

Article

Long-Term Changes in Abundance and Composition of Forest-Floor Small Mammal Communities in a Landscape with Cumulative Clearcutting

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Abstract: Responses of forest-floor small mammals to clearcutting are species-specific with generalists occupying a range of habitats, and specialists persisting on clearcuts for variable periods. We investigated the responses in abundance and species composition of small mammal communities to cumulative clearcutting of coniferous forests on a landscape that had four independent clearcutting events (*Periods 1 to 4*) over a 42-year interval from 1979 to 2020 in south-central British Columbia, Canada. We ask if the small mammal communities have changed significantly over these decades owing to removal of old-growth forest by clearcut harvesting. Hypotheses (H) predicted that the small mammal community would (H₁) increase in abundance, species richness, and diversity on new clearcuts owing to the availability of early seral post-harvest habitats from cumulative clearcutting; and (H₂) have higher mean abundance, species richness, and species diversity in clearcut than uncut forest sites, owing to availability of vegetative food and cover. A third hypothesis (H₃) predicted that abundance of (i) early seral vegetation (herbs and shrubs) and (ii) small mammal populations, will be greater in ungrazed clearcut sites than in those grazed by cattle (*Bos taurus*). Mean total numbers of small mammals on new clearcuts declined in *Periods 3* and *4*, and hence did not support the abundance part of H₁. Much of this decline was owing to low numbers of the long-tailed vole (*Microtus longicaudus*) and meadow vole (*M. pennsylvanicus*). Two generalist species: the deer mouse (*Peromyscus maniculatus*) and northwestern chipmunk (*Neotamias amoenus*), contributed to high mean species richness and diversity in *Periods 2* and *3* before these metrics declined in *Period 4*, and hence partly supported H₁. The similarity in mean total numbers of small mammals in *Periods 2* to *4* did not support the abundance prediction of H₂ that total numbers would be higher in clearcut than uncut forest sites. Higher mean species richness (*Periods 2* and *3*) and diversity (*Period 3*) measurements on clearcut than forest sites, particularly in the early post-harvest years, did support these parts of H₂. The vegetation part (i) of H₃ was not supported for herbaceous plants but it was for shrubs. The small mammal part (ii) of H₃ that populations would be higher in ungrazed than grazed clearcut sites was supported for abundance but not for species richness or diversity. The decline and near disappearance of both species of *Microtus* was possibly related to the reduction in plant community abundance and structure from grazing (at least for shrubs) and potentially from drought effects associated with climate change. Loss of microtines from these early seral ecosystems may have profound negative effects on various ecological functions and predator communities.



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1. Introduction

Conservation of mature and old-growth forests has reached a crucial point in time because there are unpredictable and large-scale losses of existing timber due to clearcut harvesting, natural disturbances from wildfire, insect epidemics, windthrow, and potentially

widespread drought owing to climate change [1–4]. Naturally disturbed forests may also have large-scale salvage harvesting that creates very large (>1000 ha) contiguous openings [5]. Clearcutting continues to be common and may reduce the abundances of some mammalian species because of a loss of food, cover, and forest stand structure [6–10].

Forest-floor small mammals are excellent ecological indicators of significant change in forest structure and function [11–14]. These functions include prey for many predators [15,16], consumers of seeds [17,18], seedlings [19,20], other plant products [21], and invertebrates [22,23], and dispersal of fungal (including mycorrhizae) spores [24,25]. Many studies have used small mammals as a model to evaluate improvements in forestry practices and sustainable management for conservation of forest biodiversity across landscapes [14,26].

Responses of forest-floor small mammals to clearcutting in North America are species-specific with generalists such as the deer mouse (*Peromyscus maniculatus*) and chipmunks (*Neotamias* spp.) occupying a range of habitats, whereas *Microtus* voles and *Sorex* shrews may persist on clearcuts for variable periods. Similarly, common species of small mammals usually increased in abundance, or were not affected, by clearcutting of temperate and boreal forests in Europe [10]. Small mammals take advantage of increased vegetation cover and food on clearcuts. Foods include herbaceous forbs and grasses, seeds, fruits, and mast of various tree and plant species, invertebrates, and fungi [17,24,27,28].

Specialists such as the southern red-backed vole (*Clethrionomys gapperi*) require closed-canopy forest and disappear on clearcuts, often within a year after harvest, at least in coniferous stands in North America [29,30]. Thus, *C. gapperi* is an important indicator species of closed-canopy forest conditions in managed landscapes [31]. This microtine does not return to old forest-level abundance for several decades [32,33]. Recent reviews by [9,26] have corroborated this pattern of response in abundance of small mammal species to clearcutting in North America.

A major limitation of determining the explanation for population changes of forest-floor small mammals is that most studies are short-term (e.g., 3–5 years). However, the crucial importance of identifying and understanding how species and ecosystems respond to environmental change requires long-term studies of many decades [34]. Research undertakings in forest ecology are long-term endeavors that may be termed “the long now” [35]. The value of long-term monitoring of ecological sites has been known for some time [36–39]. Long-term monitoring programs provide managers with input on the effectiveness of past actions (e.g., silvicultural systems) and/or environmental change (e.g., habitat alteration and climate change) that help provide input into management and policy decisions [34,39]. This feature of “the long now” allows us to look forward in a way that is informed by the past [35]. For example, long-term datasets (46 years) from the Yukon Territory have recorded major changes in northern red-backed vole (*C. rutilus*) and deer mouse numbers over several years, possibly related to climate change [40,41].

In many forest regions, the cumulative removal of forest cover by clearcutting and salvage harvesting has generated large expanses of early successional habitat on an unprecedented scale [4]. We ask what are the long-term consequences of this dramatic change in habitat for abundance and species composition of forest-floor small mammal communities? We have a unique 42-year window of a landscape from the first clearcut-harvest event in lodgepole pine (*Pinus contorta* var. *latifolia*) forest through four independent periods of cumulative clearcutting (1979 to 2020) in southern British Columbia (BC), Canada. Cover of early successional habitat progressed from 0% of the landscape in 1977 (pre-clearcutting) to $\geq 70\%$ in 2020. Conversely, cover of standing mature and old-growth coniferous forest has declined from near 100% to $\leq 30\%$. In addition, a second anthropogenic disturbance is that virtually all clearcuts are grazed by cattle (*Bos taurus*) which are ubiquitous throughout much of the inland Pacific Northwest, at least where summer forage is relatively abundant [42]. A further disturbance is climate change, which is particularly severe in arctic regions, but is affecting all ecosystems including temperate forests [43].

Firstly, we investigated the responses in abundance and species composition of small mammal communities to cumulative clearcutting of coniferous forests over a landscape that covered four independent harvest events (*Periods 1 to 4*) over a 42-year interval from 1979 to 2020. In particular, we ask if the small mammal communities have changed significantly over these decades owing to removal of old-growth forest by clearcut harvesting. Secondly, we report on changes in abundance, species richness, and diversity of small mammal communities in newly clearcut harvested sites and uncut old-growth forest sites over these same four *Periods*. Thirdly, we compared the responses in the abundance of early seral vegetation (herbs and shrubs) post-harvest and abundance, species richness, and diversity of small mammal communities in cattle-grazed and ungrazed clearcuts over three comparable periods of cumulative clearcutting at our Summerland and Golden study areas, respectively.

To better understand these long-term changes, we tested three hypotheses (H): the small mammal community would (H₁) increase in abundance, species richness, and diversity on new clearcuts owing to the availability of early seral post-harvest habitats from cumulative clearcutting; and (H₂) have higher mean abundance, species richness, and species diversity in clearcut than uncut forest sites, owing to availability of vegetative food and cover. A third hypothesis (H₃) predicted that abundance of (i) early seral vegetation (herbs and shrubs) and (ii) small mammal populations, will be greater in ungrazed than grazed clearcut sites

2. Methods

2.1. Study Areas

Studies were conducted in BC, Canada from 1979 to 2020. The long-term cumulative clearcutting (LTCC), clearcut-forest (CC-FOR), and ungrazed vs. grazed clearcut (CC-GR) studies were located at two study areas in south-central BC: (i) Summerland (LTCC + CC-FOR + CC-GR) 25 km west of Summerland and (ii) Golden (CC-GR) 25 km and 35 km east and northwest, respectively, of Golden. The Summerland area is primarily in the Montane Spruce (MS_{dm}; dry, mild) biogeoclimatic subzone with a small part in the upper Interior Douglas fir (*Pseudotsuga menziesii* var. *glauca*) (IDF_{dk}; dry, cool) subzone [44] (Table 1). Hybrid interior spruce (*Picea glauca* × *P. engelmannii*) and subalpine fir (*Abies lasiocarpa*) are the dominant shade-tolerant climax trees. Trembling aspen (*Populus tremuloides*) and black cottonwood (*Populus trichocarpa*) occur on some moist sites [44].

The Golden area is in the MS_{dk} (dry, cool) and Interior Cedar-Hemlock (ICH_{mk}; moist, cool) biogeoclimatic subzones with topography ranging from hilly to steep terrain at 1060–1350 m elevation in the lower ranges of the Rocky Mountains. Western red cedar (*Thuja plicata*) and western hemlock (*Tsuga heterophylla*) dominate mature climax forests with Douglas-fir, lodgepole pine, white spruce (*Picea glauca*), Engelmann spruce (*Picea engelmannii*), and subalpine fir common in these stands [44].

The Summerland studies were in a commercial forest landscape with clearcut harvesting of lodgepole pine beginning in 1977 and continuing periodically throughout the 1980s and 1990s in response to an outbreak of mountain pine beetle (MPB) (*Dendroctonus ponderosae*). Approximately 30% of uncut old-growth forest remained in this area, and hence approximately 70% of the original standing forest of lodgepole pine had been harvested. Thus, the clearcut harvests that initiated the four *Periods* of the LTCC and CC-FOR and three *Periods* of the CC-GR studies (1979–1982, 1997–2002, 2007–2011, and 2017–2020) included harvest of lodgepole pine and other available coniferous species.

The Golden study area was located in a similar commercial forest landscape but with some larger expanses of unbroken forest (100 s to 1000 s of ha) than at Summerland. Clearcutting was initially dominated by salvage harvesting of lodgepole pine from stands of MPB-killed and susceptible trees and then conventional harvest focussed on Douglas-fir and interior spruce. The three *Periods* (2, 3, and 4) of the CC-GR study at Golden (2004–2009, 2012–2016, and 2016–2019) were approximate matches for those at Summerland

(1997–2002, 2007–2011, and 2017–2020) with respect to number of post-harvest years after each new clearcutting.

Table 1. Characteristics of Summerland and Golden study areas and treatment sites for the cumulative clearcutting study (LTCC) and grazed vs. ungrazed clearcutting (CC-GR) studies.

Area and Replicate Sites	Mean (\pm SE) Area (ha)	Distance between Sites (km)	Year of Harvest	Period + Years	Vegetation Sampling	Grazing	Ecological Subzone	Latitude + Longitude
Summerland								
Munro—OKAE <i>n</i> = 1	20.2	0.30	1978	1 1979–1982	No	Yes	MS _{dm}	49°40' N; 119°53' W
Munro—A <i>n</i> = 3	9.2 \pm 2.4	0.30–2.46	1996	2 1997–2002	Yes	Yes	MS _{dm+} IDF _{dk}	49°40' N; 119°53' W
Munro—B <i>n</i> = 3	23.7 \pm 5.3	0.20–3.00	2006	3 2007–2011	Yes	Yes	MS _{dm}	49°40' N; 119°53' W
Munro—C <i>n</i> = 4	24.2 \pm 1.3	1.53 \pm 0.46	2016	4 2017–2020	No	Yes	MS _{dm+} IDF _{dk}	49°42' N; 119°57' W
Golden								
Roth Creek <i>n</i> = 3	15.9 \pm 3.5	0.20–0.50	2003–2004	1 2004–2009	Yes	No	MS _{dk}	51°18' N; 116°45' W
East Palliser <i>n</i> = 3	11.4 \pm 2.7	1.00–1.90	2011	2 2012–2016	Yes	No	ICH _{mk}	51°14' N; 116°41' W
Donald <i>n</i> = 3	7.7 \pm 1.8	0.20–0.50	2015–2016	3 2016–2019	No	No	ICH _{mk}	51°29' N; 117°05' W

2.2. Study and Sampling Designs

For the LTCC study at Summerland, there were 1, 3, 3, and 4 replicate sites of each treatment in *Periods*: (1) 1979–1982, (2) 1997–2002, (3) 2007–2011, and (4) 2017–2020, respectively. Timing of clearcut harvesting and mean area of clearcut sites are listed in Table 1. Pinegrass (*Calamagrostis rubescens*), Arctic lupine (*Lupinus arcticus*), fireweed (*Epilobium angustifolium*), and heart-leaved arnica (*Arnica cordifolia*) were the major herbaceous species on these 1- to 6-year-old clearcut sites. All clearcut units were aerially seeded with an agronomic grass-legume mix in the first year after harvest to enhance forage production for cattle in *Period 1* at Summerland [42]. However, this practice was dramatically reduced by 83% by the 1990s [45] and was not evident in *Periods 2, 3, or 4* in our study areas. Seasonal grazing by cattle continues to be common and relatively consistent on harvested sites, particularly clearcuts at Summerland, and may last for at least 10–15 years post-harvest [42].

The CC-FOR study at Summerland had a completely randomized design with two treatments: (a) clearcut harvest and (b) uncut old-growth forest in each of the four independent *Periods*. Forest sites were composed of a mixture of lodgepole pine and Douglas-fir with scattered interior spruce and subalpine fir in wetter sites. Mean ages of lodgepole pine ranged from 80 to 120 years and Douglas-fir and other conifers ranged from 120 to 220 years. Area of forest sites ranged from 10 to 100+ ha. Canopy closure ranged from 82% to 88%. The CC-GR study (*Periods 2, 3, and 4*) included clearcut sites at Summerland which had summer grazing by cattle and at Golden which had no history of grazing (Table 1). However, seeding of landings, road-sides, and skid-trails with an agronomic-legume mix for slope stabilization and erosion control was conducted, as an operational practice, on some harvested sites at Golden.

All clearcut sites were planted with lodgepole pine, Douglas-fir, and interior spruce seedlings at 1- or 2-years post-harvest. All sites at Summerland and Golden were spatially

segregated to enhance biological and statistical independence [46] (Table 1). Forest sites in the CC-FOR study were separated by a mean (\pm SE) of 1.79 ± 0.49 km (range 0.67–2.96 km). For the major species, very few or no voles or deer mice were captured on more than one grid or line, and hence our sites were considered independent. Sites were not considered independent for the northwestern chipmunk (*Neotamias amoenus*).

2.3. Forest-Floor Small Mammal Populations

There were nine species of forest-floor small mammals: five major species that included the deer mouse, southern red-backed vole, long-tailed vole (*Microtus longicaudus*), meadow vole (*M. pennsylvanicus*), and northwestern chipmunk; and four less common species: heather vole (*Phenacomys intermedius*), montane shrew (*Sorex monticolus*), common shrew (*S. cinereus*), and western jumping mouse (*Zapus princeps*). Two small mustelids: the short-tailed weasel (*Mustela erminea*) and long-tailed weasel (*M. frenata*) were also captured occasionally. At Summerland, populations were sampled at 3–4-week intervals on grids in clearcut and forest sites in *Period 1*: May to September or October 1979–1982; *Period 2*: May to October 1997–2002; *Period 3*: May or June to September or October 2007–2011; and on index-lines in *Period 4*: May or June to October 2017–2020. At Golden, populations were sampled on clearcut sites at 4-week intervals with grids in *Period 1*: May to September 2004–2008; at 4- to 8-week intervals with index-lines in *Period 2*: May to September 2012–2016; and *Period 3*: May to September 2016–2019.

One live-trapping grid (1 ha) or index-line was in each site. Grids had 49 (7×7) trap stations at 14.3-m intervals with 1 Longworth live-trap at each station. An index-line had 7 stations at 14.3-m intervals with four Longworth live-traps at each station [47]. Traps were baited with whole oats, a slice of carrot, and cotton as bedding. Each trap had a 30-cm \times 30-cm plywood cover for protection from sunlight (heat) and precipitation. Traps were set on the afternoon of day 1, checked on the morning and afternoon of day 2 and the morning of day 3, and then locked open between trapping periods. All animals captured were ear-tagged with serially numbered tags and point of capture recorded [48]. Animals were released immediately after processing. Unfortunately, the overnight trapping technique resulted in a high mortality rate for shrews. Therefore, shrews were collected, frozen, and later identified according to tooth patterns [49]. All handling of animals followed guidelines approved by the American Society of Mammalogists [50] and the Animal Care Committee, University of British Columbia.

2.4. Population Data Analyses

Abundance estimates of the major species (numerically dominant) were derived from the Jolly–Seber (J-S) stochastic model for open populations with small sample size corrections [51,52]. Minimum number alive was used to estimate populations of the heather vole; number of individuals was used for the montane shrew, common shrew, and western jumping mouse. We calculated the effective trapped area (ETA) for the major species on each grid based on mean maximum distance moved (MMDM) as a boundary strip method [53]. Estimates of population size were converted to a density estimate by dividing population estimates for each trapping period by the ETA. At Summerland, mean ETAs (\pm SE) (ha) in *Periods 1, 2, and 3* for deer mice in clearcut sites was 1.44 ± 0.04 and forest sites was 1.54 ± 0.09 ; for red-backed voles in forest sites was 1.28 ± 0.04 ; for long-tailed and meadow voles in clearcut sites was 1.19 ± 0.06 ; and for chipmunks, where sample size was sufficient, was 2.05 ± 0.02 in clearcut sites and 1.80 ± 0.19 in forest sites. Mean ETAs (\pm SE) (ha) for *Period 2* in clearcut sites at Golden were 1.40 ± 0.03 for deer mice, 1.27 ± 0.00 for red-backed voles, 1.09 ± 0.05 for long-tailed voles, 1.08 ± 0.00 for meadow voles, and 1.82 ± 0.07 for chipmunks.

Regression relationships of numbers of animals captured on index-lines to numbers on an ETA-adjusted 1-ha grid system were conducted for each of the major species: deer mice ($y = 8.45\ln(x) + 0.69$; $R^2 = 0.47$, $p < 0.01$) [54]; long-tailed vole ($y = 0.57x^{0.80}$; $R^2 = 0.62$, $p < 0.01$) [55]; and northwestern chipmunk: ($y = -0.14x^2 + 1.57x$; $R^2 = 0.51$, $p < 0.01$).

We consider each of these estimates to be a “density index” [53]. Jolly trappability was calculated according to [56]. Species richness was the total number of species sampled for the small mammal communities in each site [52]. Species diversity was based on the Shannon-Wiener index [52,57].

2.5. Early Seral Vegetation

Early seral vascular plants were sampled following the method of [58]. Vegetation responses were coordinated for 3 and 5 years post-harvest at Summerland (*Period 2*; 1999 and 2001) and Golden (*Period 2*; 2006 and 2008) and again for 1, 2, and 3 years post-harvest at Summerland (*Period 3*; 2007–2009) and Golden (*Period 3*; 2012–2014). All sampling was conducted in July–August and plant species were identified in accordance with [59]. No vegetation sampling was done in *Periods 1* or *4* at Summerland nor *Period 4* at Golden.

2.6. Statistical Analyses

In the LTCC study at Summerland, a repeated-measures analysis of variance (RM-ANOVA) [60] was conducted to determine the effect of clearcutting *treatment: Period (1, 2, 3, and 4)*, and *time: years 1 to 4* post-harvest, on mean annual total abundance, species richness, and species diversity of small mammals in the four years immediately post-clearcutting in each *Period*. Where significant treatment effects were detected that also had significant treatment \times time interactions over the four *Periods*, additional univariate ANOVAs were conducted within individual *Periods*.

In the CC-FOR study at Summerland, a RM-ANOVA was also conducted to determine the effect of cumulative clearcutting on mean annual total abundance, species richness, and species diversity of small mammals, as well as time and treatment \times time interactions, between clearcut and forest sites over the three *Periods (2, 3, and 4)*. Mean values were calculated for these attributes in *Period 1* (one replicate only) for comparison with mean results for *Periods 2, 3, and 4* in the RM-ANOVA. A univariate ANOVA was conducted to determine the effect of the two treatments on overall mean trappability for *P. maniculatus* and *N. amoenus* in clearcut and forest sites.

In the CC-GR study, a RM-ANOVA was conducted to determine the effect of cattle grazing on mean ground cover and abundance (crown volume index) of herb and shrub layers between grazed sites (Summerland) and ungrazed sites (Golden) for the two comparable *Periods* where vegetation data were available. This analysis was also done for mean annual total abundance, species richness, and species diversity of small mammals, as well as time and treatment \times time interactions, between grazed and ungrazed sites for the three comparable *Periods*. Where significant treatment effects were detected that also had significant treatment \times time interactions over the three *Periods*, additional univariate ANOVAs were conducted within individual *Periods*.

For all analyses, homogeneity of variance was measured by the Levene statistic. Mauchly’s *W*-test statistic was used to test for sphericity (independence of data among repeated measures) [61,62]. For data found to be correlated among years, the Huynh-Feldt (H-F) correction was used to adjust the degrees of freedom of the within-subjects *F*-ratio [63]. Duncan’s multiple range test (DMRT), adjusted for multiple contrasts, was used to compare mean values based on RM-ANOVA results for the LTCC analysis [64]. In all analyses, the level of significance was at least $p = 0.05$ [65].

3. Results

3.1. Small Mammal Populations

We conducted a total of 185 trapping periods at Summerland (120) and Golden (65) and captured an overall total of 8068 individual small mammals: *P. maniculatus* (2940), *C. gapperi* (1586), *M. longicaudus* (1541), *N. amoenus* (691), *M. pennsylvanicus* (376), *P. intermedius* (194), *S. monticolus* (553), *S. cinereus* (181), and *Z. princeps* (6). At Summerland, for the major species, overall mean (\pm SE) Jolly trappability (%) of *P. maniculatus* ranged from 84.6 ± 1.0 to 85.9 ± 3.7 in clearcut sites and from 73.3 ± 8.3 to 81.4 ± 1.0 in forest sites and for *N. amoenus*

ranged from 72.2 ± 5.7 to 75.7 ± 8.4 in clearcut sites to 55.4 ± 10.0 to 63.6 ± 7.2 in forest sites. For both species, these values were similar ($p \geq 0.21$) between treatment sites for all *Periods*, thereby meeting the homogeneity assumption related to capture probabilities. For those species captured predominantly in one treatment site, overall mean (\pm SE) trappability (%) for *C. gapperi* ranged from 78.4 ± 3.6 to 87.5 ± 2.3 in forest sites; for *M. longicaudus* ranged from 65.3 ± 4.4 to 76.8 ± 9.7 in clearcut sites; for *M. pennsylvanicus* ranged from 67.4 ± 4.2 to 73.2 ± 12.4 in clearcut sites. In clearcut sites at Golden, overall mean (\pm SE) Jolly trappability (%) of *M. longicaudus* was 68.5 ± 1.0 , *P. maniculatus* was 75.8 ± 1.9 , and *N. amoenus* was 52.0 ± 1.8 .

3.2. Small Mammals and Cumulative Clearcutting

In the LTCC study, mean total annual abundance of small mammals was significantly ($F_{3,7} = 20.59$; $p < 0.01$) different across *Periods* 1 to 4 of cumulative forest harvesting with numbers being highest (DMRT; $p = 0.05$) overall in *Period* 2 (Table 2 and Figure 1). Mean total abundance was 1.7 to 5.2 times higher in *Period* 2 than *Periods* 3 and 4, respectively, in the first two years post-harvest. This comparison of total abundance followed the same pattern ranging from 2.6 to 3.4 times higher in *Period* 1 than *Periods* 3 and 4 (Table 2). Mean total abundance declined significantly ($p < 0.01$) with time (i.e., years post-harvest). However, a significant ($p < 0.01$) effect of treatment \times time interaction was a result of higher (DMRT; $p = 0.05$) abundance in *Period* 4 than *Periods* 2 and 3 in the third year post-harvest. Furthermore, these mean values were similar between *Period* 1 (22.8) and 4 (19.8) in this third year post-harvest (Table 2). There was no difference among *Periods* in the fourth post-harvest year. Overall mean total abundance was 1.7 to 1.9 times higher in *Periods* 1 and 2 than *Periods* 3 and 4 (Table 2).

Table 2. Mean ($n = 1, 3$ or 4 replicate sites) \pm SE annual total abundance, species richness, and species diversity per ha for forest-floor small mammals during the first four years after clearcutting for each of the four *Periods* for the LTCC study in southern BC, Canada 1979 to 2020, and results of RM-ANOVA. Within a row, columns of mean values with different letters (upper-case for RM-ANOVA; lower-case for univariate ANOVA) are significantly different by Duncan’s multiple range test (DMRT), adjusted for multiple contrasts. Significant values are given in bold text.

Parameter	Treatment				Treatment		Time		Treatment \times Time	
	Period 1 (1)	Period 2 (3)	Period 3 (3)	Period 4 (4)	$F_{3,7}$	p	$F_{3,21}$	p	$F_{9,21}$	p
Total abundance	-	A	B	B	20.59	<0.01	23.03	<0.01	22.20	<0.01
Years post-harvest										
1	38.8	25.4 a \pm 3.7	13.0 b \pm 1.0	14.7 b \pm 1.6						
2	29.3	44.9 a \pm 4.1	15.8 b \pm 2.2	8.6 b \pm 1.3						
3	22.8	14.5 b \pm 1.5	13.6 b \pm 1.4	19.8 a \pm 0.9						
4	13.8	12.9 \pm 1.5	11.7 \pm 1.5	13.5 \pm 1.5						
Overall	26.2 \pm 5.3	24.4 \pm 7.4	13.5 \pm 0.9	14.2 \pm 2.3						
Species richness	-	A	B	C	16.35	<0.01	11.64	<0.01	2.66	0.03
Years post-harvest										
1	3.00	5.11 a \pm 0.15	3.83 b \pm 0.17	3.05 c \pm 0.22						
2	2.89	5.45 a \pm 0.15	4.44 b \pm 0.24	2.65 c \pm 0.35						
3	2.57	3.94 ab \pm 0.34	3.17 b \pm 0.51	2.40 bc \pm 0.16						
4	2.43	3.45 a \pm 0.40	3.47 a \pm 0.33	2.42 b \pm 0.14						
Overall	2.72 \pm 0.13	4.49 \pm 0.47	3.73 \pm 0.27	2.63 \pm 0.15						
Species diversity	-	A	A	B	10.18	<0.01	8.31	<0.01	0.66	0.74
Years post-harvest										
1	0.94	1.81 \pm 0.05	1.60 \pm 0.11	1.09 \pm 0.19						
2	0.70	1.80 \pm 0.11	1.74 \pm 0.12	1.02 \pm 0.18						
3	0.45	1.47 \pm 0.19	1.32 \pm 0.21	0.66 \pm 0.09						
4	0.61	1.35 \pm 0.19	1.52 \pm 0.19	0.84 \pm 0.04						
Overall	0.68 \pm 0.10	1.61 \pm 0.12	1.55 \pm 0.09	0.90 \pm 0.10						

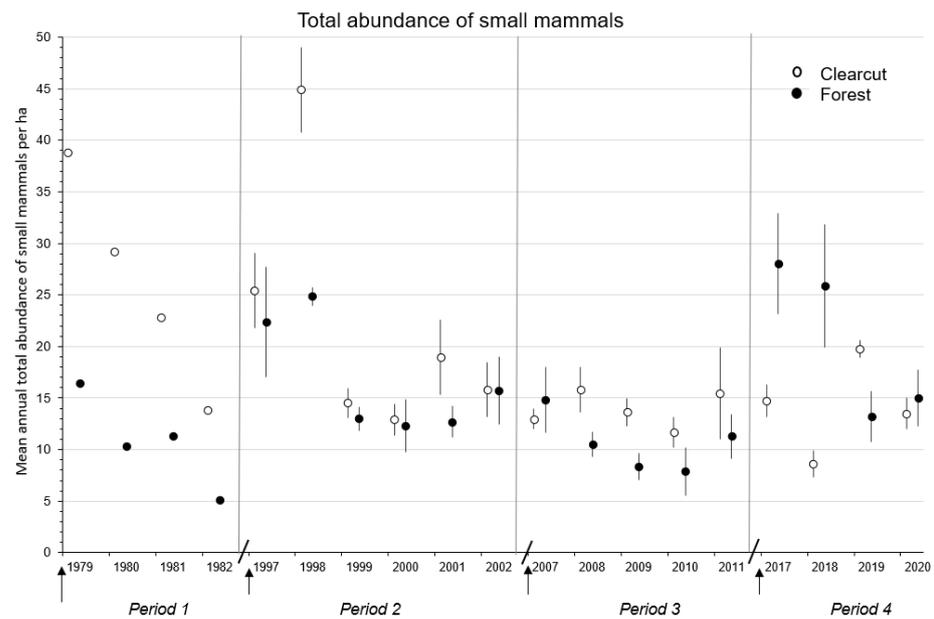


Figure 1. Mean ($n = 1, 3,$ or 4 replicate sites) \pm SE total annual abundance of forest-floor small mammals in the first four to six complete years in clearcut and uncut forest sites during the *Periods* 1979–1982, 1997–2002, 2007–2011, and 2017–2020 for the CC-FOR study in southern British Columbia, Canada. Arrow indicates time of harvesting on clearcut sites. Diagonal line separates *Periods*.

Mean annual species richness of the small mammal communities was significantly ($F_{3,7} = 16.35; p < 0.01$) different across *Periods* 1 to 4 of cumulative forest harvesting with the number of species being highest (DMRT; $p = 0.05$) overall in *Period* 2, followed by *Periods* 3 and then 4 (Table 2 and Figure 2). In terms of overall mean species richness, *Periods* 1 (2.72) and 4 (2.63) were similar. Again, there were significant ($p \leq 0.03$) effects of time and treatment \times time interaction across the three *Periods*, whereby richness generally declined with post-harvest year (Table 2).

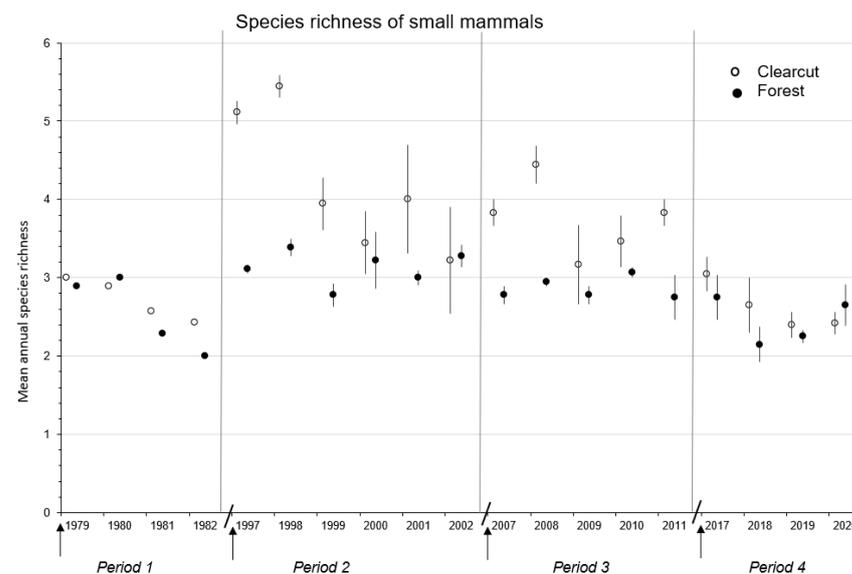


Figure 2. Mean ($n = 1, 3,$ or 4 replicate sites) \pm SE annual species richness of forest-floor small mammals in the first four to six complete years in clearcut and uncut forest sites during the *Periods* 1979–1982, 1997–2002, 2007–2011, and 2017–2020 for the CC-FOR study in southern British Columbia, Canada. Arrow indicates time of harvesting on clearcut sites. Diagonal line separates *Periods*.

Mean annual species diversity of the small mammal communities was significantly ($F_{3,7} = 10.18; p < 0.01$) different across *Periods 1* to *4* of cumulative forest harvesting with diversity being highest (DMRT; $p = 0.05$) overall in *Periods 2* and *3* (Table 2 and Figure 3). Overall mean diversity was 1.7 to 2.4 times higher in *Periods 2* and *3* than in *1* and *4*. Again, a significant ($p < 0.01$) time effect reflected the general decline in diversity with post-harvest year.

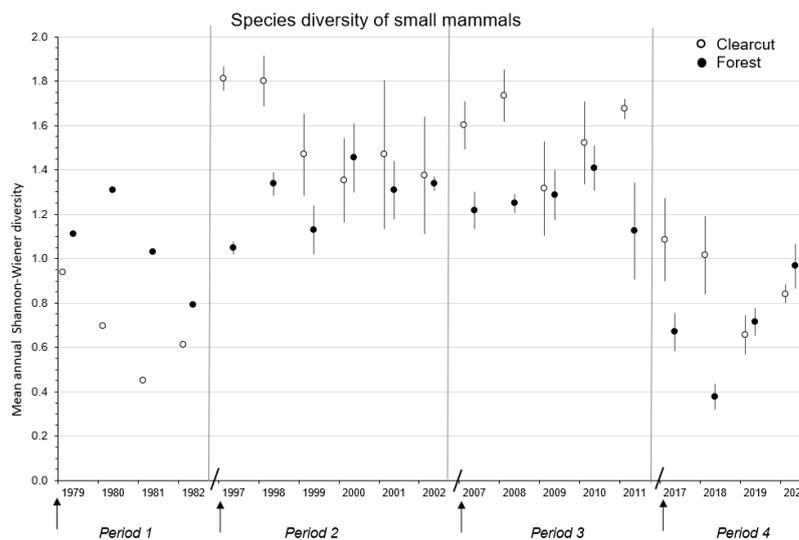


Figure 3. Mean ($n = 1, 3,$ or 4 replicate sites) \pm SE annual species diversity of forest-floor small mammals in the first four to six complete years in clearcut and uncut forest sites during the *Periods 1979–1982, 1997–2002, 2007–2011,* and *2017–2020* for the CC-FOR study in southern British Columbia, Canada. Arrow indicates time of harvesting on clearcut sites. Diagonal line separates *Periods*.

3.3. Small Mammals in Clearcut vs. Forest

In the CC-FOR study, mean total abundance of small mammals was similar between clearcut and forest sites during *Periods 2* to *4* ($p \geq 0.07$), however, mean numbers were 2.0 to 2.8 times higher in clearcut than forest sites in *Period 1* (Tables 3 and 4 and Figure 1). Mean total abundance increased to a high of 45 animals per ha in the clearcut sites in 1998 before declining through time, thereby resulting in the significant ($p < 0.01$) time and treatment \times time interactions (Figure 1). The significant ($p < 0.01$) treatment \times time interaction in *Period 4* reflected the high numbers of total animals in the forest sites in 2017 and 2018 (Table 4 and Figure 1).

Table 3. Mean ($n = 1$ replicate site) \pm SE abundance, species richness, and species diversity per trapping period for forest-floor small mammals in forest and clearcut sites during *Period 1* (1979 to 1982) for the CC-FOR study in southern BC, Canada. Number of trapping periods each year in parentheses.

Parameter	Year			
	1979 (9)	1980 (9)	1981 (7)	1982 (7)
Mean abundance				
Clearcut	38.8 \pm 5.5	29.3 \pm 4.3	22.8 \pm 1.0	13.8 \pm 2.5
Forest	16.4 \pm 3.1	10.3 \pm 2.0	11.3 \pm 1.6	5.1 \pm 0.8
Species richness				
Clearcut	3.00 \pm 0.17	2.89 \pm 0.20	2.57 \pm 0.30	2.43 \pm 0.30
Forest	2.89 \pm 0.54	3.00 \pm 0.24	2.29 \pm 0.18	2.00 \pm 0.22
Species diversity				
Clearcut	0.94 \pm 0.05	0.70 \pm 0.06	0.45 \pm 0.10	0.61 \pm 0.11
Forest	1.11 \pm 0.23	1.31 \pm 0.10	1.03 \pm 0.11	0.79 \pm 0.16

Table 4. Overall mean ($n = 3 \times 6; 3 \times 5; 4 \times 4$; sites \times years) \pm SE annual total abundance, species richness, and species diversity of forest-floor small mammals in clearcut-harvested and forest sites for the CC-FOR study in southern BC, Canada 1997 to 2020, and results of RM-ANOVA for *Periods 2, 3, and 4*. Within a row, columns of mean values with different letters are significantly different. *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. Significant values are given in bold text.

	Clearcut	Forest	Treatment		Time		Treatment \times Time	
			$F_{1,4}$	<i>p</i>	$F_{5,20}$	<i>p</i>	$F_{5,20}$	<i>p</i>
Total abundance								
<i>Period 2</i> 1997–2002	- 22.1 \pm 2.9	- 16.8 \pm 1.6	3.27	0.15	26.27	<0.01	5.20	<0.01
			$F_{1,4}$	<i>p</i>	$F_{4,16}$	<i>p</i>	$F_{4,16}$	<i>p</i>
<i>Period 3</i> 2007–2011	- 13.9 \pm 1.0	- 10.6 \pm 1.1	3.09	0.15	1.43 *	0.28	1.02*	0.42
			$F_{1,6}$	<i>p</i>	$F_{3,18}$	<i>p</i>	$F_{3,18}$	<i>p</i>
<i>Period 4</i> 2017–2020	- 14.2 \pm 1.2	- 20.5 \pm 2.6	5.08	0.07	2.18 *	0.13	7.34*	<0.01
			$F_{1,4}$	<i>p</i>	$F_{5,20}$	<i>p</i>	$F_{5,20}$	<i>p</i>
Species richness								
<i>Period 2</i> 1997–2002	A 4.20 \pm 0.25	B 3.13 \pm 0.08	9.62	0.04	6.18 *	<0.01	5.06 *	<0.01
			$F_{1,4}$	<i>p</i>	$F_{4,16}$	<i>p</i>	$F_{4,16}$	<i>p</i>
<i>Period 3</i> 2007–2011	A 3.75 \pm 0.16	B 2.86 \pm 0.07	17.87	0.01	2.77	0.06	2.46	0.09
			$F_{1,6}$	<i>p</i>	$F_{3,18}$	<i>p</i>	$F_{3,18}$	<i>p</i>
<i>Period 4</i> 2017–2020	- 2.63 \pm 0.12	- 2.45 \pm 0.12	0.58	0.48	3.87 *	<0.04	1.43 *	0.27
			$F_{1,4}$	<i>p</i>	$F_{5,20}$	<i>p</i>	$F_{5,20}$	<i>p</i>
Species diversity								
<i>Period 2</i> 1997–2002	- 1.55 \pm 0.09	- 1.27 \pm 0.05	2.47	0.19	1.16	0.36	3.46	0.02
			$F_{1,4}$	<i>p</i>	$F_{4,16}$	<i>p</i>	$F_{4,16}$	<i>p</i>
<i>Period 3</i> 2007–2011	A 1.57 \pm 0.07	B 1.26 \pm 0.05	7.44	0.05	0.72	0.59	1.75	0.19
			$F_{1,6}$	<i>p</i>	$F_{3,18}$	<i>p</i>	$F_{3,18}$	<i>p</i>
<i>Period 4</i> 2017–2020	- 0.90 \pm 0.08	- 0.68 \pm 0.06	2.76	0.15	5.24	<0.01	13.08	<0.01

Mean annual species richness was significantly ($p \leq 0.04$) higher in clearcut than forest sites in *Periods 2 and 3* but similar between treatment sites in *Periods 1 and 4* (Tables 3 and 4 and Figure 2). There were significant ($p < 0.01$) effects of time and treatment \times time interaction in *Period 2* with a univariate ANOVA detecting significantly ($p \leq 0.03$) higher species richness in clearcut than forest sites in 1997 to 1999 (Figure 2). Mean annual numbers of species was >5.0 in clearcut sites in 1997 and 1998, the highest recorded levels over the 42-year study period. A similar pattern was observed in clearcut sites in 2007, 2008, and 2011 in *Period 3* with species richness above or near 4.0 (Figure 2).

Mean annual species diversity was significantly ($p = 0.05$) higher in clearcut than forest sites in *Period 3* but was similar between treatment sites in *Periods 2 and 4* (Table 4 and Figure 3). Again, the highest diversity measurements (at or near 1.80) were recorded in 1997, 1998, 2007, and 2008 (Figure 3). The significant ($p = 0.02$) treatment \times time interaction in *Period 2* was related to the dramatic difference between clearcut and forest sites in the first two years. The significant ($p < 0.01$) effects of time and treatment \times time interaction in *Period 4* were related to the decline in diversity of small mammals in the clearcut sites in 2017 to 2019 and forest sites in 2017 to 2018 followed by an increase in both sites up to 2020 (Table 4 and Figure 3). Mean species diversity measurements of small mammals were at

similar levels in *Periods 1* and *4* (Figure 3) but were 1.2 to 2.3 times higher in the forest than clearcut sites in *Period 1* (Table 3).

3.4. Composition of Small Mammal Communities in Clearcut vs. Forest

The relative abundance of the most common species, *P. maniculatus*, was >60% in *Period 1* and near 75% in *Period 4* in clearcut sites but was approximately 40% in the two intervening *Periods* (Figures 4 and 5). In forest sites relative abundance of deer mice declined to 20% in *Period 4* after ranging from 25% to 40% in the earlier *Periods*. Relative abundance of the other common species, the red-backed vole, was <5% in clearcut sites throughout the four *Periods* but was comparable to, or higher than, the deer mouse in forest sites in *Periods 1* to *3* ranging from 40% to 56% (Figures 4 and 5). In *Period 4*, *C. gapperi* made up 76% of the forest small mammal community. *M. longicaudus* was most abundant in *Period 1* with relative measures of 32% in clearcut sites and 14% in forest sites but declined over time to <3% in *Period 4* in clearcuts and disappeared completely in forest sites (Figures 4 and 5). *M. pennsylvanicus* was relatively uncommon throughout the overall 42-year period except in *Period 2* at 17% relative abundance in clearcut sites. However, similar to *M. longicaudus*, this vole all but disappeared in *Periods 3* and *4*, despite the presence of early seral vegetation post-clearcutting. The generalist *N. amoenus* was rare in *Period 1* but increased through time to a relative abundance of 30% in clearcut sites and 12% in forest sites in *Period 3* (Figures 4 and 5). There were four uncommon species that appeared infrequently throughout the 42-year period: *P. intermedius*, *S. monticolus*, *S. cinereus*, and *Z. princeps*. The short-tailed and long-tailed weasel were also relatively rare.

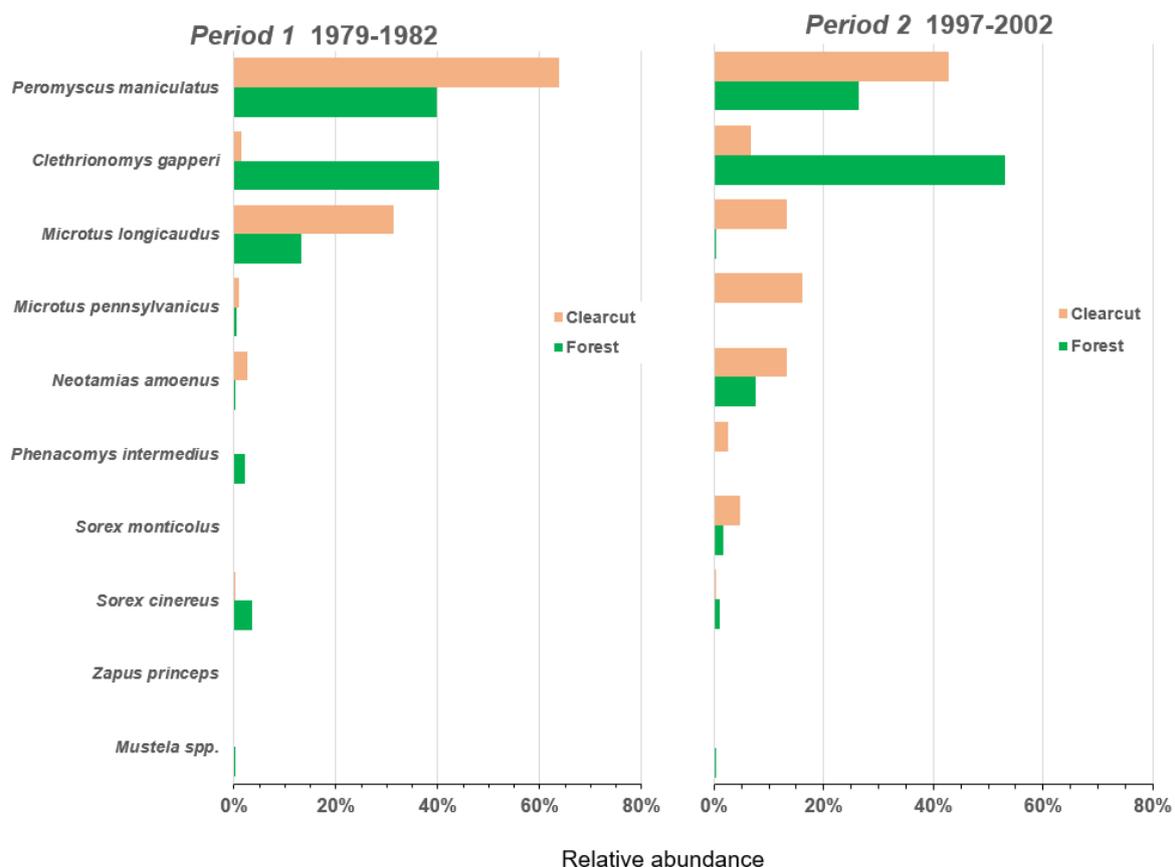


Figure 4. Relative abundance of nine species in the small mammal community in *Periods 1* to *2* (1979–1982 and 1997–2002) in clearcut and forest sites for the CC-FOR study in southern British Columbia, Canada.

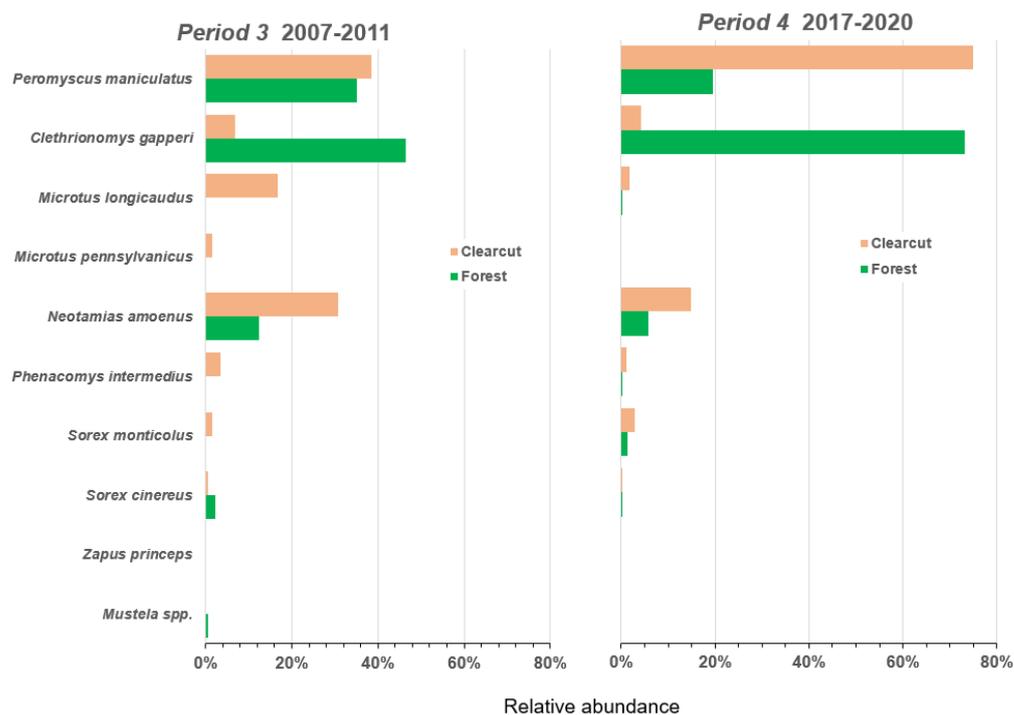


Figure 5. Relative abundance of nine species in the small mammal community in *Periods* 3 to 4 (2007–2011 and 2017–2020) in clearcut and forest sites for the CC-FOR study in southern British Columbia, Canada.

3.5. Early Seral Vegetation in Grazed and Ungrazed Sites

In the CC-GR study, mean cover and abundance of herbaceous vegetation were similar ($p = 0.57$) between grazed and ungrazed sites for the years 3 to 5 after clearcutting in comparable *Periods* at Summerland and Golden (Table 5). Pine grass and fireweed were the dominant herbs at both areas. However, mean cover ($F_{1,4} = 36.80$; $p < 0.01$) and abundance ($F_{1,4} = 18.40$; $p < 0.01$) of shrubs were significantly higher (4.4 to 7.7 times) in ungrazed than grazed sites during this period (Table 5). Red raspberry (*Rubus idaeus*), baldhip rose (*Rosa gymnocarpa*), willow (*Salix* spp.), soapberry (*Shepherdia canadensis*), snowberry (*Symphoricarpus albus*), and aspen were dominant shrubs in the ungrazed sites at Golden. Sitka alder (*Alnus sinuata*), Utah honeysuckle (*Lonicera utahensis*), birch-leaved spiraea (*Betula spiraea*), and several dwarf shrubs comprised the much lower abundance of shrubs in grazed sites at Summerland. There were no significant effects of time or treatment \times time interactions for this analysis.

In years 1 to 3 after clearcutting in the next comparable *Periods* at Summerland and Golden, mean cover and abundance of herbs were again similar ($p \geq 0.42$) between grazed and ungrazed sites. Pine grass was the dominant herbaceous species followed by aster (*Aster* spp.), heart-leaved arnica, and white-flowered hawkweed (*Hieracium albiflorum*) in the grazed sites at Summerland. Fireweed dominated the herb layer along with similar species as Summerland in the ungrazed sites at Golden; however, pine grass was minimal. In both treatment sites herb abundance increased significantly ($p < 0.01$) with time (Table 5). Mean cover ($F_{1,4} = 19.77$; $p = 0.01$) and abundance ($F_{1,4} = 16.21$; $p = 0.02$) of shrubs were again significantly higher (4.3 to 4.9 times) in ungrazed than grazed sites during this period. Utah honeysuckle, birch-leaved spiraea, and several dwarf shrubs were common in grazed sites whereas red raspberry, thimbleberry (*Rubus parviflorus*), and birch-leaved spiraea dominated the shrub layer in the ungrazed sites. There were significant ($p < 0.01$) effects of time and treatment \times time interaction with mean shrub abundance increasing over the three years (Table 5). Mean shrub abundance measurements were similar ($p \geq 0.08$) in year 1, but then significantly ($p \leq 0.04$) higher in ungrazed than grazed sites in years 2 and 3 as indicated by an univariate ANOVA.

Table 5. Overall mean ($n = 3 \times 2; 3 \times 3; \text{sites} \times \text{years}$) \pm SE cover ($\text{m}^2/0.01 \text{ ha}$) and abundance ($\text{m}^3/0.01 \text{ ha}$) of early seral vegetation (herb and shrub layers) in grazed and ungrazed clearcut sites for comparable years post-harvest for the CC-GR study in southern BC, Canada, and results of RM-ANOVA, and univariate ANOVA where applicable. *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. Significant values are given in bold text.

Parameter	Grazed	Ungrazed	Treatment		Time		Treatment \times Time	
			$F_{1,4}$	<i>p</i>	$F_{1,4}$	<i>p</i>	$F_{1,4}$	<i>p</i>
<i>Period 2: years 3 + 5 (n = 6)</i>								
Herb cover	26.9 \pm 3.6	38.4 \pm 10.2	0.39	0.57	0.05	0.83	0.59	0.49
Herb abundance	9.1 \pm 1.9	11.8 \pm 2.5	0.39	0.57	0.02	0.89	2.83	0.17
Shrub cover	17.6 \pm 2.6	78.2 \pm 6.1	36.80	<0.01	3.10	0.15	2.22	0.21
Shrub abundance	8.9 \pm 1.9	68.5 \pm 9.1	18.40	0.01	3.32	0.14	0.10	0.77
<i>Period 3: years 1 to 3 (n = 9)</i>								
Herb cover	31.5 \pm 8.9	28.6 \pm 3.2	0.01	0.94	27.66	<0.01	11.84	<0.01
Herb abundance	9.8 \pm 2.6	12.2 \pm 1.9	0.79	0.42	20.58	<0.01	0.62	0.56
Shrub cover	7.3 \pm 1.4	31.6 \pm 4.4	19.77	0.01	27.52 *	<0.01	7.73 *	0.03
Shrub abundance	2.5 \pm 0.3	12.2 \pm 2.1	16.21	0.02	28.66	<0.01	15.05	<0.01

3.6. Small Mammals in Grazed and Ungrazed Sites

Mean total abundance of small mammals was significantly ($p \leq 0.05$) higher (1.5 to 3.5 times) in ungrazed than grazed sites during *Periods 2 to 4* (Table 6 and Figure 6). Mean total abundance increased dramatically in ungrazed sites in the third to fourth years in *Period 2* and second to third years in *Period 3* before declining to lower numbers resulting in the significant ($p \leq 0.04$) time and treatment \times time interactions (Table 6 and Figure 6). A univariate ANOVA detected significantly ($p \leq 0.04$) higher total abundance in ungrazed than grazed sites in the third year (*Period 2*) and second and fourth years (*Period 3*) (Figure 6). Mean total abundance of small mammals was consistently higher in ungrazed than grazed sites in *Periods 3 and 4* (Figure 6).

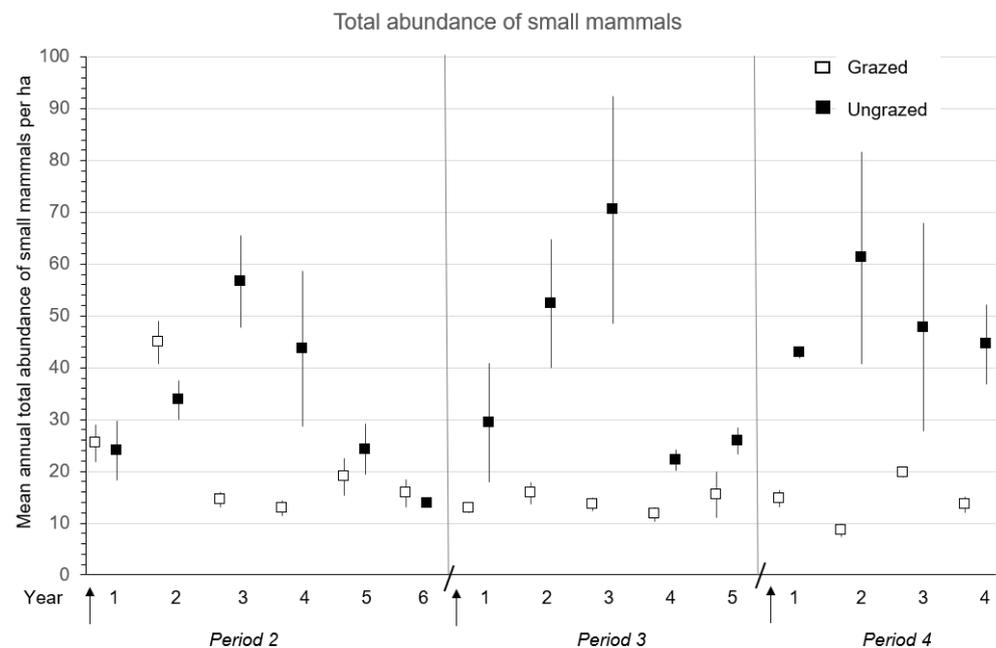


Figure 6. Mean ($n = 1, 3, \text{ or } 4$ replicate sites) \pm SE total annual abundance of forest-floor small mammals in the first four to six complete years in grazed and ungrazed sites after clearcut harvesting during the three *Periods*: 2 (1997–2002 and 2004–2009), 3 (2007–2011 and 2012–2016), and 4 (2017–2020 and 2016–2019) for the CC-GR study in southern British Columbia, Canada. Arrow indicates time of harvesting on clearcut sites. Diagonal line separates *Periods*.

Table 6. Overall mean ($n = 3 \times 6; 3 \times 5; 3 \text{ or } 4 \times 4$; sites \times years) \pm SE annual total abundance, species richness, and species diversity of forest-floor small mammals in grazed (Summerland) and ungrazed (Golden) clearcut sites for comparable years post-harvest for the CC-GR study in southern BC, Canada 1997 to 2020, and results of RM-ANOVA for *Periods* 2, 3, and 4. Within a row, columns of mean values with different letters are significantly different. *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. Significant values are given in bold text.

	Grazed	Ungrazed	Treatment		Time		Treatment \times Time	
<i>Total abundance</i>			$F_{1,4}$	<i>p</i>	$F_{5,20}$	<i>p</i>	$F_{5,20}$	<i>p</i>
<i>Period 2</i> 1997–2002 2004–2009	B 22.1 \pm 2.9	A 32.7 \pm 4.4	8.37	0.04	4.69 *	0.03	6.30 *	0.01
			$F_{1,4}$	<i>p</i>	$F_{4,16}$	<i>p</i>	$F_{4,16}$	<i>p</i>
<i>Period 3</i> 2007–2011 2012–2016	B 13.9 \pm 1.0	A 40.0 \pm 6.8	7.74	0.05	4.93 *	0.03	4.46 *	0.04
			$F_{1,5}$	<i>p</i>	$F_{3,15}$	<i>p</i>	$F_{3,15}$	<i>p</i>
<i>Period 4</i> 2017–2020 2016–2019	B 14.2 \pm 1.2	A 49.1 \pm 6.7	12.03	0.02	0.55 *	0.60	1.90 *	0.20
<i>Species richness</i>			$F_{1,4}$	<i>p</i>	$F_{5,20}$	<i>p</i>	$F_{5,20}$	<i>p</i>
<i>Period 2</i> 1997–2002 2004–2009	- 4.20 \pm 0.25	- 3.94 \pm 0.20	0.44	0.54	8.57	<0.01	3.85	0.01
			$F_{1,4}$	<i>p</i>	$F_{4,16}$	<i>p</i>	$F_{4,16}$	<i>p</i>
<i>Period 3</i> 2007–2011 2012–2016	- 3.75 \pm 0.16	- 3.20 \pm 0.19	3.73	0.13	3.59	0.03	1.84	0.17
			$F_{1,5}$	<i>p</i>	$F_{3,15}$	<i>p</i>	$F_{3,15}$	<i>p</i>
<i>Period 4</i> 2017–2020 2016–2019	- 2.63 \pm 0.12	- 3.18 \pm 0.28	3.32	0.13	3.52	0.04	12.85	<0.01
<i>Species diversity</i>			$F_{1,4}$	<i>p</i>	$F_{5,20}$	<i>p</i>	$F_{5,20}$	<i>p</i>
<i>Period 2</i> 1997–2002 2004–2009	- 1.55 \pm 0.09	- 1.42 \pm 0.07	0.61	0.48	3.55	0.02	1.76	0.17
			$F_{1,4}$	<i>p</i>	$F_{4,16}$	<i>p</i>	$F_{4,16}$	<i>p</i>
<i>Period 3</i> 2007–2011 2012–2016	A 1.57 \pm 0.07	B 0.79 \pm 0.09	35.77	<0.01	0.96 *	0.45	0.73 *	0.57
			$F_{1,5}$	<i>p</i>	$F_{3,15}$	<i>p</i>	$F_{3,15}$	<i>p</i>
<i>Period 4</i> 2017–2020 2016–2019	- 0.90 \pm 0.08	- 0.97 \pm 0.13	0.15	0.71	2.14	0.14	6.94	<0.01

Mean annual species richness was similar ($p \geq 0.13$) in grazed and ungrazed sites in all *Periods* (Table 6). There were significant time (all *Periods*) and treatment \times time (*Periods* 2 and 4) effects with a general decline in richness in grazed sites and an increase in ungrazed sites (Table 6). Mean annual species diversity was similar ($p \geq 0.48$) in grazed and ungrazed sites in *Periods* 2 and 4 and significantly ($F_{1,4} = 35.77$; $p < 0.01$) higher in grazed than ungrazed sites in *Period* 3. A significant ($p < 0.01$) treatment \times time interaction

in *Period 4* was related to a decline in diversity in the grazed sites and an increase in the ungrazed sites (Table 6).

4. Discussion

4.1. Small Mammals and Cumulative Clearcutting

The significant decline in mean total numbers of small mammals on new clearcuts in *Periods 3* and *4* did not support the abundance prediction of H_1 that abundance, species richness, and diversity would increase on new clearcuts owing to availability of early seral post-harvest habitats from cumulative clearcutting. A likely explanation for the decline in all three metrics was the major decline in mean numbers of *M. longicaudus* to ≤ 2.0 voles/ha in these two *Periods* [66]. *M. longicaudus* seems to have discordant fluctuations in abundance, without any long-term pattern, that are often triggered by forest management activities such as clearcutting and the subsequent flush of early seral vegetation 2- to 3-years post-harvest (e.g., *Periods 1* and *2* in [66]). There was also the almost complete disappearance of *M. pennsylvanicus* despite the presence of early seral vegetation, particularly grasses, during *Periods 3* and *4*. For both microtines, the influence of prolonged cattle grazing on new clearcuts may be crucial after they were relatively more abundant in *Periods 1* and *2* than in *Periods 3* and *4* (see Section 4.4).

The two generalist species: *P. maniculatus* and *N. amoenus*, contributed to the significantly higher mean species richness in *Period 2*, than other *Periods*, where along with the two vole species, richness reached >5.0 . As noted by [67,68], *P. maniculatus* tends to be widespread among the various early successional habitats associated with post-clearcut landscapes. Similarly, *N. amoenus* also occupies a wide range of early successional habitats [26,69]. Both species take advantage of increased vegetation cover and food on clearcuts, including seeds, fruits, and mast of various tree and plant species, invertebrates, and fungi [17,24,28]. The high mean species diversity in *Periods 2* and *3* on new clearcut sites reflected the presence of all five major species in relatively similar abundances plus the presence of the less common species *P. intermedius* and *S. monticolus*. Both generalist species were at relatively high abundance in *Period 4* thereby dominating the composition of the small mammal community and contributing to lower evenness, and hence diversity, in this *Period*. Similarly, the community on new clearcut sites in *Period 1* was dominated by *P. maniculatus* and *M. longicaudus* resulting in the lowest overall mean (\pm SE) diversity (0.68 ± 0.10) of all *Periods*. Thus, the species richness and diversity predictions of H_1 were supported for both measurements at least in *Periods 2* and *3*.

4.2. Small Mammals in Clearcut vs. Forest

The similarity in mean total numbers of small mammals between clearcut and forest sites in *Periods 2* to *4* did not support the abundance prediction of H_2 that abundance, species richness, and diversity would be higher in clearcut than uncut forest sites owing to availability of vegetative food and cover. The higher overall mean abundance in clearcut than forest sites in *Period 1* was supportive but based on just one replicate. Nevertheless, the high numbers of small mammals in clearcut sites in the early post-harvest years in *Periods 1* and *2*, but not later, did suggest that vegetative food and cover may have been less on clearcuts in the later *Periods*. The higher or comparable overall mean numbers of small mammals in forest than clearcut sites in 1997–1998 and 2017–2018 was owing to peak years in abundance of *C. gapperi* which has a well-defined 7- to 8-year population fluctuation [70]. Contrary to these abundance results, the higher mean species richness (*Periods 2* and *3*) and diversity (*Period 3*) measurements on clearcut than forest sites, particularly in the early post-harvest years, did support these parts of H_2 . Indeed, high relative numbers of *C. gapperi* in forest sites in the early years of *Periods 2* and *4* suppressed evenness and hence species diversity.

Most studies in North America have concluded that deer mice are more abundant (2 to 10 times) on clearcut areas than in intact forest habitat, in at least some years, and peak densities typically occur 2–5 years post-harvest [27,29,71,72]. In general, common species of

small mammals usually increased in abundance, or were not affected, by clearcutting of temperate and boreal forests in Europe [10]. Eurasian ecological counterparts to *P. maniculatus*, *Microtus* and *Clethrionomys* spp. such as the wood mouse (*Apodemus sylvaticus*), field vole (*M. agrestis*), and common vole (*M. arvalis*), respectively, increased on clearcuts whereas the bank vole (*C. glareolus*) showed no response and the gray-sided vole (*C. rufocanus*) declined in abundance similar to *C. gapperi* [10,26,73]. Declines in *Clethrionomys* may be related to the damping out or collapsing of microtine population cycles over at least the last three decades, particularly in northern and central Europe [74,75]. Fragmentation of source habitats [76,77] and climate change [78] have been advanced as possible explanations and may be particularly relevant to the disappearance of *C. gapperi* and *C. rufocanus* on clearcuts, although see [79]. *C. rufocanus* seems to require large patches (≥ 79 ha) of high-quality mature or old-growth coniferous forest [77], whereas *C. gapperi* has been maintained in late successional forest patches of 0.3 to 20 ha, at least for a 3-year period post-clearcutting [80].

4.3. Early Seral Vegetation in Grazed and Ungrazed Sites

The vegetation part (i) of H₃ that mean abundance of herbs and shrubs would be higher in ungrazed than grazed clearcut sites was not supported for herbaceous plants but it was supported for shrubs. These results were similar in the first comparable *Period* within the two MS ecological subzones, but also in different MS and ICH subzones in the second comparable *Period*, between Summerland and Golden. This pattern suggested that cattle appeared to consume shrubs as well as grasses and forbs in the grazed sites at Summerland. Although cattle feed primarily on forbs and grasses, they also will consume shrubs as browse items during certain seasons [81,82], with ranges of 50–72% grass, 23–42% forbs, and 4–20% shrubs. In recent clearcuts, cattle feed on pine grass through June but by mid-August consumption declines [83]. As pine grass matures, crude protein levels may decline to levels below minimums required for active growth of calves (12%) and for lactating cows (8.3%) [84]. It is during the late summer and fall that cattle may consume shrubs and trees such as willow, spiraea, *Rosa* spp., snowberry, Sitka alder, and aspen [81]. Further evidence for cattle consumption of shrubs was reported over a 10-year period where overall mean abundance of shrubs was 1.3 to 2.0 times higher in ungrazed (i.e., within an enclosure) than grazed sites [85].

4.4. Small Mammals in Grazed and Ungrazed sites

The small mammal part (ii) of H₃ that populations would be higher in ungrazed than grazed clearcut sites was supported for abundance but not for species richness or diversity. In addition, the abundance results also tended to support H₁, and potentially H₂, at least for ungrazed sites. In other studies, livestock disturbance appeared to have a consistently significant negative impact on small mammal abundance [86–88] and species richness or diversity [89–91]. Some variable results based on scale of habitat measurements and generalist vs. specialist species of small mammals were also reported [92,93]. In all cases, reductions in plant community abundance, composition, and structure following livestock grazing were the major factors influencing small mammal communities. Alternatively, Ref.[94] reported no effect of grazing on mean overall abundance or species diversity of the total small mammal community in young (13–23 years) stands of lodgepole pine.

However, reductions in these vegetative parameters from livestock grazing have negatively influenced *Microtus* voles in several geographic areas of North America, the United Kingdom, and northern Europe [87,88,95–97] or shown variable results [98]. Thus, it is not surprising that populations in our ungrazed sites were dominated by *M. longicaudus* and secondarily by *M. pennsylvanicus* and *P. maniculatus* in all three *Periods*. *M. longicaudus* in the grazed sites was dominant in the first two post-harvest years in *Period 2* only [66]. Thus, damping of *Microtus* population fluctuations and potentially predator communities as well may be linked to livestock grazing, at least in early successional forest sites. A major predator of voles, the short-tailed weasel (*Mustela erminea*) was reported at lower

abundance in grazed vs. ungrazed sites [94] and other predators followed this pattern in other studies [99,100].

4.5. Study Limitations

Harvested sites and stands were the size of conventional forestry operations in the southern interior of BC and in similar regions of the Pacific Northwest. Continuous sampling of all sites beyond 4 to 6 years post-harvest in each *Period* and study may have identified the presence of additional changes in the small mammal communities. Measurements of abundance, species richness, and diversity reflect May to October months only and may not have been the same during other seasons of the year. The relatively low number (9) of small mammal species suggested that species richness and diversity measurements might have been less robust than desired and that these results might simply reflect the species level abundance patterns. Additional replicates in *Period 1* would have provided precision for our measurements and allowed direct comparisons of results with the other *Periods*. Ideally, addition of ungrazed clearcut sites at Summerland and grazed clearcut sites and uncut forest sites at Golden would have balanced the study designs but were not available.

Unfortunately, we had no measurements of abundance of herbaceous and shrub vegetation in *Periods 1* or *4* for the grazed and ungrazed conditions on clearcuts at Summerland and Golden, respectively. In addition, there are three caveats regarding the vegetation and small mammal responses in the CC-GR study. Firstly, the vegetation measurements in the grazed sites at Summerland represented different sets of years: *Period 2* (1999 and 2001) and *3* (2007–2009) whereas at Golden the ungrazed sites represented *Period 2* (2006 and 2008) and *3* (2012–2014). Similarly, the small mammal measurements also covered different sets of years in the three *Periods*: *2* (1997–2002), *3* (2007–2011), and *4* (2017–2020) at Summerland; and *2* (2004–2009), *3* (2012–2016), and *4* (2016–2019) at Golden. Secondly, comparisons in *Period 2* were from similar ecosystems (MS_{dm} and MS_{dk}) whereas those in *Periods 3* and *4* were from quite different ecosystems (MS_{dm} and ICH_{mk}). However, in terms of responses of vegetation in *Periods 2* and *3*, mean abundance and cover of herbs were similar between grazed and ungrazed sites, whereas these two metrics for shrubs were higher in ungrazed than grazed sites. Thirdly, the Golden study area was located in a similar commercial forest landscape but with some larger expanses of unbroken forest (100 s to 1000 s of ha) than at Summerland. An important further note is that both areas had the same species composition of small mammal communities.

5. Conclusions

Over the 42-year period, cumulative clearcutting of the original forest resulted in creation of early successional habitat that ranged from 0% of the landscape in 1977 (pre-clearcutting) to $\geq 70\%$ in 2020. Overall mean annual abundance of forest-floor small mammals declined despite the availability of early post-seral habitats and much of this decline was owing to loss of *M. longicaudus* and *M. pennsylvanicus*, thereby not supporting H_1 . The deer mouse and northwestern chipmunk contributed to high mean species richness and diversity in *Periods 2* and *3* before these metrics declined in *Period 4*, and hence partly supported H_1 . Except for *Period 1*, numbers of small mammals were often similar in clearcut and forest sites, thereby not supporting H_2 . However, species richness and diversity remained relatively high on clearcut sites in *Periods 2* and *3*, particularly in the first two years after cutting, before declining to forest levels in *Period 4*, and hence partly supported H_2 .

Cattle grazing seemed to have a significant negative effect on overall mean abundance of small mammals in all three comparable *Periods*, and hence supported the small mammal part of H_3 . However, this difference was apparently not related to cattle consumption of herbaceous vegetation but was possibly related to the lower abundance of shrubs in grazed than ungrazed sites. Thus, the vegetation part of H_3 was supported for shrubs but not herbs. The decline and near disappearance of both species of *Microtus* was possibly

related to the reduction in plant community abundance and structure from grazing (at least for shrubs) and potentially from drought effects associated with climate change. Loss of microtines from these early seral ecosystems may have profound negative effects on various ecological functions and predator communities.

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