95% CIs abundance as an index based on minimum number alive population estimates 2014 to 2015 in three thinned, unthinned, and old-growth stands in south-central British Columbia, Canada: (a) *Tamiasciurus hudsonicus* and (b) *Glaucomys sabrinus*.

There were no significant interaction effects of treatment $\times$ time for either small mammals as a group or for tree squirrels.

4.4. Relative Habitat Use by Mule Deer

Mean relative habitat use by mule deer in pellet-groups/ha was similar ($p = 0.20$) among stands with the three thinned stands at a range of 694 to 758 and the unthinned and old-growth stands at 181 and 332, respectively (Table 2). Although not formally significant, these variable counts of pellet-groups/ha in the thinned stands (particularly in the medium-density) were 3.8 to 4.2 and 2.1 to 2.3 times higher than the unthinned and old-growth stands, respectively.

5. Discussion

5.1. Architecture of Large Trees

Our investigation of replicated large-scale thinning experiments in young lodgepole pine stands at 20- to 25-years post-treatment has resulted in large diameter crop trees with substantial crowns and relatively lower canopy closure in the low- and medium-density stands. The comparable mean diameters and abundance of total understory conifers in these heavily thinned and old-growth stands seemed to fit the prediction of a congruence of structural attributes in these different-aged stands. However, mean heights of crop trees in the young stands did not follow this pattern and remained relatively unaffected by thinning compared with the old-growth stands. Thus, H_1 , that large-scale PCT with heavy thinning to <500 stems/ha would enhance the architecture of large overstory trees was partially supported for diameter and crown dimensions.

Mean basal area was less in the low-density than old-growth stands but similar to the other thinned stands. In addition, mean merchantable volume of crop trees seemed to be higher in the old-growth than other stands (although not statistically significant) owing to greater height growth, but the medium-density, high-density and unthinned stands were comparable in this economic metric. There were high numbers of crop trees in the unthinned stands but the estimated merchantable volume was similar to the thinned stands because of the relatively small mean diameters.

A general list of old-growth structural attributes has been compiled over the last three decades and includes: (1) large dominant trees with substantial crowns, (2) multi-layered canopies of coniferous trees, (3) snags, (4) an abundance of coarse woody debris, (5) canopy gaps, and (6) understory patchiness with some herb and shrub development [73,74]. Our low- and medium-density stands seem to have achieved attributes 1, 2, 5, and 6. The structural diversity of coniferous trees (attribute 2) and understory patchiness of herbs and shrubs (attribute 6) was reported in these same stands in earlier analyses [42,56]. Clearly, the development of large trees in restored forests to emulate at least some old-growth attributes requires silvicultural interventions that substantially reduce tree density at a relatively early age and over meaningful areas of land. Such large trees, whether old- or second-growth, also have considerable implications through time for future wood supply and enhanced carbon storage [75,76].

5.2. Forest Restoration and Mammals

We evaluated the responses of forest-floor small mammals, tree squirrels, and mule deer concurrently in a range of thinned, unthinned, and old-growth stands of lodgepole pine at 20–25 years post-treatment. Despite the differences in ages, 33–42 years for the young stands and 120–167 years for the old-growth stands, mean total abundance of small mammals was similar in the low-density and old-growth stands. *M. gapperi* was the major species and also followed this pattern of abundance among stands during the two years of sampling. In addition, measurements of reproduction, recruitment, and survival of *M. gapperi*, in the one replicate reported by [56], were comparable in low-density and old-growth stands. Red-backed vole populations that reach “old-forest” levels of abundance suggested that networks of food sources (e.g., fungi) and predators (e.g., small mustelids) may also be present as components of biodiversity. Similar results were reported for this microtine with respect to canopy closure and density of understory cover in northeastern forests in Maine and Quebec [77,78]. Thus, although considered an old-forest

species, *M. gapperi* appeared to successfully inhabit the younger heavily thinned stands. Overall, the generalist species were at moderate abundance (≤ 3.1 animals/stand) and either at comparable numbers (e.g., *P. maniculatus*) among stands or at highest abundance (e.g., *N. amoenus*) in the lower density and old-growth stands. Not surprisingly, the early successional specialist species (*Microtus* spp., *Sorex* spp., and *P. intermedius*) were at low abundance (<1 animal/stand) in all stands owing to the relatively high levels of canopy closure.

In earlier studies, total abundance of eight targeted species was higher in stands that were thinned conventionally than with variable-density thinning at 4 to 5 years post-treatment [29]. In retrospective analyses, [79] reported 1.5 times as many mammals in forests managed with conventional thinning than in those with legacy retention and [80] had similar results in thinned than unthinned stands. [15] reported that heavily thinned stands up to 21 years after thinning maintained a higher level of species diversity of forest-floor small mammals than old-growth stands. This result was also recorded earlier by [81] at 10 years post-thinning, but not at 12–14 years where diversity was similar among stands [82]. A greater number of microhabitats for small mammals may have developed in the complex stand structure since the time of thinning [29,83]. However, in the current study, both measures of mean species richness and diversity of small mammals tended towards being highest in the low-density and old-growth stands, but were not formally significant. Thus, the forest-floor small mammal component of H_2 that mean total abundance would be enhanced in heavily thinned stands was supported, but species richness and diversity were not.

The similar mean abundances of *T. hudsonicus* across this array of treatment stands was also reported in a comprehensive review by [43]. *T. hudsonicus* is a common inhabitant of a broad range of temperate and boreal coniferous forests [84] and seems to persist in young managed stands. Population fluctuations of *T. hudsonicus* have been related to availability of seed crops of coniferous trees [85,86], and this pattern may have been reflected in the somewhat higher abundance in our old-growth stands.

The similarity in mean abundance of *G. sabrinus* among stands was different from the higher numbers in old-growth than young managed and unmanaged forests reported in reviews [43,87]. In terms of density of trees in managed stands, consistently low numbers of *G. sabrinus* were recorded in low-density second-growth stands in interior [15,88], but not coastal areas [60,89,90]. As reported by [91], heavy thinning decreased density of *G. sabrinus* in coastal forest. However, mean abundance of *G. sabrinus* did not differ between second-growth lodgepole pine stands ranging from 1942 to 2303 trees/ha and old-growth forest at 28–30 years after thinning [92]. Larger tree diameters and heights and enhanced understory coniferous structural diversity in thinned stands at these densities may have provided sufficient canopy closure and food and cover [92]. [93] reported that a threshold of 55% canopy cover separated stands with low- and high-density populations of *G. sabrinus* in interior forests of Washington state. Thus, H_2 that heavy thinning would enhance mean abundance of tree squirrels was not supported as numbers were similar among our treatment stands.

Our thinned second-growth stands with large diameter trees and crowns seemed to provide sufficient cover and forage for mule deer based on measurements of relative habitat use at 20- to 25-years post-thinning. Although not formally significant, this same pattern was observed at 15- to 20-years post-thinning but with similar levels of habitat use in thinned and old-growth stands [94]. Similar results were reported for moose (*Alces alces*) use of thinned “open” stands in Quebec and Scandinavia [95–97]. Our managed forests may be moving towards winter range conditions suitable for mule deer [53]. We acknowledge that cumulative collection of pellet-groups over a 5-year period did not distinguish summer and winter use by deer. Thus, our H_3 that relative habitat use by mule deer would be enhanced in heavily thinned stands compared with unthinned and old-growth stands was not supported statistically, but perhaps biologically by the somewhat higher mean numbers of pellet-groups in the thinned stands.

5.3. Decades or Centuries?

Although intensive management of pine plantations in the southern United States has been clearly demonstrated [23,98], Canadian management continues to be extensive rather than intensive. In fact, sustainable forest management is essentially considered as successful planting or natural regeneration of cutover lands with little or no silviculture intervention beyond stand establishment [13,37,99]. However, there is a strong voice for more progressive restoration directives that go beyond just revegetation of sites disturbed by forest harvesting, mineral resource extraction, or natural disturbances [14]. Clearly, an improved understanding of treatment effects and potential benefits associated with intensive silviculture is needed, particularly for northern ecosystems [37]. To this end, we have asked how do we accelerate restoration activities to grow new forests with large overstory trees in meaningful lengths of time that will provide environmental and economic benefits? For example, overly dense (e.g., >5000 trees/ha) unthinned stands may represent continuous forest cover but the quality of forest in terms of large trees, diverse coniferous structure, and functional habitat for wildlife is generally low [15,43,56]. Even conventional thinning of such dense stands to 2000–3000 trees/ha will likely require up to 80–100 years to develop harvestable, and hence large, trees in many temperate and boreal forest zones [20].

We also recognize that the species we studied represent a small fraction of the species and ecosystem processes that comprise the concept of biodiversity, and that the more rapid development of structural diversity in the low-density stands may not satisfy the habitat requirements of all old forest dependent biota. However, our results suggest that silvicultural interventions can benefit some mammalian species that are often associated with old-growth forest conditions. Other species, such as epiphytes and lichens, and the species that rely on them may require extended periods of succession and forest development before they are functional. In this context, although the stand thinning regime we studied may not represent treatments that benefit all mature and old-growth associated species, silvicultural practices should play a critical role in the design of appropriate restoration practices.

5.4. Study Limitations

To increase the degree of replication to $n = 3$ and provide a potentially wider scope of inferences that also included unthinned and old-growth stands, we combined the relevant replicate stands from three study areas: Penticton Creek (25-years after PCT) and Summerland and Kelowna (20 years after PCT). The stands were of slightly different ages and the thinning treatments started at different times. However, all measurements were conducted concurrently in treatment stands in 2013–2014 for forest-floor small mammals, 2014–2015 for tree squirrels, and 2013 for mule deer. We did not investigate the demographic variables of reproduction, recruitment, and survival for small mammals or tree squirrels, bearing in mind that density alone may not always be a significant factor in evaluation of habitat quality. However, these variables were analyzed for *M. gapperi* in an earlier publication [56]. Tree squirrel data were not sufficient to analyze these variables, except for body mass as a measure of condition, and the limited results should be viewed as preliminary. As noted above, measurement of relative habitat use by mule deer needs to be done annually to reflect summer and winter range use by these ungulates. Extrapolation of results was limited to lodgepole pine stands in the southern interior of BC.

6. Conclusions

This is the first concurrent measurement of mammal species in heavily thinned (<500 stems/ha), unthinned, and old-growth forest stands across three replicate study areas at 20–25 years post-treatment. Although not all mammal responses were significant among our treatment stands, abundance of *M. gapperi* and total forest-floor small mammals were different and highest in the low-density and old-growth stands. Other small mammal species, *T. hudsonicus*, *G. sabrinus*, and mule deer were all present in the managed stands at least at similar abundance or habitat use as the old-growth stands.

Clearly, the relationship between these mammals and forest “age” may not be nearly as important as the availability of various structural attributes associated with large trees in managed stands. Thus, there was a strong indication that restored forests via heavy thinning (<500 trees/ha) produced large overstory trees (at least for diameter and crown dimensions) after 20–25 years post-thinning in stands 33 to 42 years old. Comparable old-growth stands, albeit with crop trees of greater height and merchantable volume, ranged from 120 to 167 years of age. Restored forests with large trees capable of supporting at least these mammal species may be achieved in decades rather than centuries.

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Institutional Review Board Statement: All handling of animals followed guidelines approved by the American Society of Mammalogists [61] and the Animal Care Committee, University of British Columbia.

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Data Availability Statement: The data presented in this study are available on request from the corresponding author.

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References

1. Irwin, L.L.; Riggs, R.A.; Verschuyt, J.P. Tamm Review: Reconciling wildlife conservation to forest restoration in moist mixed-conifer forests of the inland northwest: A synthesis. *For. Ecol. Manag.* **2018**, *424*, 288–311. [\[CrossRef\]](#)
2. Cosovic, M.; Bugalho, M.N.; Thom, D.; Borges, J.G. Stand structural characteristics are the most practical biodiversity indicators for forest management planning in Europe. *Forests* **2020**, *11*, 343. [\[CrossRef\]](#)
3. Allen, C.D.; Macalady, A.K.; Chenchouni, H.; Bachelet, D.; McDowell, N.; Vennetier, M.; Cobb, N. A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. *For. Ecol. Manag.* **2010**, *259*, 660–684. [\[CrossRef\]](#)
4. Mitchell, S.J. Wind as a natural disturbance agent in forests—A synthesis. *Forestry* **2013**, *86*, 147–157. [\[CrossRef\]](#)
5. Cooke, B.J.; Carroll, A.L. Predicting the risk of mountain pine beetle spread to eastern pine forests: Considering uncertainty in uncertain times. *For. Ecol. Manag.* **2017**, *396*, 11–25. [\[CrossRef\]](#)
6. Pritchard, S.J.; Stevens-Rumann, C.S.; Hessburg, P.F. Tamm review: Shifting global fire regimes: Lessons from reburns and research needs. *For. Ecol. Manag.* **2017**, *398*, 217–233. [\[CrossRef\]](#)
7. Nabuurs, G.J.; Pussinen, A.; van Brusselen, J.; Schelhaas, M.J. Future harvesting pressure on European forests. *Eur. J. For. Res.* **2007**, *126*, 391–400. [\[CrossRef\]](#)
8. Raunikar, R.; Buongiorno, J.; Turner, J.A.; Zhu, S. Global outlook for wood and forests with the bioenergy demand implied by scenarios of the intergovernmental panel on climate change. *For. Pol. Econ.* **2010**, *12*, 48–56. [\[CrossRef\]](#)
9. Hunter, M.L.; Schmiegelow, F.K.A. *Wildlife, Forests, and Forestry*, 2nd ed.; Prentice Hall: Upper Saddle River, NJ, USA, 2011; p. 259.
10. Gotmark, F. Habitat management alternatives for conservation forests in the temperate zone: Review, synthesis, and implications. *For. Ecol. Manag.* **2013**, *306*, 292–307. [\[CrossRef\]](#)
11. Strittholt, J.R.; Dellasala, D.A.; Jiang, H. Status of mature and old-growth forests in the Pacific Northwest. *Cons. Biol.* **2006**, *20*, 363–374. [\[CrossRef\]](#) [\[PubMed\]](#)
12. Bunnell, F.L.; Dunsworth, G.B. *Forestry and Biodiversity: Learning How to Sustain Biodiversity in Managed Forests*; UBC Press: Vancouver, BC, Canada, 2009; p. 374.
13. Park, A.; Wilson, E.R. Beautiful plantations: Can intensive silviculture help Canada to fulfil ecological and timber production objectives? *For. Chron.* **2007**, *83*, 825–839. [\[CrossRef\]](#)
14. Plotkin, R. *Room for both. Realizing a Future with Sustainable Economies and Healthy Caribou Populations*; David Suzuki Foundation: Vancouver, BC, Canada, 2019.

15. Sullivan, T.P.; Sullivan, D.S.; Lindgren, P.M.F.; Ransome, D.B. Stand structure and small mammals in intensively managed forests: Scale, time, and testing extremes. *For. Ecol. Manag.* **2013**, *310*, 1071–1087. [\[CrossRef\]](#)
16. Cole, D.M.; Koch, P. *Managing Lodgepole Pine to Yield Merchantable Thinning Products and Attain Sawtimber Rotations*; USDA Forest Service, Intermountain Forest and Range Experiment Station: Ogden, UT, USA, 1996.
17. Stewart, J.D.; Salvail, J.C. *Evaluation of Precommercial Thinning of Lodgepole Pine from Long-Term Research Installations in Alberta*; Canadian Forest Service: Edmonton, AB, Canada, 2017.
18. Johnstone, W.D. Thinning lodgepole pine. In *Lodgepole Pine: The Species and Its Management*; Baumgartner, D.M., Krebill, R.G., Arnott, J.T., Weetman, G.F., Eds.; Washington State University Cooperative Extension: Spokane, WA, USA; Vancouver, BC, Canada, 1985; pp. 253–262.
19. Brockley, R.P. Effects of post-thinning density and repeated fertilization on the growth and development of young lodgepole pine. *Can. J. For. Res.* **2005**, *35*, 1952–1964. [\[CrossRef\]](#)
20. Prescott, C.; deMontigny, L.; Harper, G. Eighteen-year growth response to thinning and fertilization of a height-repressed lodgepole pine stand in interior British Columbia. *For. Chron.* **2019**, *95*, 207–221. [\[CrossRef\]](#)
21. Griess, V.C.; Man, C.D.; Polinko, A.D.; Spies, J. Mitigating midtermtimber supply shortage using commercial thinning operations. A case study from British Columbia, Canada. *For. Ecol. Manag.* **2019**, *443*, 1–18. [\[CrossRef\]](#)
22. Nohrstedt, H.O. Response of coniferous forest ecosystems on mineral soils to nutrient additions: A review of Swedish experiences. *Scand. J. For. Res.* **2001**, *16*, 555–573. [\[CrossRef\]](#)
23. Fox, T.R.; Jokela, E.A.; Allen, H.L. The development of pine plantation silviculture in the southern United States. *J. For.* **2007**, *105*, 337–347.
24. Verschuyt, J.; Riffell, S.; Miller, D.; Wigley, T.B. Biodiversity response to intensive biomass production from forest thinning in North American forests—A meta-analysis. *For. Ecol. Manag.* **2011**, *261*, 221–232. [\[CrossRef\]](#)
25. Demarais, S.; Verschuyt, J.P.; Roloff, G.J.; Miller, D.A.; Wigley, T.B. Tamm review: Terrestrial vertebrate biodiversity and intensive forest management in the U.S. *For. Ecol. Manag.* **2017**, *385*, 308–330. [\[CrossRef\]](#)
26. Carey, A.B. Restoration of landscape function: Reserves or active management? *Forestry* **2003**, *76*, 221–230. [\[CrossRef\]](#)
27. Franklin, J.F. Conserving old-growth forests and attributes: Reservation, restoration, and resilience. In *Old Growth in a New World. A Pacific Northwest Icon Reexamined*; Spies, T.A., Duncan, S.L., Eds.; Island Press: Washington, DC, USA, 2009; pp. 247–260.
28. Finnegan, L.; MacNearney, D.; Pigeon, K.E. Divergent patterns of understory forage growth after seismic line exploration: Implications for caribou habitat restoration. *For. Ecol. Manag.* **2018**, *409*, 634–652. [\[CrossRef\]](#)
29. Carey, A.B.; Wilson, S.M. Induced spatial heterogeneity in forest canopies: Responses of small mammals. *J. Wildl. Manag.* **2001**, *65*, 1014–1027. [\[CrossRef\]](#)
30. Newton, M.; Cole, L. Overstory development in Douglas-fir-dominant forests thinned to enhance late-seral features. *For. Sci.* **2015**, *61*, 809–816. [\[CrossRef\]](#)
31. United Nations. Decade on Ecosystem Restoration. Available online: <https://www.decadeonrestoration.org/> (accessed on 4 January 2021).
32. Diaz-Garcia, J.M.; Lopez-Barrera, F.; Pineda, E.; Toledo-Aceves, T.; Andresen, E. Comparing the success of active and passive restoration in a tropical cloud forest landscape: A multi-taxa fauna approach. *PLoS ONE* **2020**, *15*, e0242020. [\[CrossRef\]](#)
33. Lindgren, P.M.F.; Sullivan, T.P. Long-term responses of tree and stand growth of young lodgepole pine to pre-commercial thinning and repeated fertilization. *For. Ecol. Manag.* **2013**, *307*, 155–164. [\[CrossRef\]](#)
34. Sullivan, T.P.; Sullivan, D.S.; Lindgren, P.M.F.; Ransome, D.B.; Zabek, L. Twenty-five years after stand thinning and repeated fertilization in lodgepole pine forest: Implications for tree growth, stand structure, and carbon sequestration. *Forests* **2020**, *11*, 337. [\[CrossRef\]](#)
35. Peterken, G.F. *Natural Woodland: Ecology and Conservation in Northern Temperate Regions*; Cambridge University Press: Cambridge, UK, 1996; p. 522.
36. Hartmann, H.; Daoust, G.; Bigué, B.; Messier, C. Negative or positive effects of plantation and intensive forestry on biodiversity: A matter of scale and perspective. *For. Chron.* **2010**, *86*, 354–364. [\[CrossRef\]](#)
37. Lautenschlager, R.A. Can intensive silviculture contribute to sustainable forest management in northern ecosystems? *For. Chron.* **2000**, *76*, 293–295. [\[CrossRef\]](#)
38. Barbour, R.J.; Johnston, S.; Hayes, J.P.; Tucker, G.F. Simulated stand characteristics and wood product yields from Douglas-fir plantations managed for ecosystem objectives. *For. Ecol. Manag.* **1997**, *91*, 205–219. [\[CrossRef\]](#)
39. Moore, S.E.; Allen, H.L. Plantation forestry. In *Maintaining Biodiversity in Forest Ecosystems*; Hunter, M.L., Jr., Ed.; Cambridge University Press: New York, NY, USA, 1999; pp. 400–433.
40. Franklin, J.F.; Spies, T.A.; Pelt, R.V.; Carey, A.B.; Thornburgh, D.A.; Berg, D.R.; Chen, J. Disturbances and structural development of natural forest ecosystems with silvicultural implications, using Douglas-fir forests as an example. *For. Ecol. Manag.* **2002**, *155*, 399–423. [\[CrossRef\]](#)
41. McElhinny, C.; Gibbons, P.; Brack, C.; Bauhus, J. Forest and woodland stand structural complexity: Its definition and measurement. *For. Ecol. Manag.* **2005**, *218*, 1–24. [\[CrossRef\]](#)
42. Sullivan, T.P.; Sullivan, D.S. Acceleration of old-growth structural attributes in lodgepole pine forest: Tree growth and stand structure 25 years after thinning. *For. Ecol. Manag.* **2016**, *365*, 96–106. [\[CrossRef\]](#)

43. Sullivan, T.P.; Ransome, D.B.; Sullivan, D.S.; Lindgren, P.M.F.; Klenner, W. Tree squirrel abundance and demography in managed coniferous forests of British Columbia are within the range of natural fluctuations of old-growth stands. *Can. J. For. Res.* **2017**, *47*, 565–582. [\[CrossRef\]](#)
44. Ecke, F.; Lofgren, O.; Sorlin, D. Population dynamics of small mammals in relation to forest age and structural habitat factors in northern Sweden. *J. Appl. Ecol.* **2002**, *39*, 781–792. [\[CrossRef\]](#)
45. Pearce, J.; Venier, L. Small mammals as bioindicators of sustainable boreal forest management. *For. Ecol. Manag.* **2005**, *208*, 153–175. [\[CrossRef\]](#)
46. Zwolak, R. A meta-analysis of the effects of wildfire, clearcutting, and partial harvest on the abundance of North American small mammals. *For. Ecol. Manag.* **2009**, *258*, 539–554. [\[CrossRef\]](#)
47. Fisher, J.T.; Wilkinson, L. The response of mammals to forest fire and timber harvest in the North American boreal forest. *Mammal Rev.* **2005**, *35*, 51–81. [\[CrossRef\]](#)
48. Smith, W.P.; Anthony, R.G.; Waters, J.R.; Dodd, N.L.; Zabel, C.J. Ecology and conservation of arboreal rodents of western coniferous forests. In *Mammal Community Dynamics. Management and Conservation in Forests of Western North America*; Zabel, C.J., Anthony, R.G., Eds.; Cambridge University Press: Cambridge, UK, 2003; pp. 157–206.
49. Martin, S.K. Feeding ecology of American martens and fishers. In *Martens, Sables, and Fishers. Biology and Conservation*; Buskirk, W.W., Harestad, A.S., Raphael, M.G., Powell, R.A., Eds.; Comstock Publ. Assoc., Cornell University Press: Ithaca, NY, USA, 1994; pp. 297–315.
50. Butet, A.; Leroux, A.B.A. Effect of agriculture development on vole dynamics and conservation of Montagu's harrier in Western French wetlands. *Biol. Cons.* **2001**, *100*, 289–295. [\[CrossRef\]](#)
51. Maser, C.; Claridge, A.W.; Trappe, J.M. *Trees, Truffles, and Beasts: How Forests Function*; Rutgers University Press: Piscataway, NJ, USA, 2008.
52. Carey, A.B.; Kershner, J.; Biswell, B.; DeToledo, L.D. Ecological scale and forest development: Squirrels, dietary fungi, and vascular plants in managed and unmanaged forests. *Wildl. Monogr.* **1999**, *142*, 3–71.
53. Armleder, H.M.; Waterhouse, M.J.; Keisker, D.G.; Dawson, R.J. Winter habitat use by mule deer in the central interior of British Columbia. *Can. J. Zool.* **1994**, *72*, 1721–1725. [\[CrossRef\]](#)
54. Dawson, R.J.; Armleder, H.M.; Waterhouse, M.J. Preferences of mule deer for Douglas-fir foliage from different sized trees. *J. Wildl. Manag.* **1990**, *54*, 378–382. [\[CrossRef\]](#)
55. Meidinger, D.; Pojar, J. *Ecosystems of British Columbia*; Research Branch, Ministry of Forests: Victoria, BC, Canada, 1991.
56. Sullivan, T.P.; Sullivan, D.S. Old-growth characteristics 20 years after thinning and repeated fertilization of lodgepole pine forest: Tree growth, structural attributes, and red-backed voles. *For. Ecol. Manag.* **2017**, *391*, 207–220. [\[CrossRef\]](#)
57. Honer, T.G. Standard Volume and Merchantable Volume Tables. 1999. Available online: Flash.lakeheadu.ca/~fluckai/honer.html (accessed on 4 January 2021).
58. Englund, S.R.; O'Brien, J.J.; Clark, D.B. Evaluation of digital and film hemispherical photography and spherical densiometry for measuring forest light environments. *Can. J. For. Res.* **2000**, *30*, 1999–2005. [\[CrossRef\]](#)
59. Nagorsen, D.W. *Opossums, Shrews and Moles of British Columbia*; UBC Press: Vancouver, BC, Canada, 1996; Volume 2, p. 169.
60. Ransome, D.B.; Sullivan, T.P. Short-term population dynamics of *Glaucomys sabrinus* and *Tamiasciurus douglasii* in commercially thinned and unthinned stands of coastal coniferous forest. *Can. J. For. Res.* **2002**, *32*, 2043–2050. [\[CrossRef\]](#)
61. Sikes, R.S. Animal Care and Use Committee of the American Society of Mammalogists. Guidelines of the American Society of Mammalogists for the use of wild mammals in research and education. *J. Mammal.* **2016**, *97*, 663–688.
62. Seber, G.A. *The estimation of Animal Abundance and Related Parameters*, 2nd ed.; Charles Griffin & Co. Ltd.: London, UK, 1982.
63. Krebs, C.J. *Ecological Methodology*; Addison Wesley Longman, Inc.: Menlo Park, CA, USA, 1999.
64. Krebs, C.J.; Boonstra, R.; Gilbert, S.; Reid, D.; Kenney, A.J.; Hofer, E.J. Density estimation for small mammals from livetrapping grids: Rodents in northern Canada. *J. Mammal.* **2011**, *92*, 974–981. [\[CrossRef\]](#)
65. Burton, P.J.; Balisky, A.C.; Coward, L.P.; Cumming, S.G.; Kneeshaw, D.D. The value of managing for biodiversity. *For. Chron.* **1992**, *68*, 225–237. [\[CrossRef\]](#)
66. Côté, M.; Ferron, J. Short-term use of different residual forest structures by three sciurid species in a clear-cut boreal landscape. *Can. J. For. Res.* **2001**, *31*, 1805–1815. [\[CrossRef\]](#)
67. Sullivan, T.P.; Sullivan, D.S.; Lindgren, P.M.F.; Ransome, D.B. Influence of repeated fertilization on forest ecosystems: Relative habitat use by mule deer and moose. *Can. J. For. Res.* **2006**, *36*, 2080–2089. [\[CrossRef\]](#)
68. Harestad, A.S.; Bunnell, F.L. Persistence of black-tailed deer fecal pellets in coastal habitats. *J. Wildl. Manag.* **1987**, *51*, 33–37. [\[CrossRef\]](#)
69. IBM Corp. Inc. *IBM SPSS Statistics for Windows*; IBM Corp.: Armonk, NY, USA, 2019.
70. Fowler, J.; Cohen, L.; Jarvis, P. *Practical Statistics for Field Biology*, 2nd ed.; John Wiley and Sons: Hoboken, NY, USA, 1998; p. 259.
71. Saville, D.J. Multiple comparison procedures: The practical solution. *Am. Stat.* **1990**, *44*, 174–180.
72. Zar, J.H. *Biostatistical Analysis*; Prentice-Hall, Inc.: Englewood Cliffs, NJ, USA, 1999; p. 663.
73. Franklin, J.F.; Spies, T.A. Composition, function, and structure of old-growth Douglas-fir forests. In *Wildlife and Vegetation of Unmanaged Douglas-fir Forests*; Ruggiero, L.F., Aubry, K.B., Carey, A.B., Huff, M.H., Eds.; USDA Forest Service: Portland, OR, USA, 1991; pp. 71–80.
74. Bauhus, J.; Puettman, K.; Messier, C. Silviculture for old-growth attributes. *For. Ecol. Manag.* **2009**, *258*, 525–537. [\[CrossRef\]](#)

75. Luysaert, S.; Schultze, E.-D.; Borner, A.; Knohl, A.; Hessenmoller, D.; Law, B.E.; Clais, P.; Grace, J. Old-growth forests as global carbon sinks. *Nature* **2008**, *455*, 213–215. [[CrossRef](#)] [[PubMed](#)]
76. Ishii, H.R.; Sillett, S.C.; Carroll, A.L. Crown dynamics and wood production of Douglas-fir trees in an old-growth forest. *For. Ecol. Manag.* **2017**, *384*, 157–168. [[CrossRef](#)]
77. Fuller, A.K.; Harrison, D.J.; Lachowski, H.J. Stand scale effects of partial harvesting and clearcutting on small mammals and forest structure. *For. Ecol. Manag.* **2004**, *191*, 373–386. [[CrossRef](#)]
78. Etcheverry, P.; Ouellet, J.-P.; Crete, M. Response of small mammals to clearcutting and precommercial thinning in mixed forests of southeastern Quebec. *Can. J. For. Res.* **2005**, *35*, 2813–2822. [[CrossRef](#)]
79. Wilson, S.M.; Carey, A.B. Legacy retention versus thinning: Influences on small mammals. *Northwest Sci.* **2000**, *74*, 131–145.
80. Suzuki, N.; Hayes, J.P. Effects of thinning on small mammals in Oregon coastal forests. *J. Wildl. Manag.* **2003**, *67*, 352–371. [[CrossRef](#)]
81. Sullivan, T.P.; Sullivan, D.S.; Lindgren, P.M.F. Stand structure and small mammals in young lodgepole pine forest: 10-year results after thinning. *Ecol. Appl.* **2001**, *11*, 1151–1173. [[CrossRef](#)]
82. Sullivan, T.P.; Sullivan, D.S.; Lindgren, P.M.F.; Ransome, D.B. Long-term responses of ecosystem components to stand thinning in young lodgepole pine forest: II. Diversity and population dynamics of forest floor small mammals. *For. Ecol. Manag.* **2005**, *205*, 1–14. [[CrossRef](#)]
83. Homyack, J.A.; Harrison, D.J.; Krohn, W.B. Long-term effects of precommercial thinning on small mammals in northern Maine. *For. Ecol. Manag.* **2005**, *205*, 43–57. [[CrossRef](#)]
84. Steele, M.A. *Tamiasciurus hudsonicus*. *Mamm. Species* **1998**, *586*, 9. [[CrossRef](#)]
85. Boonstra, R.; Boutin, S.; Byrom, A.; Karels, T.; Hubbs, A.; Stuart-Smith, K.; Blower, M.; Antpoehler, S. The role of red squirrels and arctic ground squirrels. In *Ecosystem Dynamics of the Boreal Forest: The Kluane Project*; Krebs, C.J., Boutin, S., Boonstra, R., Eds.; Oxford University Press: New York, NY, USA, 2001.
86. Fletcher, Q.E.; Boutin, S.; Lane, J.E.; LaMontagne, J.M.; McAdam, A.G.; Speakman, J.R.; Krebs, C.J.; Humphries, M.M. The functional response of a hoarding seed predator to mast seeding. *Ecology* **2010**, *91*, 2673–2683. [[CrossRef](#)] [[PubMed](#)]
87. Holloway, G.L.; Smith, W.P. A meta-analysis of forest age and structure effects on northern flying squirrel densities. *J. Wildl. Manag.* **2011**, *75*, 668–674. [[CrossRef](#)]
88. Ransome, D.B.; Lindgren, P.M.F.; Sullivan, D.S.; Sullivan, T.P. Long-term responses of ecosystem components to stand thinning in young lodgepole pine forest: I. Population dynamics of northern flying squirrels and red squirrels. *For. Ecol. Manag.* **2004**, *202*, 355–367. [[CrossRef](#)]
89. Ransome, D.B.; Sullivan, T.P. Population dynamics of *Glaucomys sabrinus* and *Tamiasciurus douglasii* in old-growth and second-growth stands of coastal coniferous forest. *Can. J. For. Res.* **2003**, *33*, 587–596. [[CrossRef](#)]
90. Gomez, D.M.; Anthony, R.G.; Hayes, J.P. Influence of thinning of Douglas-fir forests on population parameters and diet of northern flying squirrels. *J. Wildl. Manag.* **2005**, *69*, 1670–1682. [[CrossRef](#)]
91. Manning, T.; Hagar, J.C.; McComb, B.C. Thinning of young Douglas-fir forests decreases density of northern flying squirrels in the Oregon Cascades. *For. Ecol. Manag.* **2012**, *264*, 115–124. [[CrossRef](#)]
92. Sullivan, T.P.; Sullivan, D.S.; Lindgren, P.M.F.; Ransome, D.B. Green-tree retention and life after the beetle: Stand structure and small mammals 30 years after salvage harvesting. *Silva Fenn.* **2010**, *44*, 749–774. [[CrossRef](#)]
93. Lehmkuhl, J.F.; Kistler, K.D.; Begley, J.S.; Boulanger, J. Demography of northern flying squirrels informs ecosystem management of western interior forests. *Ecol. Appl.* **2006**, *16*, 584–600. [[CrossRef](#)]
94. Sullivan, T.P.; Sullivan, D.S.; Lindgren, P.M.F.; Ransome, D.B. Long-term responses of mammalian herbivores to stand thinning and fertilization in young lodgepole pine (*Pinus latifolia* var. *latifolia*) forest. *Can. J. For. Res.* **2010**, *40*, 2302–2312. [[CrossRef](#)]
95. Lavsurund, S. Moose relationships to forestry in Finland, Norway, and Sweden. *Swed. Wildl. Res.* **1987**, *1*, 229–244.
96. Ball, J.P.; Danell, K.; Sunesson, P. Response of a herbivore community to increased food quality and quantity: An experiment with nitrogen fertilizer in boreal forest. *J. Appl. Ecol.* **2000**, *37*, 247–255. [[CrossRef](#)]
97. Leblond, M.; Dussault, C.; St-Laurent, M.-H. Low-density spruce plantations increase foraging by moose in a northeastern temperate forest. *For. Ecol. Manag.* **2015**, *347*, 228–236. [[CrossRef](#)]
98. Jokela, E.J.; Martin, T.A.; Vogel, J.G. Twenty-five years of intensive management with southern pines: Important lessons learned. *J. For.* **2010**, *108*, 338–347.
99. Ter-Mikaelian, M.T.; Colombo, S.J.; Chen, J. Fact and fantasy about forest carbon. *For. Chron.* **2008**, *84*, 166–171. [[CrossRef](#)]