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## Diversifying clearcuts with green-tree retention and woody debris structures: conservation of mammals across forest ecological zones

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### Highlights

- Species diversity of small mammals increased with structural complexity left on clearcut sites.
- Productivity of red-backed vole populations was higher in sites with green-tree retention (GTR) and windrows of woody debris.
- GTR and windrows may provide additive effect for providing habitat to conserve mammals on clearcuts.

### Abstract

We tested the hypotheses (H) that on newly clearcut-harvested sites, (H<sub>1</sub>) abundance and species diversity of the forest-floor small mammal community, and (H<sub>2</sub>) abundance, reproduction, and recruitment of red-backed voles (*Myodes gapperi* Vigors), would increase with higher levels of structural retention via green-tree retention (GTR) and woody debris (dispersed and constructed into windrows). Study areas were located in three forest ecological zones in southern British Columbia, Canada. For H<sub>1</sub>, mean total abundance did generally increase with the gradient of retained habitat structure. Mean species richness and diversity were similar among treatment sites but did show an increasing gradient with structural complexity. For H<sub>2</sub>, mean abundance, reproduction, and recruitment of *M. gapperi* were higher in GTR and windrow sites than those without retained structures. There was a positive relationship between mean abundance of *M. gapperi* and total volume of woody debris across treatments. This study is the first investigation of the responses of forest-floor small mammals to an increasing gradient of retained habitat structure via GTR and woody debris on clearcuts. Our assessment of a combination of these two interventions suggested a potentially strong additive effect that could be cautiously extrapolated across three forest ecological zones. With the advent of low levels of GTR on clearcuts, woody debris structures should help provide some habitat to conserve forest mammals on harvest openings.

**Keywords** clearcutting; coniferous forests; ecological zones; green-tree retention; *Myodes gapperi*; population dynamics; red-backed voles; small mammals; woody debris structures

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## 1 Introduction

Clearcutting of temperate zone forests is the dominant harvesting system in much of North America and northern Europe. However, maintaining mammal diversity, as a component of biodiversity is a major conservation goal in commercial forest landscapes. An array of harvesting systems that leaves residual live trees after harvest (green-tree retention (GTR)) has evolved to help achieve that goal (Franklin et al. 1997; Rosenvald and Lohmus 2008). Retention patterns may be dispersed or aggregated across harvest units, often including seed-tree, shelterwood, patch, and selection cutting systems and their variants (Smith 1986; Larsen 1995; Franklin et al. 1997). These alternative harvesting systems are more aligned with natural processes by retaining large live trees, snags, and downed logs after harvest (Franklin et al. 1997, 2002; Bunnell and Dunsworth 2009). Conservation of residual live trees increases structural diversity and provides attributes of mature forest habitat that develop sooner than in sites managed by clearcutting (McComb et al. 1993; Franklin et al. 2000).

Woody debris on the forest floor is another potential source of habitat creation on new clearcuts. It accumulates as a result of stand development and by natural (wildfire, insect outbreaks, wind events) and human-caused disturbances such as harvesting (Spies et al. 1988). Woody debris provides many important functions that are essential to maintaining biodiversity and long-term ecosystem productivity such as the slow release of nutrients “tied up” in the fines of post-harvest slash and the contribution of organic matter to soil structure and modification of near-ground microclimate (Harmon et al. 1986; McComb and Lindenmayer 1999; Bunnell and Houde 2010). Excess woody debris from felling operations is typically burned to reduce a perceived fire hazard. However, woody debris contributes to habitat quality for a wide range of mammal species (McComb 2003).

Ecological indicators of significant change in forest structure and function include terrestrial small mammals which are widespread across temperate and boreal forest ecosystems (Carey and Harrington 2001; Ecke et al. 2001, 2002; Pearce and Venier 2005). These functions include prey for many predators (Martin 1994), consumers of plants, plant products (Carey et al. 1999), and invertebrates (Gunther et al. 1983), and dispersal of fungal spores (Maser et al. 1978). Responses to clearcutting in North America are species-specific with generalists that occupy a variety of habitats such as the deer mouse (*Peromyscus maniculatus* Wagner), northwestern chipmunk (*Neotamias amoenus* Allen), and *Microtus* voles persisting on clearcuts, although some for variable periods. Specialists such as the southern red-backed vole (*Myodes gapperi* Vigors) require closed-canopy forest and disappear on clearcuts, often within a year after harvest, at least in western North America (Fisher and Wilkinson 2005; Zwolak 2009). Thus, *M. gapperi* is an important indicator species of closed-canopy forest conditions in managed landscapes. This microtine commonly inhabits late successional coniferous and deciduous forests across temperate and boreal North America (Merritt 1981), and hence is a good candidate species for evaluation of the development of “old forest” structural attributes in young stands. The presence of red-backed vole populations at mature or old-growth “forest” levels of abundance suggests that networks of food sources and predators (e.g., short-tailed weasel (*Mustela erminea* L.) and American marten (*Martes americana* Turton) may also be present as components of biodiversity.

Suitable habitat conditions for red-backed voles have been maintained in partially cut forests with GTR levels of  $> 15 \text{ m}^2/\text{ha}$  BA or 30% uncut forest across a variety of forest ecosystems as reviewed by Sullivan et al. (2008). However, responses of *M. gapperi* to GTR levels to these and lower thresholds have been variable and short-term ( $\leq 3$  years post-harvest) (Sullivan et al. 2008). Gitzen et al. (2007) also noted that some of this variability may be related to flexibility in habitat occupancy and changes in forest-floor conditions. Although these partial cutting results are encouraging for maintenance of *M. gapperi*, clearcutting still dominates as a harvesting system, even with

some degree of GTR. Thus, we ask: Is there a habitat creation approach that could be combined with relatively modest levels of GTR (i.e., < 5 m<sup>2</sup>/ha BA or 5% uncut forest) to diversify clearcuts? Some studies indicate that *M. gapperi* seem to select forest sites with large amounts of woody debris that moderate moisture, temperature, and cover for foraging (Tallmon and Mills 1994; Vanderwel et al. 2010; Fauteux et al. 2012). To this end, construction of piles and windrows of woody debris on new clearcuts has significantly enhanced populations of forest-floor small mammals, including *M. gapperi*, and some of their predators (Sullivan et al. 2012). Thus, could a combination of low, but common, levels of GTR and woody debris structures enhance habitat conditions for *M. gapperi* and the overall forest-floor small mammal community in newly clearcut sites?

We tested the hypotheses (H) that on newly clearcut sites, (H<sub>1</sub>) abundance and species diversity of the forest-floor small mammal community, and (H<sub>2</sub>) abundance, reproduction, and recruitment of *M. gapperi*, will increase with higher levels of structural retention via GTR and woody debris. A third hypothesis (H<sub>3</sub>) predicted that the above response variables on sites with GTR and windrows of debris would be comparable to or higher than those in uncut mature/old growth forest.

## 2 Methods

### 2.1 Study areas

Three replicate study areas (blocks) were located in the southern interior of British Columbia (BC), Canada: 1) East Munro (49°40'27"N; 119°51'49"W) and 2) Kathleen Lake (49°44'57"N; 120°06'13"W) on the Okanagan Plateau 25 and 47 km, respectively, west of Summerland, BC, and 3) Blaeberry River (51°28'25"N; 116°58'59"W) in the Rocky Mountains 20 km northeast of Golden, BC. Biogeoclimatic ecological zones were 1) Interior Douglas-fir (IDF<sub>dk</sub>), 2) Montane spruce (MS<sub>dm</sub>), and 3) Interior Cedar-Hemlock (ICH<sub>mk</sub>) (Meidinger and Pojar 1991). General topography at 1) and 2) is rolling hills at 1300–1520 m elevation, and at 3) ranges from hilly to steep terrain at 870–890 m elevation.

The upper IDF and MS have a cool, continental climate with cold winters and moderately short, warm summers. The average temperature is below 0 °C for 2–5 months, and above 10 °C for 2–5 months, with mean annual precipitation ranging from 300 to 900 mm. Open to closed mature forests of Douglas-fir (*Pseudotsuga menziesii* (Mirbel) Franco. var. *glauca* (Beissn.) Franco) cover much of the IDF zone, with even-aged post-fire lodgepole pine (*Pinus contorta* Dougl. ex Loud. var. *latifolia* Engelm.) stands at higher elevations. The MS landscape has extensive young and maturing seral stages of *Pinus contorta*, which have regenerated after wildfire. Hybrid interior spruce (*Picea glauca* × *P. engelmannii* (Moench) Voss) and subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.) are the dominant shade-tolerant climax trees. *Pseudotsuga menziesii* is an important seral species in zonal ecosystems and is a climax species on warm south-facing slopes in the driest ecosystems. Trembling aspen (*Populus tremuloides* Michx.) is a common seral species and black cottonwood (*Populus trichocarpa* T. & G.) occurs on some moist sites (Meidinger and Pojar 1991). The ICH has an interior, continental climate with cool wet winters and warm dry summers. Mean annual temperature ranges from 2 to 8.7 °C. The temperature averages below 0 °C for 2–5 months and above 10 °C for 3–5 months of the year. Mean annual precipitation is 500–1200 mm, 25–50% of which falls as snow. Upland coniferous forests dominate the ICH landscape and comprise the highest diversity of tree species of any zone in BC. Western red cedar (*Thuja plicata* Donn ex D. Don) and western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) dominate mature climax forests with *Pseudotsuga menziesii*, *Pinus contorta*, *Picea glauca*, *Picea engelmannii*, their hybrids, and *A. lasiocarpa* common in these stands (Meidinger and Pojar 1991).

Prior to harvesting, stands at study areas 1) and 2) were composed of a mixture of *Pinus contorta* with variable amounts of *Pseudotsuga menziesii*, *Picea*, and some *A. lasiocarpa*, and at area 3) primarily *Pseudotsuga menziesii* with some of the other coniferous species. Mean ages of *Pinus contorta* ranged from 80 to 120 years and for *Pseudotsuga menziesii* ranged from 120 to 220 years. Mean tree heights ranged from 10.5 to 19.5 m for *Pinus contorta* and from 16.7 to 27.5 m for *Pseudotsuga menziesii*. There were no site preparation treatments on any of these harvested sites, prior to planting. Mean area of sites ranged from 4.5 to 5.8 ha.

## 2.2 Experimental design

Initially, each of the three study areas was considered a regional replicate (block) with a randomized complete block design of the following five treatments (all harvested sites clearcut): (a) no GTR or windrows of woody debris (dispersed debris only); (b) GTR (5–15 trees/ha) without windrows of woody debris (c) no GTR but with woody debris distributed into windrows, (d) GTR (5–15 trees/ha) and woody debris distributed into windrows, and (e) uncut mature/old-growth forest (Fig. 1). The



**Fig. 1.** Photographs (fall 2009) of treatment sites (a) dispersed woody debris, (b) dispersed woody debris with green-tree retention, (c) windrows of woody debris, (d) windrows of woody debris with green-tree retention, and (e) uncut old forest.

15 sites (5 treatments × 3 replicates) were selected on the basis of operational scale, harvest sites that were the size of typical forestry operations, and reasonable proximity of sites to one another within a study area. However, there was a significant treatment by block interaction indicating that each block (study area) and its constituent treatments should be analyzed separately as outlined in the statistical analysis. All treatments within a study area were reasonably separated to enhance statistical independence: East Munro a mean ( $\pm$ SE) of  $0.31 \pm 0.07$  km; Kathleen a mean ( $\pm$ SE) of  $0.40 \pm 0.09$  km; and Blaeberry a mean ( $\pm$ SE) of  $0.23 \pm 0.03$  km. A measure of this independence was that no *M. gapperi* were captured on more than one trapping line.

### 2.3 GTR and woody debris treatments

Timber harvesting at East Munro and Kathleen was targeted at *Pinus contorta* salvage after, or impending, mountain pine beetle (*Dendroctonus ponderosae* Hopk.) attack; at Blaeberry the target was primarily *Pseudotsuga menziesii*. Harvesting system was clearcut with no residual timber, and clearcut with reserves of *Pseudotsuga menziesii* trees as GTR units. Harvesting and subsequent woody debris treatments were installed in autumn 2009 at all study areas. Windrows were created during processing of cut timber, or by site preparation work with an excavator. At East Munro and Kathleen, windrows averaged 2–3 m in height and 7–9 m in diameter or width. At Blaeberry, windrows were smaller than the other areas, averaging 1–2 m in height and 6–7 m in width. Volumes of downed wood ( $\geq 1$  cm in diameter) in the dispersed treatments were measured using the line-intersect method of Van Wagner (1968) in three plots, each of which was an equilateral triangle with 20 m sides. Location of plots was randomly chosen along the small mammal sampling line on each site. Volume of woody debris in a windrow was measured by the method of Hardy (1996), first estimating the volume of a window and then using the method discussed in Sullivan et al. (2011).

### 2.4 Small mammals

Forest-floor small mammals were sampled at 4-week intervals from May to October 2010, 2011, and 2012 at East Munro and Kathleen, and at 4- to 8-week (2010–2012) intervals at Blaeberry. Each of the 15 sites had a 143-m transect for efficient sampling of community composition of small mammals (Pearson and Ruggiero 2003). Each transect had 10 trap stations at 14.3-m intervals with four Longworth live-traps at each station. Traps were supplied with whole oats, a slice of carrot, and 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 morning and afternoon of day 2 and morning of day 3, and then locked open between trapping periods. Small mammal species sampled by this procedure included the southern red-backed vole, long-tailed vole (*Microtus longicaudus* Merriam), meadow vole (*M. pennsylvanicus* Ord), heather vole (*Phenacomys intermedius* Merriam), deer mouse, northwestern chipmunk, montane shrew (*Sorex monticolus* Merriam), masked shrew (*S. cinereus* Kerr), and short-tailed weasel. All animals captured (except shrews and weasels) were ear-tagged with serially numbered tags, breeding condition noted, weighed on Pesola spring balances, and point of capture recorded (Krebs et al. 1969). The duration of the breeding season was noted by palpation of male testes and the condition of mammarys of the females (Krebs et al. 1969). Animals were released on the lines immediately after processing. The overnight trapping technique resulted in a high mortality rate for shrews. Therefore, shrews were collected, frozen, and later identified according to tooth patterns (Nagorsen 1996). All handling of animals was in accordance with the Animal Care Committee, University of British Columbia.

## 2.5 Demographic and diversity parameters

Abundance estimates of animals were derived from the Jolly-Seber (J-S) stochastic model for open populations with small sample size corrections (Seber 1982; Krebs 1999). The J-S model assumes marked and unmarked animals have the same capture probability in each sampling session (Krebs 1999). Because our traps were locked open between trap sessions, we expected that trap responses of animals dissipated between our monthly sampling sessions. The reliability of the Jolly-Seber model declines when population sizes are very low and no marked animals are captured (Seber 1982). Number of individual animals captured was used as the population estimate for the first and last sampling weeks, and for the enumeration of the relatively less common meadow vole, heather vole, the two shrew species, and the short-tailed weasel. Jolly trappability of *M. gapperi* was calculated according to the estimate discussed by Krebs and Boonstra (1984). There were three summer (May-September) and two winter (October-April) periods.

Red-backed voles were classified by age when the body mass of obvious juveniles when first captured was compared with the mass of these animals as they recruited into the population and first showed signs of sexual maturity: juvenile = 1–18 g; adult  $\geq$  19 g. Juveniles were considered to be young animals recruited during the study. Measurements of recruitment (new animals that entered the population through reproduction and immigration), number of successful pregnancies, and early juvenile survival were derived from the sample of animals captured in each trapping session and then summed for each summer period. A pregnancy was considered successful if a female was lactating during the period following the estimated time of birth of a litter. Early juvenile survival is an index relating recruitment of young into the trappable population to the number of lactating females (Krebs et al. 1969). A modified version of this index is number of juvenile animals at week  $t$  divided by the number of lactating females caught in week  $t$ .

Species richness was the total number of species sampled for the small-mammal community in each site (Krebs 1999). Species diversity was calculated using the estimated abundance of each species for a given sampling session and then averaged over the total sampling sessions for each year. This measure of diversity was based on the Shannon-Wiener index which is well represented in the ecological literature (Magurran 2004).

## 2.6 Statistical analysis

A repeated-measures analysis of variance (RM-ANOVA) (SPSS 21.0 SPSS Institute Inc., 2013) was used to determine the effect of GTR and woody debris treatments on mean values of total abundance, species richness, and species diversity of the small mammal communities among the five treatments at each of the three study areas. There were five temporal samples (May to September) for each of the three years to compare treatments at each of the Munro and Kathleen study areas. There were three temporal samples (May, July, and September) for each of the three years to compare treatments at the Blaeberry study area. This same analysis tested for differences in mean values of abundance, number of recruits, number of successful pregnancies, and index of juvenile survival for the red-backed vole. The latter two attributes were compared among treatments at Munro and Kathleen areas only, as there were insufficient data at Blaeberry. A randomized block two-way ANOVA-Model III (Zar 1999) with factor treatment as a fixed effect and factor block as a random effect was used to detect differences in dimensions of windrows among treatments. Where necessary, data were transformed ( $\log_{10}$ ) to better approximate normal distribution and homogeneity of variance as measured by the Levene statistic (Fowler et al. 1998). Transformed datasets included abundance, recruits, and pregnancies for red-backed voles. Mauchly's  $W$ -test

statistic was used to test for sphericity (independence of data among repeated measures) (Littel 1989; Kuehl 1994). For data found to be correlated among years, the Huynh-Feldt (H-F) correction was used to adjust the degrees of freedom of the within-subjects  $F$ -ratio (Huynh and Feldt 1976). Logarithmic (ln based) regression analyses were conducted to determine the relationship and upper limits between mean total abundance, species richness, and species diversity of small mammals, as well as mean abundance of *M. gapperi*, with total volume of woody debris (dispersed and windrow treatments with and without GTR) (Zar 1999). Overall mean values ( $n=9$ ; 3 study areas  $\times$  3 years) were calculated for total abundance, species richness and diversity, and for abundance of each of the individual mammal species. Duncan's multiple range test (DMRT), adjusted for multiple contrasts, was used to compare mean values based on ANOVA results. In all cases, the level of significance was at least  $P=0.05$ .

### 3 Results

#### 3.1 GTR and woody debris treatments

Mean diameters and heights of residual *Pseudotsuga menziesii* trees in GTR units ranged from 46–48 cm and 30–31 m, respectively (Table 1). In the forest sites, three additional tree species included *Pinus contorta*, *A. lasiocarpa*, and *Picea* spp. as well as *Pseudotsuga menziesii* with a range of diameters from 25 to 38 cm and heights from 24 to 30 m. The mean number of residual trees in GTR units ranged from 5–15/ha with a basal area of  $< 5$  m<sup>2</sup>/ha; and was 340 overstory ( $\geq 20$  m height) trees/ha in the uncut forest. Area of treatment sites was similar (Table 1). For woody debris, total volume and volume/ha were significantly ( $P \leq 0.02$ ) lower in the dispersed treatments

**Table 1.** Mean ( $n=3$  study areas)  $\pm$  SE diameter (cm), height (m), and stand density of overstory ( $\geq 20$  m height) coniferous trees, measurements of woody debris treatments, and results of analyses. Mean values followed by different letters are significantly different by DMRT.

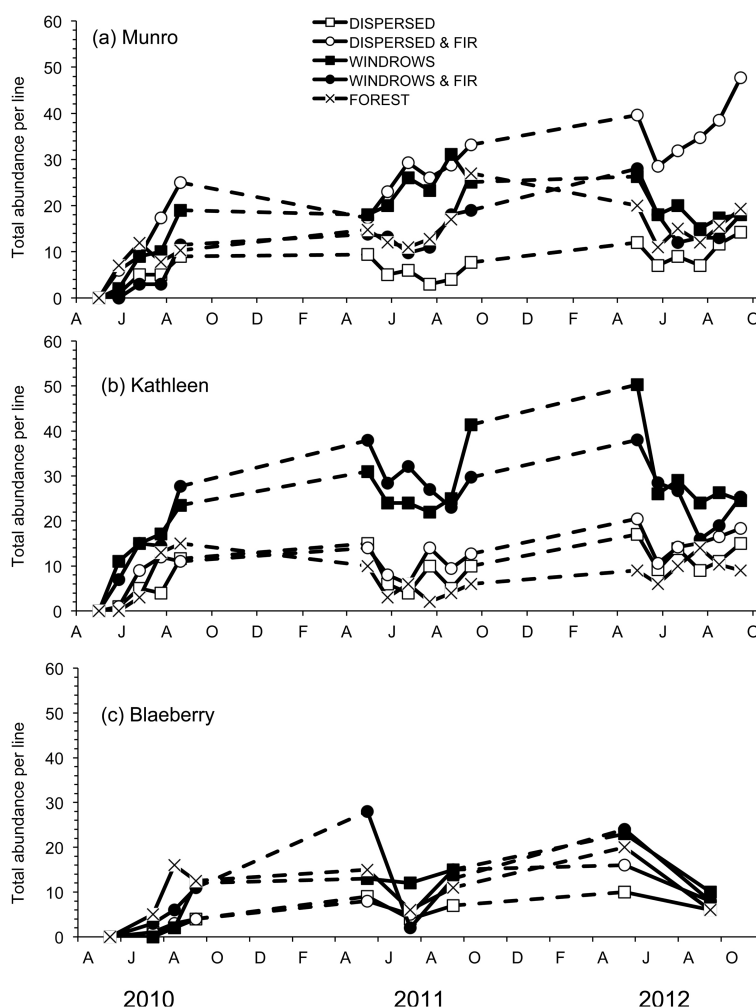
Parameter and species	DISP	DISP+GTR	WINDR	WINDR+GTR	FOREST	Analysis	
<b>Overstory conifers</b>							
Mean diameter							
<i>Pseudotsuga menziesii</i>	-	48.2 $\pm$ 1.9	-	46.3 $\pm$ 4.3	38.1 $\pm$ 3.5	-	-
Mean height							
<i>Pseudotsuga menziesii</i>	-	30.9 $\pm$ 1.0	-	29.6 $\pm$ 1.2	29.2 $\pm$ 2.4	-	-
Trees/ha	-	5–15	-	5–15	340 $\pm$ 87	-	-
						F <sub>3,6</sub>	P
Area (ha)	4.47 $\pm$ 0.23	4.63 $\pm$ 0.03	5.83 $\pm$ 1.34	5.77 $\pm$ 1.38	100+	0.92	0.49
<b>Woody debris</b>							
Total volume (m <sup>3</sup> )	735b $\pm$ 106	1084b $\pm$ 257	2504a $\pm$ 483	2996a $\pm$ 296	-	21.76	<0.01
Volume/ha (m <sup>3</sup> )	167.9b $\pm$ 33.8	234.4b $\pm$ 56.5	504.1a $\pm$ 165.3	589.3a $\pm$ 148.3	-	6.81	0.02
						F <sub>1,2</sub>	P
Windrow length (m)	-	-	256.1 $\pm$ 22.6	411.7 $\pm$ 77.8	-	6.85	0.12
Volume (m <sup>3</sup> ) per m of windrow	-	-	10.23 $\pm$ 2.62	8.06 $\pm$ 2.14	-	1.18	0.39
Windrow height (m)	-	-	2.26 $\pm$ 0.34	2.01 $\pm$ 0.35	-	6.81	0.12
Windrow width (m)	-	-	8.03 $\pm$ 0.97	7.32 $\pm$ 0.83	-	0.43	0.58

DISP=Dispersed debris; DISP+GTR=Dispersed debris and green-tree retention; WINDR=Windrow of debris; WINDR+GTR=Windrow of debris and green-tree retention.

than in windrows (Table 1). Mean length of windrow and volume of debris per meter of length were similar ( $P > 0.05$ ) between windrow treatments, as were mean height and width of windrows.

### 3.2 Small mammal communities

A total of nine species of forest-floor small mammals, composed of 1553 individuals, were captured. *M. gapperi* was the most common species captured with 599 individuals, followed by *P. maniculatus* (274), *N. amoenus* (201), *M. longicaudus* (171), *S. monticolus* (157), *S. cinereus* (63), *P. intermedius* (38), *M. pennsylvanicus* (35), and *M. erminea* (15). Mean total abundance of small mammals per index-line was significantly different among treatment sites at Munro ( $F_{4,20} = 17.05$ ;  $P < 0.01$ ) and Kathleen ( $F_{4,20} = 23.99$ ;  $P < 0.01$ ), but not at Blaeberry (Table 2 and Fig. 2). At Munro, mean total abundance was highest (DMRT;  $P = 0.05$ ) in the dispersed+GTR site at 26 animals per line, followed by the windrow, forest, and windrow-GTR sites (Table 2). At Kathleen, mean total abundance was highest (DMRT;  $P = 0.05$ ) in the windrow and windrow-GTR sites at 24 animals per line. The other three sites ranged from 7–11 animals per line. The sites at Blaeberry tended to



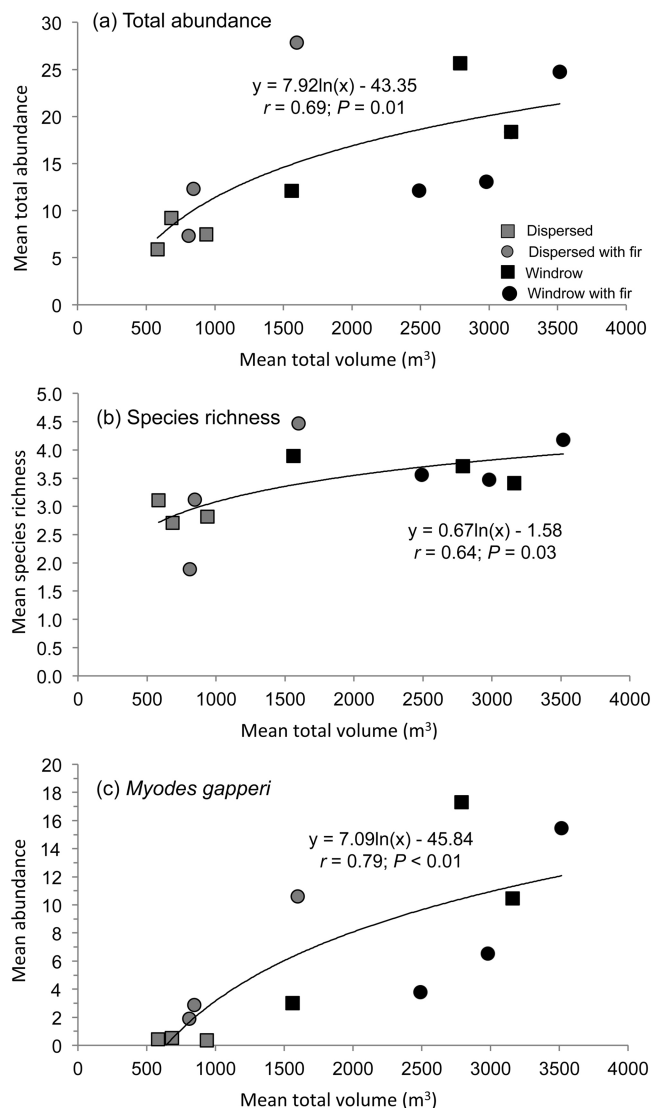
**Fig. 2.** Total abundance per line of forest-floor small mammals for the five treatments for each of the study sites: a) Munro, b) Kathleen, and c) Blaeberry 2010 to 2012. A=April, J=June, A=August, O=October, D=December, F=February.



**Table 2.** Mean±SE (*n*=3 or 5 samples) total abundance, species richness, and diversity of small mammals during 2010–2012 and results of RM-ANOVA for each block (study area). Within a row, columns with different letters are significantly different by Duncan's multiple range test (DMRT), adjusted for multiple contrasts. No data were found to be correlated among years.

Parameter and area	Site			Treatment		Analysis Time		Treatment × time			
	DISP	DISP+GTR	WINDR	WINDR+GTR	FOREST	<i>F</i> <sub>4,20</sub>	<i>P</i>	<i>F</i> <sub>2,40</sub>	<i>P</i>	<i>F</i> <sub>8,40</sub>	<i>P</i>
<b>Total abundance</b>											
Mumro	6.93 <sup>d</sup> ±0.88	26.41 <sup>a</sup> ±2.81	18.12 <sup>b</sup> ±1.87	11.75 <sup>cd</sup> ±1.5	13.63 <sup>bc</sup> ±1.27	17.05	<0.01	54.61	<0.01	9.53	<0.01
Kathleen	8.64 <sup>b</sup> ±1.11	11.45 <sup>b</sup> ±1.13	24.25 <sup>a</sup> ±1.81	23.85 <sup>a</sup> ±2.08	7.42 <sup>b</sup> ±1.19	23.99	<0.01	4.24	0.02	1.74	0.12
Blaeberry	6.13±1.25	7.75±1.89	12.13±2.92	12.25±3.37	12.75±2.42	0.78 <sup>1)</sup>	0.56	7.49 <sup>2)</sup>	<0.01	2.07 <sup>3)</sup>	0.09
<b>Species richness</b>											
Mumro	2.53 <sup>b</sup> ±0.2	4.27 <sup>a</sup> ±0.33	3.40 <sup>ab</sup> ±0.27	3.33 <sup>ab</sup> ±0.35	3.33 <sup>ab</sup> ±0.27	3.58	0.02	13.64	<0.01	2.29	0.04
Kathleen	2.53±0.22	3.00±0.31	3.53±0.32	4.00±0.32	3.33±0.39	2.08	0.12	6.42	<0.01	2.15	0.05
Blaeberry	3.00±0.60	2.00±0.27	3.75±0.67	3.38±0.60	2.25±0.16	1.20 <sup>1)</sup>	0.37	14.62 <sup>2)</sup>	<0.01	4.03 <sup>3)</sup>	<0.01
<b>Species diversity</b>											
Mumro	1.03±0.15	1.59±0.13	1.27±0.15	1.35±0.13	1.54±0.10	2.51	0.07	9.28	<0.01	1.86	0.09
Kathleen	1.07±0.13	1.21±0.13	1.16±0.15	1.27±0.18	1.46±0.14	0.84	0.51	16.02	<0.01	3.87	<0.01
Blaeberry	1.13±0.30	0.75±0.17	1.54±0.26	1.37±0.20	0.88±0.07	1.28 <sup>1)</sup>	0.34	6.88 <sup>2)</sup>	<0.01	2.24 <sup>3)</sup>	0.07

1) *F*<sub>4,10</sub>; 2) *F*<sub>2,20</sub>; 3) *F*<sub>8,20</sub>  
 DISP Dispersed; DISP+GTR Dispersed with green tree retention; WINDR Windrow; WINDR+GTR Windrow with green tree retention.



**Fig. 3.** Regression relationship of mean a) total abundance and b) species richness of forest-floor small mammals, and c) abundance of *Myodes gapperi*, with mean total volume of woody debris in dispersed and windrow treatments with and without GTR.

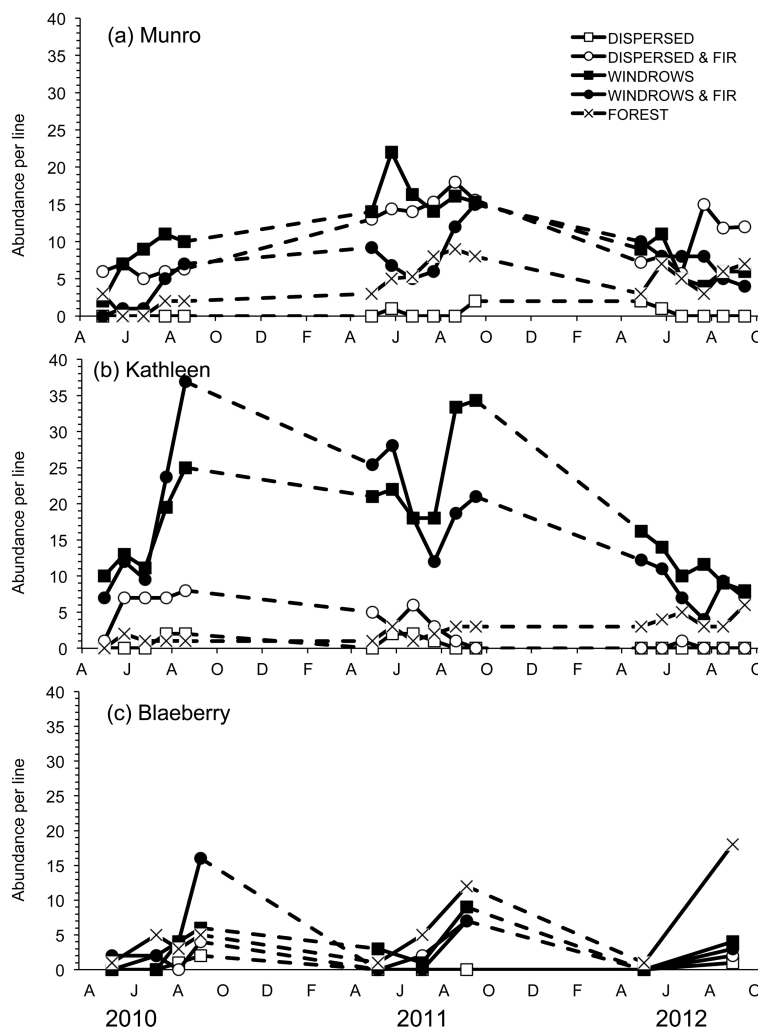
follow this latter pattern with 12 animals per line in the windrow, windrow+GTR, and forest sites, and 6–7 in the other two sites, but with generally lower numbers overall than the other two study areas. All study areas had significant ( $P \leq 0.02$ ) changes in total abundance with time (Table 2). There was a significant ( $F_{8,40} = 9.53; P < 0.01$ ) treatment  $\times$  time interaction at Munro owing to changes in number of animals in the windrow and windrow+GTR sites (Fig. 2a).

Mean species richness was significantly ( $F_{4,20} = 3.58; P = 0.02$ ) different among treatment sites at Munro, but not at Kathleen or Blaeberry (Table 2). Mean species richness was significantly (DMRT;  $P = 0.05$ ) higher in the dispersed+GTR site than dispersed site, with the other sites being similar to both of these. Mean species diversity was similar ( $P > 0.05$ ) among sites at all three study areas (Table 2). Both richness and diversity measures increased significantly ( $P < 0.01$ ) with time at all study areas. Although not formally significant, the highest levels of species richness (4.39 and 4.28) and diversity (1.85 and 2.05) overall occurred in the windrow and windrow+GTR treatments, respectively, in 2012.

There was a positive relationship ( $r=0.69$ ;  $P=0.01$ ) between mean total abundance of small mammals and total volume of woody debris across the dispersed and windrow treatments with and without GTR (Fig. 3a). A similar relationship was recorded for mean species richness ( $r=0.64$ ;  $P=0.03$ ) with mean total volume of woody debris (Fig. 3b). Mean species diversity also followed this pattern but was not significant.

### 3.3 Red-backed voles

Susceptibility to capture was measured by Jolly trappability estimates with mean values ranging from 71.4 to 88.4% for *M. gapperi* in the sites where this species was common. Mean abundance of *M. gapperi* was significantly different among treatment sites at Munro ( $F_{4,20}=83.08$ ;  $P<0.01$ ) and Kathleen ( $F_{4,20}=114.20$ ;  $P<0.01$ ), but not at Blaeberry (Table 3 and Fig. 4). At Munro, mean abundance of *M. gapperi* was highest (DMRT;  $P=0.05$ ) in the dispersed+GTR and windrow sites at 10 voles per line, and at Kathleen was highest in the windrow and windrow+GTR sites at 16



**Fig. 4.** Abundance per line of *Myodes gapperi* for the five treatments for each of the study sites: a) Munro, b) Kathleen, and c) Blaeberry 2010 to 2012. A=April, J=June, A=August, O=October, D=December, F=February.

**Table 3.** Mean ± SE (*n* = 3 or 5 samples) abundance per line, number of recruits, successful pregnancies, and early juvenile survival for *Myodes gapperi* during 2010–2012 and results of RM-ANOVA for each block (study area). *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. Within a row, columns of mean values with different letters are significantly different by Duncan's multiple range test (DMRT), adjusted for multiple contrasts.

Parameter and area	Site				RM-ANOVA results			
	DISP	DISP+GTR	WINDR	FOREST	Treatment <i>F</i> <sub>4,20</sub> <i>P</i>	Time <i>F</i> <sub>2,40</sub> <i>P</i>	Treatment × time <i>F</i> <sub>8,40</sub> <i>P</i>	
<b>Abundance</b>								
Munro	0.27 <sup>d</sup> ± 0.15	10.18 <sup>a</sup> ± 1.14	10.43 <sup>a</sup> ± 1.39	4.09 <sup>s</sup> ± 0.70	83.08 <0.01	22.94* <0.01	2.59* 0.03	
Kathleen	0.60 <sup>c</sup> ± 0.24	3.27 <sup>b</sup> ± 0.80	16.79 <sup>a</sup> ± 1.74	2.20 <sup>b</sup> ± 0.35	114.20 <0.01	11.32* <0.01	6.13* <0.01	
Blaeberry	0.38 ± 0.26	2.13 ± 0.85	2.88 ± 1.17	6.00 ± 2.15	1.31 <sup>1)</sup> 0.33	0.16 <sup>2)</sup> 0.85	3.26 <sup>3)</sup> 0.02	
<b>Total recruits</b>								
Munro	0.13 <sup>c</sup> ± 0.09	3.73 <sup>ab</sup> ± 0.75	4.07 <sup>a</sup> ± 0.70	1.93 <sup>b</sup> ± 0.43	10.40 <0.01	6.48 <0.01	1.75 0.12	
Kathleen	0.40 <sup>c</sup> ± 0.16	1.73 <sup>b</sup> ± 0.50	6.13 <sup>a</sup> ± 1.19	1.40 <sup>b</sup> ± 0.29	17.25 <0.01	14.91 <0.01	2.88 0.01	
Blaeberry	0.28 ± 0.15	2.00 ± 0.76	2.44 ± 1.03	6.17 ± 1.96	1.27 <sup>1)</sup> 0.35	0.12 <sup>2)</sup> 0.89	1.33 <sup>3)</sup> 0.29	
<b>Successful pregnancies</b>								
Munro	0.07 <sup>c</sup> ± 0.07	2.47 <sup>a</sup> ± 0.40	1.67 <sup>ab</sup> ± 0.45	0.73 <sup>bc</sup> ± 0.25	5.25 <0.01	3.51 0.04	4.78 <0.01	
Kathleen	0.07 <sup>c</sup> ± 0.07	0.67 <sup>bc</sup> ± 0.32	3.27 <sup>a</sup> ± 0.73	0.87 <sup>bc</sup> ± 0.31	6.05 <0.01	4.49 0.02	3.78 <0.01	
<b>Juvenile survival</b>								
Munro	0.00	0.57 ± 0.19	0.68 ± 0.53	0.07 ± 0.07	-	-	-	
Kathleen	0.00	0.13 ± 0.09	0.42 ± 0.16	0.07 ± 0.07	-	-	-	

1) *F*<sub>4,10</sub>; 2) *F*<sub>2,20</sub>; 3) *F*<sub>8,20</sub>  
 DISP Dispersed; DISP+GTR Dispersed with green tree retention; WINDR Windrow; WINDR+GTR Windrow with green tree retention.

voles per line (Table 3). Again, mean numbers of *M. gapperi* were generally lower at Blaeberry than at Munro or Kathleen, but with a relative increase in voles across sites with greater retention (Table 3). Munro and Kathleen had significant ( $P < 0.01$ ) changes in abundance of *M. gapperi* with time, and all three study areas had significant ( $P \leq 0.03$ ) treatment  $\times$  time interactions (Table 3 and Fig. 4).

Mean number of recruits also followed this pattern of abundance, with significant differences among treatment sites at Munro ( $F_{4,20} = 10.40$ ;  $P < 0.01$ ) and Kathleen ( $F_{4,20} = 17.25$ ;  $P < 0.01$ ) (Table 3). At Munro, mean number of recruits was highest (DMRT;  $P = 0.05$ ) in the dispersed+GTR, windrow, and windrow+GTR sites, with the GTR sites being similar to the forest. At Kathleen, mean number of recruits was highest (DMRT;  $P = 0.05$ ) in the windrow and windrow+GTR sites, followed by the dispersed+GTR and forest sites. At both of these study areas, the lowest number of recruits of *M. gapperi* was in the dispersed sites. At Blaeberry, recruit numbers were less than the other areas, but tended to increase with retention (Table 3). Munro and Kathleen had significant ( $P < 0.01$ ) changes in mean number of recruits with time. Mean number of successful pregnancies and early juvenile survival followed the pattern of recruitment at Munro and Kathleen (Table 3). There were insufficient data to analyze pregnancies or juvenile survival for *M. gapperi* at Blaeberry, and similarly too few data for juvenile survival to be analyzed at Munro and Kathleen. There was a positive relationship ( $r = 0.79$ ;  $P < 0.01$ ) between mean abundance of *M. gapperi* and total volume of woody debris across treatments (Fig. 3c).

## 4 Discussion

### 4.1 GTR, woody debris and small mammals

This study is the first investigation of the responses of forest-floor small mammals to an increasing gradient of retained habitat structure via GTR and woody debris on clearcuts. Hypothesis (1), that abundance and species diversity of the forest-floor small mammal community would increase with higher levels of structural retention via GTR and woody debris seemed to be partly supported. Mean total abundance was higher in the two windrow treatment sites than the dispersed sites and did generally increase with the gradient of retained habitat structure. An exception was the dispersed+GTR site at Munro which had the highest number of small mammals at that study area. This result was likely owing to a relatively high volume (*ca.* twice as much) of dispersed woody debris for that particular treatment site. Although mean species richness and diversity were generally similar among treatment sites, the highest levels of species richness and diversity were recorded in windrow and windrow+GTR treatments in 2012, as these measurements increased significantly during the 3-year study. In addition, all nine species of small mammals were present in the various treatments in terms of overall mean abundance (Table 4).

This pattern of higher values for the small mammal community was also reported for substantial piles and windrows of debris than dispersed debris by Sullivan et al. (2012). However, increasing levels of GTR, without woody debris structures, had no effect on abundance, richness, or diversity for the small mammal community in mixed *Pinus contorta* – *Pseudotsuga menziesii* forest similar to this study at three years (Sullivan and Sullivan 2001) and eight years (Sullivan et al. 2008) post-harvest. At 4-to 6-years post-harvest in this same forest type, even relatively high densities (73–127 trees/ha) and basal area (mean of 14.7 m<sup>2</sup>/ha) of residual trees, without woody debris, showed similar levels of total abundance and diversity in GTR and clearcut sites (Sullivan and Sullivan 2011). Much of this lack of positive responses to GTR is related to the species-specific responses of small mammals to harvesting strategies with habitat generalist and early successional

**Table 4.** Responses (overall mean values $\pm$ SE,  $n=9$ ; 3 study areas  $\times$  3 years) of small mammal communities to GTR and woody debris treatments 2010–2012.

Parameter	Dispersed	Dispersed+GTR	Windrow	Windrow+GTR	Uncut forest
Mean abundance per line					
<i>Myodes gapperi</i>	0.43 $\pm$ 0.12	5.08 $\pm$ 1.61	10.15 $\pm$ 2.50	8.40 $\pm$ 2.23	4.35 $\pm$ 0.91
<i>Peromyscus maniculatus</i>	2.07 $\pm$ 0.55	3.80 $\pm$ 0.76	1.55 $\pm$ 0.74	1.80 $\pm$ 0.83	3.95 $\pm$ 0.91
<i>Neotamias amoenus</i>	3.03 $\pm$ 0.87	4.89 $\pm$ 1.62	2.34 $\pm$ 0.71	2.28 $\pm$ 0.73	1.68 $\pm$ 0.76
<i>Phenacomys intermedius</i>	0.34 $\pm$ 0.11	0.02 $\pm$ 0.02	0.15 $\pm$ 0.11	0.36 $\pm$ 0.26	0.16 $\pm$ 0.07
<i>Microtus longicaudus</i>	0.53 $\pm$ 0.28	0.80 $\pm$ 0.61	2.61 $\pm$ 0.82	1.97 $\pm$ 0.65	0.74 $\pm$ 0.50
<i>Microtus pennsylvanicus</i>	0.45 $\pm$ 0.33	0.56 $\pm$ 0.27	0.00 $\pm$ 0.00	0.07 $\pm$ 0.07	0.06 $\pm$ 0.06
<i>Sorex monticolus</i>	0.58 $\pm$ 0.16	0.32 $\pm$ 0.17	1.45 $\pm$ 0.22	0.79 $\pm$ 0.19	0.29 $\pm$ 0.14
<i>Sorex cinereus</i>	0.14 $\pm$ 0.05	0.15 $\pm$ 0.09	0.51 $\pm$ 0.20	0.57 $\pm$ 0.20	0.26 $\pm$ 0.15
<i>Mustela erminea</i>	0.04 $\pm$ 0.02	0.04 $\pm$ 0.04	0.05 $\pm$ 0.04	0.16 $\pm$ 0.07	0.04 $\pm$ 0.03
Total	7.61 $\pm$ 0.74	15.66 $\pm$ 3.58	18.81 $\pm$ 2.50	16.40 $\pm$ 2.38	11.53 $\pm$ 1.23
Species richness	2.89 $\pm$ 0.15	3.14 $\pm$ 0.43	3.70 $\pm$ 0.30	3.72 $\pm$ 0.21	3.01 $\pm$ 0.27
Species diversity	1.16 $\pm$ 0.07	1.19 $\pm$ 0.16	1.39 $\pm$ 0.16	1.51 $\pm$ 0.17	1.29 $\pm$ 0.13

species dominating clearcuts and closed-canopy specialists like *M. gapperi* disappearing (Fisher and Wilkinson 2005; Zwolak 2009).

## 4.2 Red-backed voles

Hypothesis (2), that abundance, reproduction, and recruitment of *M. gapperi* would increase with higher levels of structural retention via GTR and woody debris, seemed to be supported. Mean abundance, recruitment, and number of successful pregnancies of *M. gapperi* increased significantly with GTR and amounts of woody debris in windrows. In terms of GTR, *M. gapperi* has persisted for 2–3 years in several forest types that have been harvested by selection, patch, and shelterwood systems (Steventon et al. 1998; Von Trebra et al. 1998), but not at 3–8 years post-harvest in seed-tree systems (Sullivan et al. 2008). However, several other studies reported that red-backed voles commonly inhabit older clearcuts that did not have intensive site preparation or conifer release treatments (Gagne et al. 1999; Fuller et al. 2004; Ransome et al. 2009). *M. gapperi* habitat seemed ameliorated further when these parameters were augmented by advanced coniferous regeneration (Potvin et al. 1999), substantial woody debris on harvest openings (Sullivan et al. 2012) and in partially cut stands (Fauteux et al. 2012), and variable levels of both dispersed and aggregated GTR (Gitzen et al. 2007).

## 4.3 Diversifying clearcuts

Hypothesis (3), that responses of the forest-floor small mammal community and *M. gapperi*, on sites with GTR and windrows of debris, would be comparable to or higher than those in uncut mature/old growth forest was also supported, at least for this initial 3-year post-harvest window of investigation. The presence of *M. gapperi* populations at mature or old-growth “forest” levels of abundance suggested that networks of food sources and predators may also have been present as components of biodiversity, however, we did not collect data on these aspects. Abundances of mammalian carnivores, and hence degree of predation, are also reduced by clearcutting with loss of preferred prey species, den sites, and other components of forest stand structure (Fisher and Wilkinson 2005). In terms of mammalian biodiversity, carnivores such as coyotes (*Canis latrans* Say), red foxes (*Vulpes vulpes* L.), lynx (*Lynx canadensis* Kerr), cougars (*Felis concolor* L.),

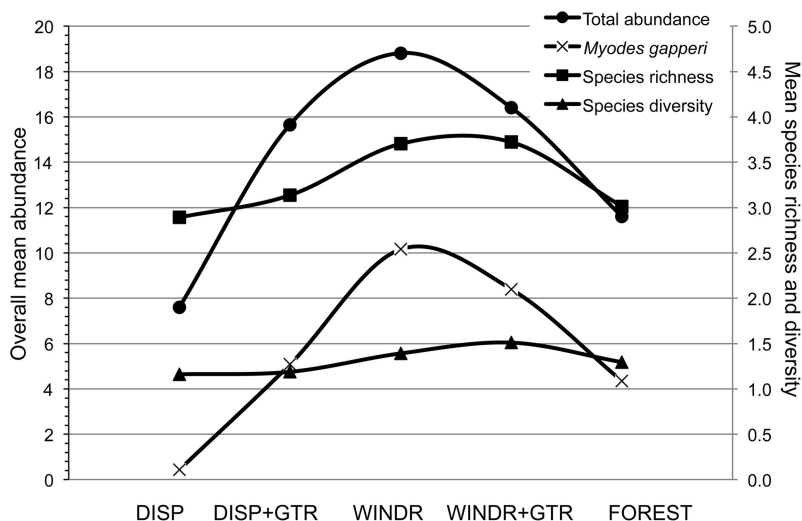
weasels, and American martens also use woody debris, particularly logs, as habitat for denning, nesting, and foraging (McComb 2003). Weasels and marten seem to use incidental debris piles in reports reviewed by Bunnell and Houde (2010). Thus, strategic management of post-harvest woody debris could help maintain abundance and diversity of forest mammals, both predator and prey species, on clearcuts. Large-scale salvage harvesting of those forests influenced by wildfire and insect outbreaks typically create large (> 100 ha) openings where habitat creation is much needed (Lindenmayer et al. 2008).

#### 4.4 Study design

The three study areas were originally to act as regional replicates in a randomized complete block design. However, a significant treatment by block interaction necessitated analysis of each block (study area) separately. As noted, small mammals at the Munro and Kathleen study areas exhibited reasonably similar patterns of responses to the different treatments. Mammal responses to treatments at the Blaeberry study area tended to follow the same pattern but small sample sizes may have limited the detection of significant differences. Thus, inferences of results from these study areas should be cautiously extrapolated across the different forest ecological zones. However, it is important to note that these inferences reflect small mammal responses to habitat structures during summer and fall (May to October) only. Population changes resulting from these treatments may not have been the same during other seasons of the year. The 3-year study duration did suggest that there were no dramatic changes in abundance of small mammals from one year to the next during the overwinter periods when data were not available. As with many ecological studies, additional replicates and years of study may have improved the precision of our estimates and duration of observed results, but were not possible due to funding and logistical constraints.

#### 4.5 Conclusions

There are two methods of intervention, at the time of harvest, to produce “old-forest” habitat and diversify clearcuts for mammals: 1) green-tree retention and 2) strategic management of post-harvest woody debris. Each method has been tried in certain situations, but our assessment of a combination of these two interventions suggested a potentially strong additive effect that appeared to be common to the three forest ecological zones examined (Fig. 5). The potential for both of these forest practices to be implemented in innovative strategies, to maintain or enhance habitat for forest mammals, is well within the scope of current industrial operations. However, planting of seedlings to regenerate cutover areas needs to avoid the perimeter of windrows where voles may feed on trees immediately adjacent to woody debris (Sullivan and Sullivan 2014). In the absence of woody debris as retained structures on new clearcuts, density and basal area of residual trees need to be increased substantially beyond the common levels examined in our study. Levels of GTR at  $\geq 25$  m<sup>2</sup>/ha basal area and  $\geq 30\%$  uncut forest seem to be GTR targets to maintain some aspects of habitat for forest mammals (Klenner and Sullivan 2009). In addition, the risk of windthrow of GTR structures also needs to be considered (Scott and Mitchell 2005; Lavoie et al. 2012). However, economic constraints suggest that clearcutting may continue as the dominant harvest system in temperate and boreal forests with relatively low amounts of GTR. Hence, woody debris structures should help provide some habitat to conserve forest mammals on harvest openings.



**Fig. 5.** Overall mean ( $n=9$ ; 3 study areas  $\times$  3 years) abundance for total small mammals and *Myodes gapperi* and species richness and diversity for the five treatments 2010 to 2012. DISP=Dispersed, DISP+GTR=Dispersed with green tree retention, WINDR=Windrow, WINDR+GTR=Windrow with green tree retention.

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