

Understorey protection harvest expedites recolonisation of boreal forest stands by North American red squirrels

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Abstract

Clearcut harvesting removes old-forest structure from stands, rendering these habitats unsuitable for tree-dependent mammal species such as North American red squirrels (*Tamiasciurus hudsonicus*). Unsuitability of boreal mixedwood forest clearcuts may persist for almost a century, longer than most harvest rotations in this region. In these systems, one alternative to clearcutting is mixedwood understorey protection (MUP) harvesting. MUP harvesting selectively removes mature deciduous canopy trees, retaining some mature and immature trees in the overstorey and understorey, and promoting release of understorey conifers. Live tree retention may also serve to promote early recolonisation by tree squirrels. We compared red squirrel abundance and demography before and after MUP harvest, and between different stand types, in the boreal forest of northern Alberta, Canada. Red squirrels were mark-recaptured in MUP, mixedwood reserve, deciduous, and conifer stands June–July 2001–2003. Red squirrel abundance and masses differed between stand types within years. Abundance and masses did not differ between pre- and post-harvest mixedwood stands across years. Across all stand types, red squirrel abundance was predicted by abundance of spruce trees and fungi. Our results indicate that MUP harvesting retains forest structure required by red squirrels, thus allowing persistence of red squirrel populations; it thus holds promise as a component of the natural disturbance model for maintaining arboreal sciurid populations in managed landscapes.

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1. Introduction

The human requirement for timber and pulp often clashes with forest-dwelling species' requirements for trees in which to forage, den, and reproduce. Clearcut harvesting removes all trees and shrubs, and disturbs most ground vegetation in a forested stand. In boreal mixedwood stands typical of northern Alberta, Canada – stands usually dominated by a canopy of trembling aspen (*Populus tremuloides*) with a subcanopy of white spruce (*Picea glauca*) – clearcutting results in a loss of future harvesting opportunity for spruce (Navratil et al., 1994). In the short-term, clearcutting often initiates regrowth along an aspen trajectory (Peterson and Peterson, 1992), thus 'unmixing' the mixedwood forest.

The clearcutting of forests also has the effect of re-initialising forest succession to an earlier seral stage, eliminating the in-stand

old-forest structure required by many forest-dwelling animal species. Recovery of the old-forest mammalian species assemblage to pre-harvest states can take over a century in boreal mixedwood stands (Fisher and Wilkinson, 2005). This time span is often much greater than rotation age in Canada's boreal landscape, particularly in the aspen-dominated mixedwood forests of northern Alberta. The natural disturbance model, wherein forest harvesting is implemented to spatially mimic forest fire at the landscape level, has been suggested as a tool to mitigate loss of species through forest harvest.

1.1. Sustainable harvest alternatives

Hunter (1993) suggested harvesting could be made to emulate fire by implementing harvest patterns that match (1) fire frequency; (2) fire size (mean and variance); and (3) retention rates of snags, live trees, and downed woody material of harvest. Although burn rates can be highly variable (Armstrong, 1999), the first measure would generally allow the 'overmaturation' of forests into old growth phases where growth and yield curves have reached a plateau. The third

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measure would necessarily leave valuable timber on the block (Lee et al., 1997), which may not be economically viable; this may also influence the successional trajectory of stands post-harvest, particularly in species-rich forest communities. The second measure has perhaps proved most popular; it was advocated by Hunter (1993), and has, for example, been adopted in mixedwood boreal forests of northern Alberta.

However, embracing spatial patterns while neglecting stand age and in-stand structure may be fostering a false pretence of conservation. Fisher and Wilkinson's (2005) review revealed that when in-stand structure after harvest fails to approximate in-stand structure after fire, and when stands are not allowed to reach old-growth stages, these factors may negate landscape-scale harvest patterning designed to mitigate species loss—particularly for forest mammals. They suggested that where live residual trees are retained, stands achieve old-growth characteristics (from a wildlife perspective) faster, though still not fast enough to allow the exclusion of old-growth stages in harvested landscapes.

A potential alternative to this conflict between economy and wildlife would involve the implementation of timber harvesting that does not mimic fire at the stand level, but rather 'accelerates' the ageing process of the stand; or rather, that does not reset the stand to early successional habitat as clearcutting does. One option under scrutiny in the mixedwood boreal forest is mixedwood understorey protection (MUP) harvesting. MUP harvesting selectively removes large mature deciduous trees from the canopy, retaining some mature deciduous trees in the canopy, and immature conifer in the subcanopy, while creating forest gaps. This releases light-suppressed understorey conifer into the overstorey; under these growing conditions, it is expected that spruce trees will reach merchantability sooner than if left to grow naturally (Navratil et al., 1994). MUP harvest retains significant numbers of mature or decadent trees and snags, which in turn allows for the persistence of lichen, fungi, mature seed trees, and tree nesting cavities. This practice may support wildlife populations that would otherwise be absent from clearcuts.

A rigorous test of the efficacy of MUP stands to support wildlife necessarily examines those species most heavily impacted by forest harvesting. Arboreal sciurids constitute the species group that is perhaps most heavily impacted by the removal of trees from a stand (see review in Fisher and Wilkinson, 2005). As forest-dependent species, the diversity of arboreal sciurids is often used as an indicator of forest structural complexity and ecosystem function (Carey et al., 1999). In Alberta's northern boreal mixedwood forest, the most abundant arboreal sciurid is the North American red squirrel, *Tamiasciurus hudsonicus*.

1.2. Red squirrel ecology

Red squirrels are conifer specialists, feeding on seeds contained in the cones of *Abies*, *Picea*, and *Pinus* spp. (Smith, 1968; Kemp and Keith, 1970; Rusch and Reeder, 1978; Riege, 1991). Although red squirrels also feed on mushrooms, berries, and nuts (Gurnell, 1983; Yahner, 1987), they require conifer

cones for overwinter survival (Rusch and Reeder, 1978). Squirrels collect cones in the late summer and early fall, and cache them in middens (Hurly and Robertson, 1990; Dempsey and Keppie, 1993). Red squirrel middens are located on territories that are relatively permanent (Rusch and Reeder, 1978) and heavily defended (Stuart-Smith and Boutin, 1994). Squirrels without a permanent territory containing mature conifer trees, and thus a reliable source of over-wintering food, have a low probability of survival (Rusch and Reeder, 1978).

The removal of mature cone-bearing trees from harvested stands has a demonstrated deleterious effect on red squirrel abundance (see review in Fisher and Wilkinson, 2005). Kirkland's (1990) review found that red squirrel abundance was much reduced in clearcuts; Thompson et al. (1989) found that red squirrels were significantly less abundant in young clearcuts than in old-forest stands. Fisher (1999) found that resident red squirrels were absent from clearcut mixedwood boreal forest stands. As harvesting practices that remove the majority of in-stand forest structure are shown to have a significant negative impact on red squirrel populations, red squirrels provide a good model with which to test the effects of alternative harvesting strategies that manipulate in-stand tree retention and canopy composition.

1.3. Objectives and hypotheses

Our goal was to compare the abundance and demography of red squirrels in MUP stands, with unharvested reserves with differing dominant tree species and forest structure. We tested two hypotheses:

- (1) Post-harvest MUP stands will retain reproductive adult red squirrels in numbers similar to unharvested mixedwood stands (whereas clearcuts will not).
- (2) Post-harvest MUP stands will contain fewer red squirrels than old-growth (*ca.* 150 years old) conifer stands, mirroring the relationship between unharvested mixedwood and conifer stands.

In addition, we wished to eliminate the possibility that differences between stands were artefacts of disturbance activity rather than selection for in-stand habitat attributes. Therefore, we conducted multiple regression analyses across all stand types to examine the consistency of correlations between in-stand structure and red squirrel presence. Positive habitat correlations across harvested and unharvested stands would implicate in-stand structure, rather than the harvesting process, as the mechanism behind differential habitat use of stand types.

2. Methods

2.1. Study area

We conducted this study in two areas within the boreal forest of northwestern Alberta. The study area south of Grande Prairie (Fig. 1; 118°45'0W; 54°48'50N) encompassed two forest types: (1) pure deciduous stands dominated by aspen (*P. tremuloides*

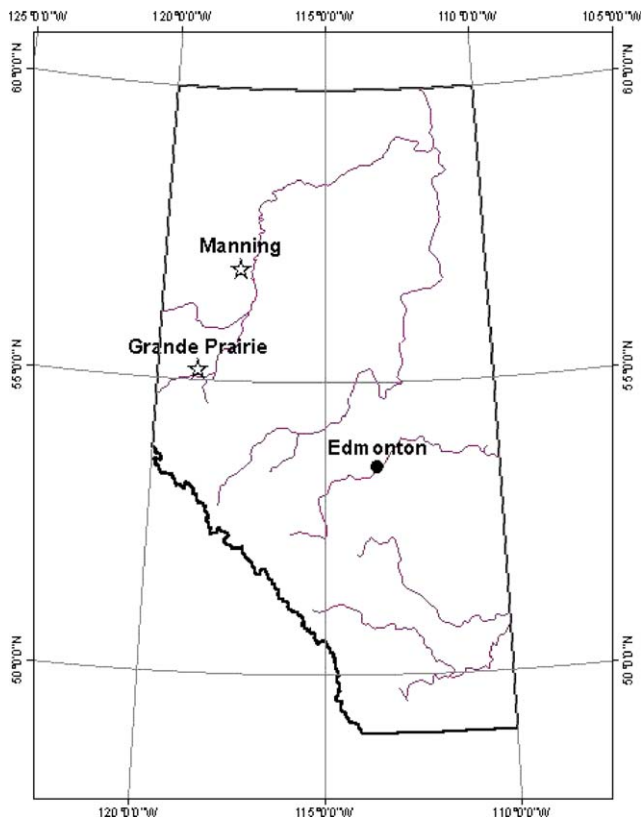


Fig. 1. Province of Alberta, Canada, showing latitude, longitude, major rivers, and the city of Edmonton for reference. Study areas are marked with an asterisk.

Michx.), but with small pockets of balsam poplar (*Populus balsamifera* L.) and (2) mixedwood stands with an aspen-dominated canopy and white spruce understorey [*P. glauca* (Moench) Voss]. Twelve stands, all approximately 105 years old, ranging in size from 20.2 to 57.6 ha, with a mean of 40.1 ha, were established in the Grande Prairie study area. The six mixedwood stands and six deciduous stands were further divided into harvest stands and control stands (hereafter termed 'reserves'; Table 1).

In the Grande Prairie study area, harvest stands were cut between September 2000 and February 2001. Deciduous cutblocks were clearcut and mixedwood stands were MUP harvested, removing *ca.* 70% of the deciduous stems while protecting the majority of coniferous understorey. Skid trails were 25 m apart. Areas with heavy coniferous understorey and

minor deciduous volume were left unharvested. Merchantable coniferous stems that reached or exceeded the height of the deciduous canopy were harvested.

The study area northwest of Manning (Fig. 1; 117°49'60W; 57°8'58N) contained two forest types. Conifer stands were dominated by mature white spruce (approximately 150 years old) with pockets of aspen, balsam poplar and lodgepole pine (*Pinus contorta* Loudon var. *latifolia* Engelm.). These stands were considered old-growth, possessing forest structure characteristic of old-growth forests. The second forest type in this area was boreal mixedwood with an aspen overstorey and white spruce understorey. Canopy trees in the mixedwood stands were approximately 75 years old. Twelve stands ranging from 11 to 49 ha, with a mean of 27.3 ha, were delineated using forest inventory maps. The six conifer and six mixedwood stands were further divided into harvest stands and reserve stands (Table 1). Thus, there were three replicates of each stand type.

In the Manning study area, cut stands were harvested in November and December 2001. Coniferous cutblocks were clearcut (followed by site preparation to expose mineral soil, and tree-planting), whereas mixedwood stands were MUP harvested. The objective of the MUP harvest was to remove 85% of the deciduous stems while protecting at least 55% of the conifer understorey. Skid trails were cut 25 m apart. Areas with heavy coniferous understorey and minor deciduous volume were left unharvested.

2.2. Forest structure and fungal sampling

This paper describes part of a multi-species project that examined several biotic responses to mixedwood understorey protection harvesting. To encompass all the plant, fungi, and animal species being studied, sampling protocols for each were overlaid in each stand. Due to the variation in size and shape of pre-harvest stands, the sampling patterns differed between the Grande Prairie and Manning study areas. In the Grande Prairie study area, a grid pattern of 10 contiguous hectares was established in the centre of each stand; in the Manning study area a strip transect of seven continuous hectares was established in the centre of each stand. All pre- and post-harvest sampling was conducted along transects within each grid (Grande Prairie) or strip (Manning).

Snag, tree and tall shrub (species that tend to grow taller than 3 m in height) sampling occurred June–July 2000 and 2002 in

Table 1
Forest structural attributes (stem density or abundance per hectare \pm S.E.) of experimental and control stands from the Grande Prairie (GP) and Manning (MN) study areas, June–August 2001–2003

Stand type	Area	Alder	Birch	<i>Picea</i>	<i>Populus</i>	<i>Salix</i>	Snag	Fungal abundance
Deciduous reserve (DR)	GP	2042 \pm 448	827 \pm 139	17 \pm 6	651 \pm 47	660 \pm 113	121 \pm 8	1303 \pm 242
Mixedwood reserve (MR)	GP	474 \pm 113	216 \pm 40	866 \pm 96	605 \pm 44	148 \pm 46	146 \pm 8	690 \pm 131
Mixedwood understorey protection stand (MUP)	GP	25 \pm 20	112 \pm 28	587 \pm 62	772 \pm 136	480 \pm 88	69 \pm 6	650 \pm 172
Mixedwood reserve (MR)	MN	235 \pm 128	3 \pm 3	983 \pm 117	1564 \pm 164	322 \pm 96	86 \pm 13	153 \pm 29
Mixedwood understorey protection stand (MUP)	MN	0 \pm 0	0 \pm 0	689 \pm 75	75 \pm 63	76 \pm 26	29 \pm 3	260 \pm 74
Conifer reserve (CR)	MN	0 \pm 0	5 \pm 5	1173 \pm 126	422 \pm 115	109 \pm 41	120 \pm 14	785 \pm 148

Notes: Alder refers to *Alnus tenuifolia*; birch refers to *Betula papyrifera*; *Picea* includes *P. glauca* and *P. mariana*; *Populus* includes *P. tremuloides* and *P. balsamifera*. All snags and fungi were pooled regardless of species.

both the Grande Prairie and Manning study areas. Sampling was executed along a transect that connected the squirrel trapping locations. Each sampling site (centred around the squirrel traps) was delineated into three different sized plots: (1) a 50 m × 20 m plot (1000 m²) for all snags above 1.3 m in height and >45° from horizontal; (2) a 50 m × 3 m plot (150 m²) for trees and tall shrubs above 10 m; and (3) a 50 m × 2 m plot (100 m²) for trees and tall shrubs below 10 m. In each plot, all tree and tall shrub species were sampled; only trees and tall shrubs with more than half of their stem within the plot boundary were measured. For each trapping location, stem densities were scaled up to units representing stems per hectare.

Due to time limitations only epigeous (above-ground) macro-fungal sporocarps were sampled. Each stand was sampled throughout the growing season along a 500 m × 2 m belt transect connecting squirrel-trapping locations within that stand. All sporocarps found along the belt transect were identified and counted, yielding sporocarp abundance values per species. Specimens not identified in the field were collected, spore prints were made, and samples were dried to assist in later identification.

2.3. Squirrel sampling

Red squirrels were live trapped using Tomahawk 102 and 201 live traps (Tomahawk Livetraps Co., Tomahawk, Wisconsin) in June and July 2001–2003. An analysis of previous and concurrent red squirrel call surveys showed red squirrels, as expected, were absent from clearcut stands (J. Fisher, unpublished data). Given these data and logistical considerations, clearcut stands were not trapped. In all other stand types, ten trap stations were established in each stand and overlapped the fungal transects. There were three replicates of each stand type; however, due to flooding, one conifer stand was rendered unusable.

On the rectangular grids (Grande Prairie), trap stations were placed 50 m apart on each gridline, with the two gridlines 100 m apart. On the linear transects (Manning), trap stations were placed 50 m apart along the length of the transect. At each trap station, two traps were erected: one at the base of the tree or at squirrel sign within 5 m of the base of the tree, and one nailed to the bole of the tree approximately 1.5 m above the ground. Traps were baited with peanut butter and sunflower seeds, stuffed with cotton bedding, and covered in clear plastic to prevent exposure. Traps were set between 18:00 and 22:00 h and checked the next morning between 06:00 and 11:00 h for six to seven consecutive nights per stand per year.

Captured animals were tagged with Monel #1 eartags and weighed with a Pesola scale. Gender and reproductive condition were assessed *via* external features, a reliable method for assessment of gender of small mammals (McCravy and Rose, 1992).

2.4. Statistical analysis among stand types

Red squirrel captures were standardised by effort (number of effective trap nights) to yield captures per 100 trap nights.

Abundance data were [ln + 1]-transformed as required to conform to normality. Abundance data were compared between years (2001–2003) and between stands using a repeated measures MIXED ANOVA procedure in the program SAS (SAS Inc.) with YEAR as the within-subjects (fixed) factor. STAND TYPE and STAND TYPE × YEAR were included as between-subjects factors. This all-encompassing repeated measures factorial ANOVA design controls for effect of YEAR, compensates for experiment-wise error rates associated with performing multiple tests across years, and is robust to any potentially existing error structure in the data. Tukey–Kramer post hoc tests were used to evaluate differences between stand types.

Red squirrel data for Grande Prairie were obtained in 2002 only, and not across several years; we tested for differences between stand types in Grande Prairie and Manning within 2002 (one-way ANOVA, SPSS Inc.).

As abundance can be a misleading indicator of habitat quality (van Horne, 1983), mass and reproductive status of red squirrels were compared across stands. Red squirrels adults were discriminated from juveniles using a threshold mass of 180 g (M. Wheatley, University of Alberta, unpublished data). Masses of red squirrel adults were normally distributed and were analysed for differences between stand types (one-way ANOVA, SPSS Inc.). The percentage of reproductive females, also a potential index of habitat quality, was also analysed for differences between stands (Kruskal–Wallis, SPSS Inc.).

2.5. Logistic regression analysis for habitat associations

Employing a multi-factorial ANOVA design assumes that there may be detectably greater differences between stands due to treatment effect, than differences within stands due to natural heterogeneity. Potential treatment effects may not be detectable in this highly heterogeneous system, so we employed multiple logistic regression models to examine relationships between red squirrel presence/absence, and forest structure within MUP and unharvested stands. First-time captures of squirrels were regressed against fungal abundance, and the number of stems per hectare of each tree species, around each trap station. Recaptures were omitted to prevent pseudoreplication (Hurlbert, 1984).

The number of stems of alder (*Alnus tenuifolia*; LNALD), birch (*Betula papyrifera*; LNBIR), *Picea* spp. (including *P. glauca* and *P. mariana*; LNSPR), *Populus* spp. (including *P. tremuloides* and *P. balsamifera*; LNPOP), and willow (*Salix* spp.; LNWIL); the number of dead decaying trees (snags) of any species (LNSNAG); and fungal abundance (LNFUNG) were [ln + 1]-transformed and entered into a multiple logistic regression model (SPSS Inc.). As the ratio of presence:absence of red squirrels was unbalanced (red squirrels present = 55, absent = 115), we randomly subsampled within absences to create a balanced model with equal presences and absences. We used a forward conditional procedure designed to select those variables that explained the most variation in the squirrel dataset. The inclusion criterion for red squirrels was $\alpha = 0.05$.

Table 2
Red squirrel capture rates per 100 trap nights, by stand type, for each year of trapping near Grande Prairie and Manning, Alberta, Canada

Stand	2001	2002	2003
GP-DR	0.30	0.97	–
GP-MUP	0.00*	4.29	–
GP-MR	0.00	8.71	–
MN-CR	8.10	13.50	21.36
MN-MUP	5.80	0.90*	0.82
MN-MR	4.04	3.35	4.13

The first year post-harvest is marked with an asterisk. '–' no data.

3. Results

3.1. Red squirrel abundance

In 2001, 46 red squirrels were captured 113 times; 68% of these were reproductive (Table 2). Forty-five red squirrels were captured in Manning; only 1 was captured in Grande Prairie. We suspected the paucity of red squirrels in Grande Prairie was due to environmental variability (*i.e.*, a cone crop failure), and not to differences in stand quality or treatment effect, so Grande Prairie 2001 stands were dropped from further analyses. In 2002, 84 red squirrel individuals were captured 132 times; 60% of these were reproductive (Table 2). Forty-three red squirrels were captured in Grande Prairie, and 41 were captured in Manning. In Manning in 2003, 64 red squirrels were captured 128 times (Table 2); 80% were reproductive.

Both STAND TYPE and STAND TYPE \times YEAR were significant terms in the red squirrel abundance repeated measures ANOVA model (STAND TYPE $F = 9.69$; d.f. = 2, 4.58; $p = 0.0226$; STAND TYPE \times YEAR $F = 4.73$; d.f. = 4, 8.96; $p = 0.0251$). Tukey–Kramer pairwise comparisons show a marginally statistically significant difference between 2001 and 2002 for MUP stand types ($p = 0.0694$). YEAR was not significant in the model ($F = 0.49$; d.f. = 2, 8.96; $p = 0.6275$).

Within years, mixedwood reserve stands and MUP stands were not significantly different from one another in either year. However, conifer stands had significantly more red squirrels per trap night than MUP stands ($p = 0.0196$), and marginally more red squirrels than mixedwood reserve stands ($p = 0.0738$). MUP stands did not differ from mixedwood reserve stands ($p = 0.3475$). In 2002, conifer stands had significantly more red squirrels per trap night than did MUP stands in the first year

after harvest ($p = 0.0279$). In 2003, conifer stands had significantly more red squirrels per trap night than did MUP stands in the second year after harvest ($p = 0.0080$).

Northern flying squirrels, *Glaucomys sabrinus*, were also captured in conifer, mixedwood reserve, and MUP stand types, but in numbers too small to permit analysis.

3.2. Red squirrel masses and reproductive status

In 2001 adult red squirrel masses (Table 3), with deciduous stands removed due to a single capture in these stands, differed between stand types (one-way ANOVA; $F = 3.502$; d.f. = 2, 35; $p = 0.041$). Post hoc comparisons detected marginal differences in red squirrel masses between conifer stands and MUP stands (Tukey's HSD; $p = 0.092$), and between conifer and mixedwood reserve stands ($p = 0.080$), but no differences between pre-harvest MUP stands and mixedwood reserve stands ($p = 0.971$). There were no significant differences in percentage of reproductive individuals between stand types in Manning (K–W; $X^2 = 3.915$; d.f. = 2; $p = 0.141$).

In 2002, with deciduous stands removed due to low sample size, adult red squirrel masses (Table 3) were significantly different between stands types (ANOVA; $F = 5.864$; d.f. = 4, 48; $p = 0.001$). Red squirrel masses in conifer stands were significantly greater than both GP-MUP and MN-MUP post-harvest stands (Tukey's HSD; $p = 0.003$ and 0.050 , respectively), were marginally greater than MN mixedwood reserve stands ($p = 0.080$), but not different from GP mixedwood reserve stands ($p = 0.131$). There were significant differences in percentage of reproductive individuals between stand types (K–W; $X^2 = 11.613$; d.f. = 5; $p = 0.040$), with Grande Prairie MUP stands having fewer (zero) reproductive individuals than Manning MUP stands (Mann–Whitney U ; $U < 0.000$; $n = 3, 2$; $p = 0.046$) or conifer stands ($U < 0.000$; $n = 2, 3$; $p = 0.053$).

In Manning in 2003 there were no significant differences in adult red squirrel masses (Table 3) between stand types (one-way ANOVA; $F = 0.460$; d.f. = 2, 53; $p = 0.634$). Of the red squirrels captured, the majority were reproductive animals. All animals captured in MUP stands in 2003 were reproductive, as in 2002. Conversely, sex ratios in mixedwood reserve stands were skewed towards males, unlike ratios seen in other years. There were no significant differences in percentage of reproductive animals between stand types (K–W; $X^2 = 4.808$; d.f. = 2; $p = 0.090$).

Table 3
Red squirrel mean mass and reproductive condition by stand type and year near Grande Prairie and Manning, Alberta, Canada

Stand type	2001		2002		2003	
	Mean mass in g (S.D.)	% Reproductive (total)	Mean mass in g (S.D.)	% Reproductive (total)	Mean mass in g (S.D.)	% Reproductive (total)
GP-DR	–	–	158.0 (24.9)	0.0 (3)	–	–
GP-MUP	–*	–*	161.1 (28.4)	0.0 (13)	–	–
GP-MR	–	–	168.4 (39.5)	56.2 (25)	–	–
MN-CR	220.5 (13.7)	64.7 (17)	218.7 (22.0)	81.5 (27)	206.7 (12.6)	76.6 (47)
MN-MUP	202.5 (20.7)	76.5 (17)	194.7* (5.9)	100.0 (3)*	200.0 (12.3)	100 (3)
MN-MR	207.6 (15.8)	60.0 (11)	198.5 (21.7)	90.0 (10)	205.0 (10.8)	85.7 (14)

The first year after harvest is marked with an asterisk. $N = 3$ for each stand type except for CR stands, in which $n = 2$. '–' no data.

Table 4

Multiple logistic regression model (forward conditional: SPSS) of In-transformed red squirrel presence against tree density across several forest stand types near Grande Prairie and Manning, Alberta, Canada

Variable	B	S.E.	Wald	d.f.	Significance	R	Exp (B)
LNSPR	0.42	0.12	12.25	1	0.0005	0.2592	1.52
LNFUNG	0.44	0.19	5.60	1	0.0180	0.1535	1.56
Constant	-2.95	0.84	12.26	1	0.0005		

$N = 110$ with equal presences and absences. Model – 2 log likelihood = 130.354; $p < 0.0001$; Nagelkerke $R^2 = 0.243$.

3.3. Logistic regression analysis

Across all stand types red squirrel presence was significantly related to LNSPR, the density of spruce trees, and LNFUNG, fungal abundance, surrounding a trap station (Table 4; model – 2LL = 130.354; model $X^2 = 22.138$; d.f. = 2; significance < 0.0001). Nagelkerke (1991) R^2 for this model was 0.243; model prediction was 68.18% correct. No other variables were significant with an $\alpha = 0.05$ inclusion criterion.

4. Discussion

4.1. Relative suitability of mixedwood understory protection harvest stands

Although we observed numerical differences in red squirrel abundance before and after MUP harvest, and between harvested and mixedwood reserve stands (Table 2), these differences were not statistically significant. This may suggest that MUP stands are able to support red squirrel populations in numbers approximating unharvested mixedwood stands. However, as a note of caution, statistical significance and biological significance are not synonymous, particularly when sample sizes are small as they are here. Further research on population dynamics beyond the first 2 years after harvest should be conducted to investigate the importance of the observed numerical drop in abundance. As it stands, the data presented here appear to substantiate the first of our research hypotheses.

Additional evidence for recolonisation of MUP stands is provided by squirrel mass and reproductive potential, which did not statistically differ between mixedwood reserves and MUP stands. Poor habitats can be occupied by abundant dispersing juveniles or non-reproductive individuals in poor condition, with low masses and high probabilities of mortality (Wheatley et al., 2002). Differences in masses between habitats have been observed in Eurasian red squirrels *Sciurus vulgaris* (Wauters and Dhondt, 1989) and North American red squirrels (Rusch and Reeder, 1978). Larger masses generally correlate with increased reproductive and recruitment rates in red squirrels (Rusch and Reeder, 1978; Wauters et al., 1990). Our results suggest MUP stands represent good quality habitat for large, fit, reproductive animals capable of sustaining a viable population.

The second of our hypotheses was also substantiated; MUP stands were of equal relative quality to unharvested mixedwood reserve stands, when compared to conifer and deciduous stands.

Conifer stands had more squirrels, larger and more frequently reproductive individuals than did mixedwood reserves, pre-harvest MUP stands, and harvested MUP stands. Deciduous stands had few or no squirrels. These results are identical to previously established relationships of stand quality between conifer, mixedwood, and aspen stands (Smith, 1968; Kemp and Keith, 1970; Rusch and Reeder, 1978; although see Wheatley et al., 2002), and are further evidence that MUP stands provide effective red squirrel habitat similar to unharvested mixedwood counterparts.

Some variability did exist across study areas. In the first years after harvest in Grande Prairie, MUP stands were occupied by non-reproductive individuals; in Manning, however, there were no differences in red squirrel masses or percent reproductive individuals between conifer stands, mixedwood reserves or MUP stands. Recapture data suggest that some resident squirrels remained in-stand and attained a greater mass and better reproductive condition 1 year after MUP harvest, and that other squirrels in better condition annexed territories in these stands. The source of the variability is unclear, but may be related to the cone crop failure suspected to have occurred in Grande Prairie in 2001 that resulted in absence of squirrel captures.

Regression indicates that red squirrel abundance within stands is related to abundance of mature conifers and fungal fruiting bodies; these are red squirrels' primary and secondary food sources, and are both components indicative of mature-forest structure. These results are consistent with past studies (Kemp and Keith, 1970; Fisher et al., 2005), which maintain that old conifer stands (in particular, white spruce) provide the highest quality forage for red squirrels, and support the largest and most dense populations. In Alberta's central boreal forest, red squirrels were most abundant in mature mixed spruce stands, followed by jack pine, and then aspen stands (Rusch and Reeder, 1978). The existence of this habitat relationship across harvested and unharvested stands further implicates the retention of forest structural components after MUP harvesting as the factor facilitating persistence of red squirrels after harvest. As MUP is designed to increase the percentage of spruce in the canopy, the abundance of red squirrels in these stands is expected to increase through time.

The persistence of red squirrels in MUP stands is sharply contrasted with clearcutting, which renders the stand unsuitable for red squirrels (Thompson et al., 1989) until these stands reach maturity after several decades (Crête et al., 1995; review in Fisher and Wilkinson, 2005). Likewise, other studies examining live-tree retention – thinning or partial cutting – have shown that species are better maintained relative to clearcutting. Sullivan et al. (2001) found that thinned stands maintained small mammal populations comparable to old-growth stands. Ransome and Sullivan (2002) found no differences in Douglas squirrel (*T. douglasii*) and northern flying squirrel (*G. sabrinus*) density and demography between thinned and unthinned conifer stands. Ransome et al. (2004) suggested that red and flying squirrel abundances would be maintained over the long-term in thinned stands, at levels comparable to old-growth stands. Similarities between partial harvest and unharvested stands (as opposed to

clearcuts) have been found for other forest biota including forest songbirds (Harrison et al., 2005) and ectomycorrhizal diversity and density (Lazaruk et al., 2005). MUP may be superior to thinning then cutting; increased light levels in MUP stands are anticipated to accelerate the maturation of conifers within the stand. MUP stands may even assume older forest characteristics sooner than more traditional partial cuts (Bradbury, 2004).

In addition to accelerating habitat suitability for older-forest species, MUP harvesting has potential applications in forest restoration. For example, a long history of harvesting in the montane red spruce (*Picea rubens*) forests of Appalachia has resulted in regeneration of many regions to *Tsuga* and *Acer* spp. (Schuler et al., 2002). The loss of red spruce communities may have consequences for now-endangered species reliant on those communities. MUP allows release of understorey trees from shading canopy trees, thus allowing suppressed tree species to again become dominant in the forest canopy. This may allow lost communities to reform, and endangered species to recover. The long-term implications of understorey release on forest structure and vegetation communities are currently being explored in the boreal forest (S. Bradbury, unpublished data) and should be explored in other forest systems.

We caution that our sample sizes were small, potentially allowing lack of statistical significance to mask biological significance. The numerical differences in capture rates between harvested and unharvested stands, particularly old-growth stands, suggest that MUP harvesting does not equal old growth or unharvested stands in terms of suitability. Our results should be considered preliminary; further observations throughout successional time are required to ascertain whether acceleration of stand maturity and thus suitability does occur. Nonetheless, our results indicate that mixedwood understorey protection harvesting maintains reproductive red squirrel populations 2 years after harvest, in numbers not statistically different from unharvested mixedwood stands. These results imply that MUP stands have the potential to achieve acceleration of stand suitability for red squirrels. The retention of live trees (young and old), a relatively intact understorey, high fungal abundance and diversity, and other old-forest characteristics, suggest that MUP stands may achieve this acceleration for other old-growth dependent species as well (S. Song, Alberta Research Council, unpublished data).

5. Conclusion

Understorey protection harvesting accelerates the ability of regenerating harvest stands to maintain populations of the mature-forest species *T. hudsonicus*. Accelerated maturity of regenerating stands is of potential application within a natural disturbance model. Employing the spatial component of the natural disturbance model – mimicking fire size and shape – while neglecting the in-stand structure and disturbance frequency typical of fires, will likely lead to the failure of stands harvested under this model to achieve biodiversity objectives. Stands without live and dead residual trees do a poor job of mimicking fire for mammals (Fisher and Wilkinson, 2005) and birds (J. Schieck, Alberta Research Council, unpublished data). Clear-

cutting has failed (as measured by water quality parameters) to emulate fire in riparian systems, whereas partial cuts have succeeded, by retaining forest structural components that influence water chemistry (Nitschke, 2005).

Perhaps more importantly, instituting a harvest rotation that is less than average fire frequency can prevent full recolonisation of old-stand-dependent biota. Integrating MUP harvesting within a natural disturbance model—which would retain in-stand live and dead residuals, and accelerate forest maturity to within harvest rotation timeframes, in addition to mimicking landscape-level fire size and shape—may achieve the aims of the natural disturbance model more effectively than employing clearcutting in the same model.

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