



Contents lists available at SciVerse ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

Small mammal responses to coarse woody debris distribution at different spatial scales in managed and unmanaged boreal forests

Dominique Fauteux^{a,*}, Louis Imbeau^a, Pierre Drapeau^b, Marc J. Mazerolle^a

^a Centre for Forest Research, Université du Québec en Abitibi-Témiscamingue, Département des sciences appliquées, 445 boul. de l'Université, Rouyn-Noranda, Québec, Canada J9X 5E4

^b Centre for Forest Research, Université du Québec à Montréal, Département des sciences biologiques, C.P. 8888 Succ. Centre-Ville, Montréal, Québec, Canada H3C 3P8

ARTICLE INFO

Article history:

Received 24 June 2011

Received in revised form 10 November 2011

Accepted 13 November 2011

Keywords:

Dead wood decay

Partial cut

Rodent

Shrew

Spatial scale

Boreal forest

ABSTRACT

Dead wood such as stumps and logs found on the forest floor is a key structural element that is used by a broad spectrum of organisms and contributes to soil nutrient cycling. The complexity of the forest floor in the boreal forest is largely dependent on coarse woody debris (CWD), but actual forestry practices may compromise the future recruitment of this resource. The main goal of our study was to determine the effects of CWD on small mammals in stands of varying green-tree retention levels. Since small mammals are associated with microhabitat components at multiple spatial scales, our secondary goal was to assess the effects of scale on small mammal relationship with CWD. Five trapping sessions were conducted in the boreal forest of western Québec, Canada during the summers of 2009 and 2010 in four managed forest blocks. Each block was composed of 12 independent trapping grids equally distributed in three treatments: clearcuts (0% green-tree retention), partial cuts (30% green-tree retention) and controls (undisturbed). We live-trapped small rodents and used pitfall traps for shrews in trapping sub-grids (fine-scale; 50 m) nested in larger grids (stand-scale; 300 m). Southern red-backed vole (*Myodes gapperi*) and deer mouse (*Peromyscus maniculatus*) abundances were positively associated with sites with high volumes of well decayed CWD in all treatments, at the fine-scale. Southern bog lemming (*Synaptomys cooperi*) abundance was positively associated with well decayed CWD, at both scales, but mainly in clear-cut areas. Masked shrew (*Sorex cinereus*) abundance increased with high volumes of well decayed CWD in clearcuts but only at the stand-scale. In contrast, meadow voles were more abundant in sites with high volumes of well decayed CWD in controls than in sites with small volumes at the stand-scale. Patches of partial cuts with high volumes of well decayed CWD were characterized by high abundances of red-backed voles and this clearly indicates that volume and decay of CWD are important drivers that can mitigate the impacts of tree removal. We found different scale-dependent responses of small mammals to volumes of well decayed CWD, which indicates that associations were found at the individual as well as at the population level. We suggest that partial cuts composed of regularly distributed patches of high volumes of CWD ($\geq 11.4 \text{ m}^3$ in patches of 0.03 ha) might have a high potential to maintain red-backed voles, a species associated with mature forests.

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1. Introduction

Dead wood plays an important role in maintaining vital natural processes such as nutrient cycling and is often a key structural element of habitat for plants and animals (Maser et al., 1979). Decaying snags, stumps, branches and logs are good substrates for fungi (Amaranthus et al., 1994), mosses (Rambo and Muir, 1998), lichens (Botting and DeLong, 2009) and other plants. Dead wood also provides nest sites, cover, food and humidity for insects (Hjalten et al.,

* Corresponding author. Permanent address: 702, des Aulnes, Amos, Québec, Canada J9T 3Y8. Tel.: +1 581 994 4456; fax: +1 819 797 4727.

E-mail addresses: dominique.fauteux2@uqat.ca (D. Fauteux), louis.imbeau@uqat.ca (L. Imbeau), drapeau.pierre@uqam.ca (P. Drapeau), marc.mazerolle@uqat.ca (M.J. Mazerolle).

2010), amphibians (Blomquist and Hunter, 2010), birds (Imbeau and Desrochers, 2002; Martin et al., 2004; Drapeau et al., 2009), mammals (Loeb, 1999; Pearce and Venier, 2005), and fish (Ahrenstorff et al., 2009). Dead wood is so crucial for maintaining biodiversity that several organisms have dramatically declined as a consequence of its disappearance or rarefaction in managed forests. For example, at the end of the 20th century, approximately 25% of all endangered Scandinavian species were associated with dead wood (Virkalla and Toivonen, 1999). Maintaining dead wood in managed stands is currently a challenge considering that several widely-used silvicultural practices such as ground preparation for plantations and clearcuts reduce dead wood volumes as well as its future recruitment within stands (Pedlar et al., 2002; Hautala et al., 2004).

Among boreal forest-associated vertebrates, small mammals are often identified as one group of species that strongly depends on dead wood. Coarse woody debris (CWD), defined here as large diameter logs and stumps, are indeed used by most of these species (Hayes and Cross, 1987; Bowman et al., 2000; Etcheverry et al., 2005; Vanderwel et al., 2010). The stage of decay of CWD has also been reported as an important variable whereas well decayed logs and stumps are more frequently used by small mammals than those in early decay stages (Gunderson, 1959; Barnum et al., 1992; Bowman et al., 2000; Brannon, 2000; Kaminski et al., 2007). Benefits provided by decaying logs and stumps for small mammals include abundant food such as fungi and insects, humidity as well as better cover against predators (Maser et al., 1979). As a result, sites with higher volumes of CWD are strongly used at fine (e.g., home range) spatial scales (Kaminski et al., 2007; Thompson et al., 2009; Vanderwel et al., 2010), although such associations are not clearly demonstrated at the stand-scale (i.e., population level associations).

For example, three related studies conducted in Oregon report varying responses through time of three species of shrews (*Sorex* spp.) in stands with different volumes of early decay class CWD (McCay and Komoroski, 2004; Moseley et al., 2008; Davis et al., 2010). Deer mice (*Peromyscus maniculatus*) and southern red-backed voles (*Myodes gapperi*) also responded both positively (Menzel et al., 1999; Pearce and Venier, 2005) or neutrally (Sullivan and Sullivan, 2001; Fuller et al., 2004; Zwolak and Foresman, 2008) to different CWD volumes at the stand-scale. This lack of consistency between results at the stand-scale may depend on the effect of hierarchical habitat selection (i.e., second-order and third-order selection; Johnson, 1980). Specifically, associations between microhabitat attributes such as CWD and small mammals are dependent of the spatial scale because responses may be observed at the individual and at the population level.

Microhabitat associations, such as the use of CWD, are reflected by the spatial distribution of small mammals. Two related studies (Oatway and Morris, 2007; Morris and MacEachern, 2010) observed a strong spatial structure in enclosures at the scale of 50 m with meadow voles. Whereas Bowman et al. (2001) found a similar pattern (from spatial autocorrelation analyses) for southern red-backed voles at the scale of 125 m in open forests, the pattern became weak at distances of more than 533 m. These distances match daily movements of voles and mice inside their home range (Tallmon and Mills, 1994; Ribble et al., 2002; Thompson et al., 2009). The observations made by Bowman et al. (2001) indicate that populations of small mammals may aggregate in high habitat quality patches and form a series of small communicating meta-populations. Krohne and Burgin (1990) also suggested that the abundance of *Peromyscus leucopus* is homogeneous over short distances while segregation over larger distances creates a more heterogeneous spatial structure. Thus, strong positive associations to microhabitat components, such as CWD, at fine-scales may be observed due to resource use by individuals while population level responses may be observable at larger spatial scales (e.g., stand-scale).

The effects of CWD on the abundance of small mammals have received increasing attention over the last decade, especially in the context of new silvicultural practices that have been proposed to stop the dwindling stocks of woody debris in managed boreal forests. Partial cuts are one of these practices proposed as an alternative to clearcuts in boreal forests in order to ensure a long-term recruitment of dead wood and CWD within harvested stands (Bergeron et al., 2002, 2007; Bouchard, 2008). This type of treatment was also proposed to maintain a forest structure more similar to old forests that represent more than 50% of the forest cover in landscapes under natural disturbance regimes (Bergeron et al., 2007). The effects of partial cuts on small mammals have

been well studied (reviews in Vanderwel et al., 2009; Zwolak, 2009) and species show varying responses to different green-tree retention treatments. For example, southern red-backed voles, a species often associated with old and mature coniferous forests, responded both negatively (Fuller et al., 2004; Sullivan et al., 2008) and positively (Steventon et al., 1998; Kaminski et al., 2007) to tree removal. Interestingly, most of these studies observed a strong positive relationship between CWD and the abundance of red-backed voles. Thus, this forest floor resource may have the potential to explain variations in the responses of small mammals to silvicultural operations. Although other factors may explain discrepancies between study results, there is a lack of information on the effects of CWD at multiple scales, overlooking the possibility that response to CWD is scale-dependent.

In this study, our main objective was to assess and compare the effects of CWD on small mammals in managed and unmanaged boreal forests of western Québec. We investigated the effects of CWD at different levels of tree retention by comparing small mammal abundances found in clearcuts, partial cuts, and undisturbed stands (controls) with a spatially and temporally structured trapping system. We first hypothesized that the abundance of voles and shrews depends on the amount and decay of CWD in all treatments. We also hypothesized that associations between boreal small mammals and CWD depends on the spatial scale. In the context of this study, fine-scale associations represent the non-random distribution of individuals inside an area equal to the approximate mean home range size of most small mammals while stand-scale associations represent the non-random distribution of small mammal populations between forest stands. Our first prediction was that (1) captures of small mammals increase with volumes of CWD, especially with those of later decay stages. Indeed, several small mammal species use well decayed CWD more often than CWD of early decay classes. We also predicted that (2) this positive relationship is observable in all treatments since CWD probably compensate the negative impacts of loss of forest cover induced by harvesting. Finally, we predicted that (3) most species will be associated with CWD at the fine-scale rather than at the stand-scale, as a consequence of previously documented strong resource use by small mammals at fine-scales.

2. Material and methods

2.1. Study area

We used a network of partial cuts, consisting of several forest blocks that were managed to study the effects of this silvicultural practice on biodiversity and forest productivity in western Québec, Canada (Fenton et al., 2009). We chose four managed forest blocks from the network (Puisseaux: 78°58'1"W;49°36'15"N, Gaudet: 78°47'33"W;49°52'58"N, Fenelon: 78°33'51"W;49°59'24"N, and Cramolet: 77°30'48"W;49°14'41"N) on the basis of their accessibility and large treated surface (35–90 ha) (Fig. 1). All four managed blocks occurred in the Clay Belt of eastern North America and in the spruce-moss bioclimatic domain (Gauthier et al., 2000). The forest stands were mainly composed of black spruce (*Picea mariana*) and trembling aspen (*Populus tremuloïdes*). Balsam fir (*Abies balsamea*), white birch (*Betula papyrifera*), and jack pine (*Pinus banksiana*) were also sparsely found. The understory vegetation was composed of alders (*Alnus* spp.), Labrador tea (*Rhododendron groenlandicum*), raspberry (*Rubus idaeus*), and blueberry (*Vaccinium myrtilloïdes*). The ground-level vegetation was mostly composed of sphagnum and other mosses. Our study area is paludified, which is the result of gradual accumulation of thick organic (mostly sphagnum) layers on the soil (Fenton et al., 2005). In the Clay Belt region of eastern North America, paludification can dramatically reduce

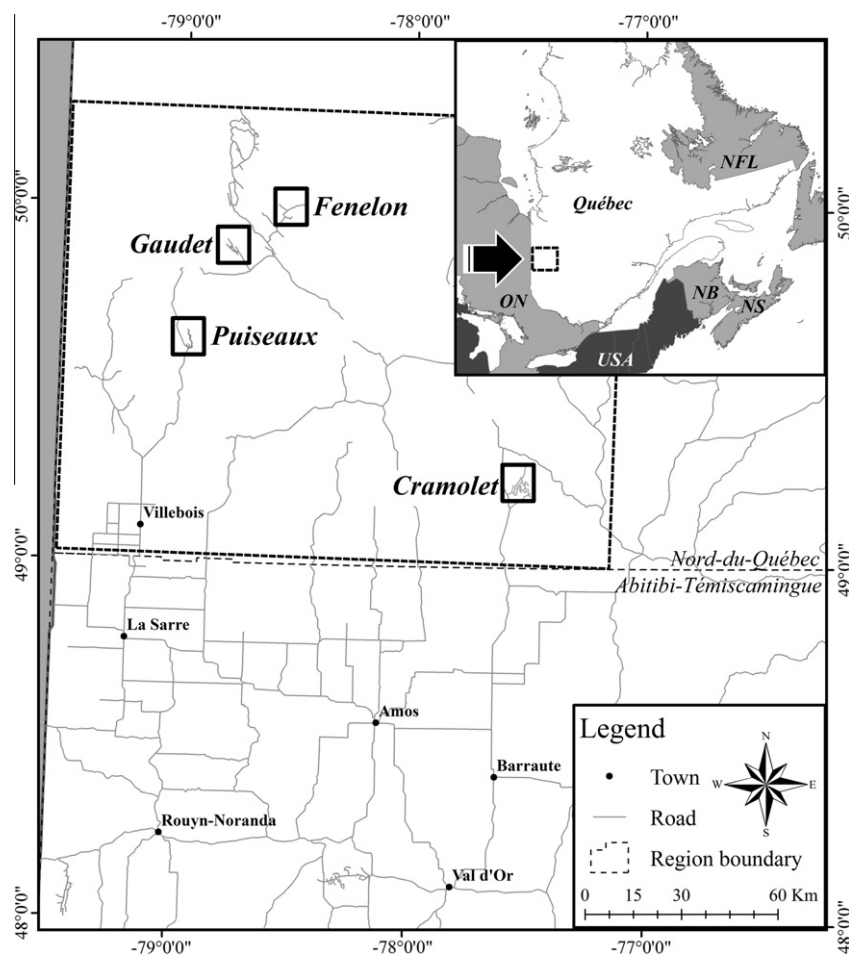


Fig. 1. Location of the study area in the Nord-du-Québec administrative region, Québec, Canada.

tree growth, which often creates open areas with few commercially sized trees. Consequently, blackspruce-feather moss forests are characterized by small live tree basal areas and low herbaceous cover compared to other parts of the boreal forest (Bescond et al., 2011).

Each block consisted of one clearcut (0% green-tree retention), one partial cut (approximately 30% green-tree retention), and one control (no recent anthropogenic disturbance) for a total of 12 sample sites (four replicate blocks \times three treatments). Because treatments are large (>35 ha), they were considered as being several smaller continuous stands in which we positioned our trapping grids. Treatments inside each managed block were separated by small distances (>0.1 km and <2.0 km) in order to reduce the effect of environmental variability. Partial cuts consisted of alternating harvested and non-harvested strips, uniformly leaving 30% of commercially-sized trees (DBH > 9 cm) across the whole stand. Operations in Puiseaux, Gaudet, and Fenelon blocks were done during the winter of 2003–2004, whereas the Cramolet block was cut during the 2007–2008 winter. No scarification or other silvicultural treatments were conducted after harvesting.

2.2. Small mammal trapping design

Stand-scale microhabitat associations with small mammals were assessed using 50 \times 50 m trapping grids (0.25 ha; Fig. 2). We chose this grid size based on the approximate mean home range size reported in previous studies for several small mammal species (Merritt, 1981; Linzey, 1983; Ribble et al., 2002; Whitaker, 2004). Four trapping grids were assigned to each sample site for a

total of 48 grids (four replicate blocks \times three treatments \times four grids). Grids were randomly established in all sample sites with spatial constraints by using Hawth's Analysis Tools (Beyer, 2006) in ArcGIS 9.2 (ESRI, 2006). Based on Bowman et al. (2001) recommendations, we separated all trapping grids by a minimum distance of 250 m to ensure spatial independence. We also considered edge effects by locating all grids at a minimum of 30 m from stand edges and 20 m from roads. Similar distances were also used in other studies (40 m, Loeb, 1999; 30 m, Butts and McComb, 2000; 20 m, Manning and Edge, 2004). Each trapping grid was a replicate for each treatment and was considered as being located in a separate stand. Thus, comparison of data between trapping grids (*i.e.*, stands) were at the stand-scale.

We divided each 0.25 ha trapping grid in four smaller sub-grids and arranged them as presented in Fig. 2 to analyze fine-scale microhabitat associations. Sub-grids were designed to represent four spatially separated microhabitats inside the area of an average small mammal home range that can potentially be visited and selected by individuals. Pitfall traps (10 L plastic buckets) were used to capture shrews, whereas small collapsible galvanized Sherman traps were used for mice and voles. Each sub-grid consisted of one central pitfall trap and one central Sherman trap. To increase our trapping effort for rodents, we located four other Sherman traps 5 m north, south, east and west from the centre of the sub-grid. Thus, every grid was composed of 20 Sherman traps and four pitfall traps.

We sampled small mammals during two consecutive summers. In 2009, surveys were done from July to August. Captures in 2010 were conducted from June to August. Two surveys of three trap-

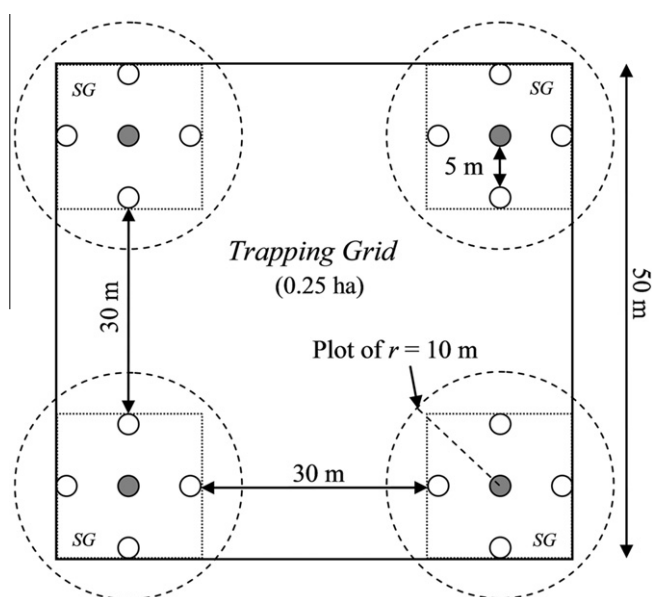


Fig. 2. Representation of one spatially independent grid divided into four sub-grids (SG). Empty circles (○) represent one Sherman trap, filled circles (●) represent one Sherman trap and one pitfall trap, dotted circles represent plots in which microhabitat was characterized. Sub-grids (dotted squares) and grids (large square) are also shown.

nights were conducted at each site during 2009 and these sites were also surveyed three times in 2010, for a total of five surveys. We sampled mammals one block at a time to avoid confounding effects of treatments and weather variables. During the first day of each survey, 240 Sherman traps and 48 pitfall traps were deployed and activated simultaneously. Traps remained open during the three following nights and were checked every day (between 06:00 and 17:00). Pitfall traps were filled with 3–4 inches of water to drown shrews. We baited all Sherman traps with peanut butter for food, a piece of apple for water, as well as a small ball of cotton batting for nest-building and isolation to ensure better survival for rodents (Drickamer and Paine, 1992). All traps (including pitfall traps) were considered as providing an effort of 1 trap night, but those accidentally sprung were noted as providing an effort of 0.5 trap night (Nelson and Clark, 1973).

We noted the site of capture of all dead shrews and rodents, and placed them in a freezer for further lab identification according to cranial characteristics (Lupien, 2001, 2002). Live shrews were immediately released on site and excluded from our analyses because identification of live individuals was often impossible. Live rodents were located (trap site), identified to species, weighed, sexed, and checked for pregnancy. Live mice and voles were identified according to a modified version of a key by Lupien (2002). Specifically, we added a new criterion based on white hairs found over the claws of the hind feet of red-backed voles. This criterion helped to distinguish dirty and wet dark-colored red-backed voles from meadow voles that rarely have these white hairs. Our key was tested on dead specimens that were first identified with external morphological characteristics (e.g., fur) and subsequently identified with cranial and dental characteristics. Identification of 97.5% ($n = 352$) of red-backed voles and 93.5% ($n = 124$) of meadow voles matched when the two methods were compared (Fauteux et al., unpublished results).

All rodents that were captured were ear-tagged with a unique-number 1005-1 Monel tag (National Band & Tag Company) before release. Recaptured individuals were counted only once during each of the five trapping sessions. In other words, individuals were not counted twice in a single session. Thus, the number of individ-

uals was used for analyzing small mammal abundance. Lethal captures of rodents in both pitfall and Sherman traps were pooled with live captures. Finally, during the fourth day of all sessions, traps were removed and relocated on the next managed block. All manipulations adhered to the Canadian Council on Animal Care Guidelines and were approved by the institutional animal care review committee at the Université du Québec en Abitibi-Témiscamingue (UQAT, permit #2009-04-30).

2.3. Microhabitat sampling

Microhabitats were characterized at the level of sub-grids. Circular plots of 10 m radius were centered on all sub-grids. In each 10 m plot, we measured the total basal area occupied by commercially-sized (DBH ≥ 9 cm diameter) live trees using a diameter tape. We visually interpreted the relative (%) shrub cover by employing three 1 m² plots (one in the center, one 5 m to the east and one 5 m to the west) in all 10 m plots. The average of the three percentages was calculated for each sub-grid. The basal area occupied by all stumps was measured on all 10 m plots. Downed logs found in the 10 m plots were inventoried. Two diameters, one at the small end and one at the large end, were measured on all logs, as well as the length between the two ends. We only considered logs with a large end ≥ 9 cm diameter and with a length ≥ 1 m. If a log was crossing the plot boundary and the large end was found outside the plot, we sampled the part of the log inside the plot only if the diameter of the log at the boundary was ≥ 9 cm. Otherwise, the log was ignored. Logs or snags with an inclination of less than 75° from vertical were considered inaccessible for small mammals. Logs that were completely (100%) covered by sphagnum were also ignored. Volumes of logs were calculated using the conic-paraboloid formula (Fraver et al., 2007) which reduces bias caused by irregular forms of well decayed logs.

All stumps and logs were associated with one of four decay classes from least (1) to most decayed (4). Classes were built according to those of previous studies (Maser et al., 1979; Fraver et al., 2002), but with some adaptations for regional differences (e.g., paludification). Logs of decay class 1 were hard, round, often with complete branches, mostly covered with bark (>75%), and only the tip of a knife could penetrate the wood. Class 2 logs were mostly hard (>75%), round with variable amounts of bark, most often without branches and a knife could penetrate <0.5 cm into the wood. Logs of class 3 were soft (>25%), possibly deformed (i.e., oval shaped), with variable amounts of bark easily removable if present, and a knife could penetrate <5 cm into the wood. Finally, class 4 logs were completely soft, often oval shaped, bark was sometimes present but easily removed, and a knife could completely penetrate the wood. To classify stumps into a decay category, we used the same criteria as for logs except for the form and branches which are absent in stumps.

2.4. Statistical analyses

2.4.1. Microhabitat evaluation

All statistical analyses were conducted with the R software (R Development Core Team, 2010). Microhabitat characteristics of clearcuts, partial cuts, and controls were compared at the sub-grid level (fine-scale). A Pearson correlation analysis was first used to detect any possible collinearity between numeric explanatory variables. Whenever two variables were collinear ($r \sim 0.7$), we kept the variable that was most easy to interpret and most biologically relevant for our analyses.

We reduced the number of variables in our analyses by summing the volumes of logs of early decay classes (classes 1 and 2) together as well as the volume of logs of late decay classes (classes 3 and 4). With these operations, we ended up with two categories

Table 1

Candidate generalized linear mixed models with Poisson distribution used to model small mammal abundance.

Model	Parameters	K_{fine}	K_{stand}
A	EDLV + LDLV	8	7
B	EDLV + LDLV + STUMPS	9	8
C	STUMPS	7	6
D	EDLV + TREES + EDLV:TREES	9	8
E	LDLV + TREES + LDLV:TREES	9	8
F	TREES + SHRUBS	8	7
Global 1	EDLV + LDLV + STUMPS + TREES + SHRUBS + EDLV:TREES	12	11
Global 2	EDLV + LDLV + STUMPS + TREES + SHRUBS + LDLV:TREES	12	11

Models are built with the following measured variables: early decay class log volume (EDLV), late decay class log volume (LDLV), late decay class stumps basal area (STUMPS), live tree basal area (TREES) and relative cover occupied by shrubs (SHRUBS). Note that K denotes the number of parameters in the model: models at the fine-scale had three random effects (block, grid within block, and sub-grid within grid within block), whereas those at the stand-scale had one parameter less (no random effect for sub-grid).

of log volumes: early decay class and late decay class. The same process was applied on stump basal areas so that we ended up with two decay categories of stumps. The basal area occupied by early decay class stumps was correlated (Pearson $r = -0.66$) with live tree basal area. Although both variables may represent the effects of harvesting, we eliminated the variable for the basal area of early decay class stumps because the effect of residual live tree basal area is easier to interpret.

Linear mixed-effects models with a Gaussian distribution were used to model the effects of treatment on the microhabitat response variables at the fine-scale. To account for the spatial dependence of units nested in larger units, we included random effects that consisted of block, treatment nested in block, grid nested in treatment nested in block, and sub-grid nested in grid nested in treatment nested in block. All response variables, except the relative cover of shrubs, were log-transformed to normalize residuals and to increase homoscedasticity. Parameters were estimated by maximum likelihood with the nlme package for R (Pinheiro et al., 2011). We used Tukey honestly significant difference (HSD) multiple comparisons to find differences among treatments implemented with the multcomp package (Hothorn et al., 2008). Similarly, we determined whether volumes of logs were different between treatments or not. Similar log volumes among treatments would indicate that it is possible to assess the effects of logs on a certain live-tree basal area gradient in subsequent analyses (described in Sections 2.4.2 and 2.4.3). In contrast, a difference in log volumes across treatments would indicate that log volume and treatment are confounded thereby forcing the interpretation of log volumes for each treatment separately.

2.4.2. Fine-scale microhabitat associations

Small mammal abundances were analyzed using generalized linear mixed-effects models (GLMM) with a Poisson distribution (Zuur et al., 2009). For the analyses of habitat use at the fine-scale, we compared the abundances of small mammals between sub-grids (192 sampling points). Using an information-theoretic approach (Burnham and Anderson, 2002; Mazerolle, 2006), we built eight candidate models to determine the effects of vegetation and CWD (Table 1). An offset variable was included in all models to account for the capture effort at the sub-grid level (6 trap-nights per sub-grid). In this context, an offset results in the estimation of capture rates instead of raw counts (McCullagh and Nelder, 1989). Preliminary analyses indicated that for each decay class, volumes of logs did not differ among all three treatments due to high variability. Moreover, all volumes of logs were well distributed in all three treatments. Four of the eight candidate models included the interaction between treatment and early or late decay class log volume to verify if the effect of log volume differed across treatments. We included a random effect for block, grid nested in block, and sub-grid nested in grid nested in block. We included year and Julian day in all models as fixed effects to reduce the var-

iability due to time. One sub-grid was eliminated from our data due to unusual extreme values, which means that 191 sampling points (instead of 192) were analyzed across the five sampling periods. We log-transformed the live tree basal area parameter to obtain a linear relationship with the log of abundance of red-backed voles and masked shrews.

The package lme4 was used to estimate the parameters of all models with the Laplace approximation (Bates and Maechler, 2010), whereas the package AICcmodavg was used for model selection and multimodel inference (Mazerolle, 2010). Models were ranked based on the second-order Akaike's information criterion (AICc). We then calculated each model delta AICc (ΔAICc) as well as Akaike weights (w_i) to verify the strength of evidence in favor of each model. If one model had an Akaike weight of more than 90%, it was considered as the most parsimonious model of all tested models. Otherwise, we calculated model-averaged estimates and unconditional 95% confidence intervals with multimodel inference (Burnham and Anderson, 2002; Mazerolle, 2006).

Our analyses on counts do not estimate the probability of detection explicitly (e.g., Mazerolle et al., 2007; Urban and Swihart, 2011). Although N-mixture models can deal with counts and imperfect detection (Royle, 2004), our design was nested, potentially invalidating the independence assumption for fine-scale analyses (Royle, 2004; Mazerolle et al., 2007). To overcome this problem, we decided to use random effects to model the variability in the data potentially due to imperfect detection.

2.4.3. Stand-scale microhabitat associations

Similarly to the analyses conducted at the fine-scale, we used GLMMs with a Poisson distribution to study the effects of CWD on the abundance of small mammals at the stand-scale (i.e., between trapping grids). We summed the number of captures per grid while habitat characteristics were averaged. The offset variable was calculated at the grid level (24 trap-nights per grid). A total of 48 trapping grids were used in the stand-scale analyses, compared to 191 in the fine-scale analyses. Again, we considered eight candidate models with the same fixed effects structure as for the fine-scale analysis above. Models at the stand-scale only differed in their random effects, which consisted of block, and grid nested within block (no random effect of sub-grid at the stand-scale). Following the estimation of parameters, we conducted model selection with AICc to select the most parsimonious model from our eight candidate models.

3. Results

3.1. Microhabitat sampling

Clearcuts, partial cuts, and controls mainly differed according to the live tree basal area (Table 2). Mean residual live tree basal areas for clearcuts, partial cuts, and controls were 1, 8, and 21 m² ha⁻¹,

respectively. The treatments did not differ statistically in terms of surface occupied by shrubs and stumps as well as in terms of volumes of both log decay classes.

3.2. Small mammals trapping survey

We captured a total of 2418 small mammals during the trapping campaigns of 2009 and 2010. In 2009, we captured 339 small rodents (mice, voles, and lemmings) and 605 shrews with a total effort of 5764 Sherman trap-nights and 1148 pitfall trap-nights. During our second campaign (2010), we captured 1068 small rodents and 406 shrews with a total effort of 8642 Sherman trap-nights and 1726 pitfall trap-nights. Five sampled species represented 97% of our total captures: masked shrew (40%; *Sorex cinereus*), southern red-backed vole (33%), meadow vole (14%), deer mouse (6%), and southern bog lemming (4%; *Synaptomys cooperi*). Other species that were captured sporadically included rock vole (*Microtus chrotorrhinus*), northern boreal lemming (*Synaptomys borealis*), heather vole (*Phenacomys intermedius*), woodland jumping mouse (*Napaeozapus hudsonicus*), meadow jumping mouse (*Zapus hudsonicus*), pygmy shrew (*Sorex hoyi*), arctic shrew (*Sorex arcticus*), smoky shrew (*Sorex fumeus*), water shrew (*Sorex palustris*), and northern short-tailed shrew (*Blarina brevicauda*).

We captured fewer rodents during the summer of 2009 than in 2010 ($n_{2009} = 4.64$ per 100 trap-nights; $n_{2010} = 10.3$ per 100 trap-nights), probably as a consequence of regular population fluctuations found near our study area (Cheveau et al., 2004). In fact, we captured approximately 2.5 times more red-backed voles in 2010 ($n_{2010} = 6.25$ per 100 trap-nights) compared to 2009 ($n_{2009} = 2.46$ per 100 trap-nights). We also captured 1.5–3.0 times more of the other rodent species. In contrast, masked shrews were captured twice more often in 2009 compared to 2010 ($n_{2009} = 8.54$ per 100 trap-nights; $n_{2010} = 3.87$ per 100 trap-nights).

3.3. Fine-scale microhabitat association

For all species, no single model had all the support (Table 3). Thus, we based our inference on the entire model set, by computing model averaged estimates and unconditional standard errors for each variable appearing in the top models (Table 4).

Red-backed voles ($\beta_{\log.TREES} = 0.4624$, CI = [0.3360, 0.5888]) and masked shrews ($\beta_{\log.TREES} = 0.1039$, CI = [0.0141, 0.1937]) were captured more often in sub-grids with a high live tree basal area. In contrast, meadow voles were more abundant in open sub-grids ($\beta_{TREES} = -0.0462$, CI = [-0.0636, -0.0289]). Masked shrew abundance was positively associated with shrubs in all treatments ($\beta_{SHRUBS} = 0.7723$, CI = [0.3460, 1.1985]). Masked shrew abundance was positively associated with sub-grids composed of a high basal area of late decay class stumps ($\beta_{STUMPS} = 0.0197$, CI = [0.0025, 0.0370]). Red-backed vole abundance was positively associated with early decay class logs in all treatments ($\beta_{EDLV} = 0.0018$,

CI = [0.0005, 0.0032]) as well as late decay class logs ($\beta_{LDLV} = 0.0020$, CI = [0.0007, 0.0034]). Model averaged predictions indicate that the abundance of red-backed voles found in sub-grids (0.03 ha) of partial cuts with 11.4 m³ or more of well decayed logs was equal to the abundance found in controls with fewer logs (Fig. 3A). Deer mice abundance was positively associated with late decay class logs in all treatments ($\beta_{LDLV} = 0.0054$, CI = [0.0014, 0.0094]; Fig. 3B). Southern-bog lemmings were more abundant in sub-grids with high volumes of early decay class logs when there was a high live tree basal area ($\beta_{EDLV:TREES} = 0.0002$, CI = [<0.0001 , 0.0005]). As shown in Fig. 3C, southern bog lemmings abundance was positively associated with sub-grids composed of high volumes of well decayed logs and a small live tree basal area ($\beta_{LDLV:TREES} = -0.0006$, CI = [-0.0010, -0.0004]).

3.4. Stand-scale microhabitat association

Small mammals expressed different patterns of microhabitat associations at the stand-scale compared to the fine-scale but some similarities persisted (Table 4, Fig. 4). Red-backed voles ($\beta_{\log.TREES} = 0.4950$, CI = [0.3319, 0.6581]) were more abundant in grids with a high live tree basal area while meadow vole abundance was negatively associated with these grids ($\beta_{TREES} = -0.0388$, CI = [-0.0583, -0.0193]). Red-backed vole abundance increased with the volume of late decay class stumps ($\beta_{STUMPS} = 0.0505$, CI = [0.0030, 0.0979]). Meadow vole abundance was positively associated with grids composed of high volumes of early decay class logs ($\beta_{EDLV} = 0.0048$, CI = [0.0001, 0.0094]) and their abundance increased with the volume of well decayed logs, especially in grids with a high live tree basal area ($\beta_{LDLV:TREES} = 0.0005$, CI = [<0.0001 , 0.0011]; Fig. 4A). Southern bog lemming ($\beta_{LDLV:TREES} = -0.0007$, CI = [-0.0014, -0.0001]) and masked shrew ($\beta_{LDLV:TREES} = -0.0029$, CI = [-0.0049, -0.0010]; Fig. 4B) abundances were positively associated with well decayed logs in grids composed of a small live tree basal area. Deer mice were highly abundant in grids with high volumes of well decayed logs ($\beta_{EDLV} = 0.0098$, CI = [0.0027, 0.0170]).

4. Discussion

4.1. Boreal small mammal associations with CWD

In this study, our first hypothesis was that the abundance of small mammals depended on the amount and decay stage of CWD. Our first prediction (1), which stated a positive response of boreal small mammals to volumes of well decayed CWD in western Québec boreal forests, was supported by showing increasing abundance for all five species that were sampled (i.e., red-backed voles, meadow voles, southern bog lemmings, deer mice, and masked shrews) considering both spatial scales. Our study extends the findings previously reported for a more limited number of spe-

Table 2
Multiple comparison tests (Tukey HSD) on microhabitat characteristics measured in the three treatments.

Response variable	Clearcut		Partial cut		Control	
	Mean	SE	Mean	SE	Mean	SE
EDLV (m ³ ha ⁻¹)	103.62 ^a	10.94	110.60 ^a	9.92	107.33 ^a	13.97
LDLV (m ³ ha ⁻¹)	80.23 ^a	11.19	108.57 ^a	16.18	70.46 ^a	11.74
STUMPS (m ² ha ⁻¹)	8.29 ^a	0.90	8.37 ^a	1.04	5.49 ^a	0.53
TREES (m ² ha ⁻¹)	1.36 ^a	0.44	7.54 ^b	1.41	20.72 ^c	1.83
SHRUBS (relative cover)	0.37 ^a	0.04	0.36 ^a	0.04	0.37 ^a	0.03

All linear mixed-effects models included random effects that consisted of block, treatment nested in block, grid nested in treatment nested in block, and sub-grid nested in grid nested in treatment nested in block. Means with different letters are statistically different compared to means of other treatments. Acronyms are as follows: early decay class log volume (EDLV), late decay class log volume (LDLV), late decay class stumps basal area (STUMPS), live tree basal area (TREES) and relative cover occupied by shrubs (SHRUBS). All parameters, except SHRUBS, were log-transformed to linearize the relationship.

Table 3
Four top-ranked generalized linear mixed models with Poisson distribution of fine and stand-scale microhabitat associations for each of the five small mammal species. Model names refer to those described in Table 1.

Species	Fine-scale					Stand-scale				
	Model	K_i	AIC _c _i	Δ_i	w_i	Model	K_i	AIC _c _i	Δ_i	w_i
Red-backed voles	Global 1	12	1129.98	0.00	0.44	Global 1	11	453.14	0.00	0.64
	Global 2	12	1130.17	0.19	0.40	D	8	455.76	2.61	0.17
	E	9	1133.31	3.33	0.08	Global 2	11	456.55	3.40	0.12
	D	9	1133.47	3.49	0.08	E	8	457.85	4.71	0.06
Meadow voles	E	9	914.42	0.00	0.39	D	8	407.62	0.00	0.69
	F	8	914.68	0.27	0.34	E	8	410.53	2.91	0.16
	D	9	916.70	2.28	0.12	Global 1	11	412.47	4.85	0.06
	Global 2	12	917.32	2.91	0.09	Global 2	11	412.94	5.32	0.05
Deer mice	E	9	471.00	0.00	0.29	E	8	275.53	0.00	0.41
	Global 2	12	471.42	0.41	0.24	A	7	276.75	1.23	0.22
	B	9	471.53	0.53	0.22	Global 2	11	277.79	2.26	0.13
	A	8	471.93	0.93	0.18	B	8	277.85	2.33	0.13
Southern bog lemmings	E	9	390.84	0.00	0.54	E	8	208.94	0.00	0.40
	Global 2	12	393.39	2.56	0.15	C	6	209.47	0.53	0.31
	C	7	394.03	3.19	0.11	A	7	212.02	3.08	0.09
	D	9	394.98	4.15	0.07	F	7	212.67	3.74	0.06
Masked shrews	F	8	1315.14	0.00	0.43	E	8	513.17	0.00	0.57
	Global 1	12	1315.42	0.28	0.38	C	6	514.74	1.57	0.26
	Global 2	12	1316.88	1.74	0.18	Global 2	11	517.31	4.14	0.07
	C	7	1323.42	8.28	0.01	B	8	518.49	5.32	0.04

Table 4
Model averaged estimates (β) of explanatory variables at the fine-scale with their respective unconditional standard errors (\pm SE) for each sampled species.

Species	Scale	Microhabitat variable						
		EDLV β (\pm SE)	LDLV β (\pm SE)	STUMPS β (\pm SE)	TREES β (\pm SE)	SHRUBS β (\pm SE)	EDLV:TREES β (\pm SE)	LDLV:TREES β (\pm SE)
Red-backed vole*	Fine	0.0018 ± 0.0007	0.0017 ± 0.0007	0.0102 ± 0.0107	0.4624 ± 0.0645	0.3411 ± 0.2740	0.0002 ± 0.0005	0.0000 ± 0.0006
	Stand	0.0022 ± 0.0016	-0.0001 ± 0.0013	0.0579 ± 0.0220	0.4950 ± 0.0832	0.6170 ± 0.6026	0.0023 ± 0.0012	-0.0015 ± 0.0180
Meadow vole	Fine	0.0002 ± 0.0011	-0.0026 ± 0.0014	0.0264 ± 0.0169	-0.0462 ± 0.0088	-0.2495 ± 0.3703	0.0000 ± 0.0004	0.0001 ± 0.0002
	Stand	0.0048 ± 0.0024	-0.0022 ± 0.0022	0.0035 ± 0.0316	-0.0388 ± 0.0100	0.1989 ± 0.7846	0.0004 ± 0.0001	0.0005 ± 0.0003
Southern bog lemming	Fine	-0.0024 ± 0.0018	0.0012 ± 0.0018	0.0294 ± 0.0225	0.0209 ± 0.0112	0.4961 ± 0.6222	0.0002 ± 0.0001	-0.0006 ± 0.0002
	Stand	0.0026 ± 0.0030	0.0003 ± 0.0026	0.0488 ± 0.0322	0.0181 ± 0.0128	0.4737 ± 0.9890	0.0004 ± 0.0002	-0.0007 ± 0.0003
Deer mouse	Fine	0.0022 ± 0.0019	0.0053 ± 0.0020	0.0518 ± 0.0290	-0.0178 ± 0.0183	-0.9177 ± 0.8125	-0.0001 ± 0.0002	0.0005 ± 0.0003
	Stand	0.0008 ± 0.0530	0.0099 ± 0.0036	0.0751 ± 0.0622	-0.0229 ± 0.0217	-2.7741 ± 1.6859	-0.0002 ± 0.0003	0.0006 ± 0.0005
Masked shrew*	Fine	-0.0003 ± 0.0006	0.0000 ± 0.0006	0.0202 ± 0.0087	0.1039 ± 0.0458	0.7730 ± 0.2163	0.0006 ± 0.0005	-0.0001 ± 0.0005
	Stand	0.0000 ± 0.0012	-0.0004 ± 0.0011	0.0269 ± 0.0142	0.0383 ± 0.0541	0.3769 ± 0.3805	-0.0002 ± 0.0010	-0.0029 ± 0.0010

Estimates in bold indicate that the 95% CI interval did not include 0, indicating strong effects. Species followed by a * indicate that live tree basal area was log-transformed to linearize the relationship.

cies in the boreal forest of eastern North America (Pearce and Venier, 2005; Vanderwel et al., 2010). Although our study was limited to summer periods of 2009 and 2010, associations between red-backed voles and CWD may have been even stronger during spring, as observed by Vanderwel et al. (2010). The authors showed stronger associations between red-backed voles and well decayed CWD in boreal forests of Ontario during spring than summer. The first surveys of our study (mid-June to mid-July) probably allowed us to detect strong resource associations. Small mammals that successfully overwintered were probably distributed in high quality sites (i.e., good cover against predators, abundant food) where high volumes of CWD were found.

We found that red-backed vole and meadow vole abundances were positively associated with logs of early decay classes. Hard logs with branches may act as effective barriers against predators and Andruskiw et al. (2008) suggested that red-backed voles may reduce their visibility to avian predators by moving along CWD. Recently fallen logs may also be used by saproxylic insects and their associated predators (Vanderwel et al., 2006; Jacobs et al., 2007), which may attract small insectivores (i.e., shrews) and certain occasional insect-eating rodents (e.g., red-backed voles).

Although early decay class logs can provide good cover against predators, well decayed CWD may offer more fungi for food, humidity, and nesting sites for small mammals. Our results indicate that red-backed voles and deer mice were found in high abundance in sub-grids with high volumes of well decayed CWD. By effectively retaining humidity, this type of CWD may provide a good substrate for fungi growth (Amaranthus et al., 1994; Clarkson and Mills, 1994) and favor fungivores, such as red-backed voles and deer mice in coniferous forests (Claridge et al., 1999; Orrock and Pagels, 2002). Hypogeous mycorrhizal fungi are the main fungi eaten by red-backed voles and deer mice in some regions (Ovaska and Herman, 1986; Gagne et al., 1999; Orrock and Pagels, 2002). Other dead-wood inhabiting fungi found in our study area, such as *Fomitopsis* species, are also consumed by small rodents (Rhoades, 1986). Moreover, Lepidoptera insects, which are important food for shrews (Bellocq et al., 1994), reproduce on *Fomitopsis pinicola* in other boreal regions (Jonsell et al., 1999).

Humidity itself is a factor that may affect the use of well decayed logs by small mammals. In fact, most of our sampled species have high water needs which may explain their search for humid microhabitats (Getz, 1961a,b, 1968). Microhabitats composed of high volumes of woody debris, especially those that

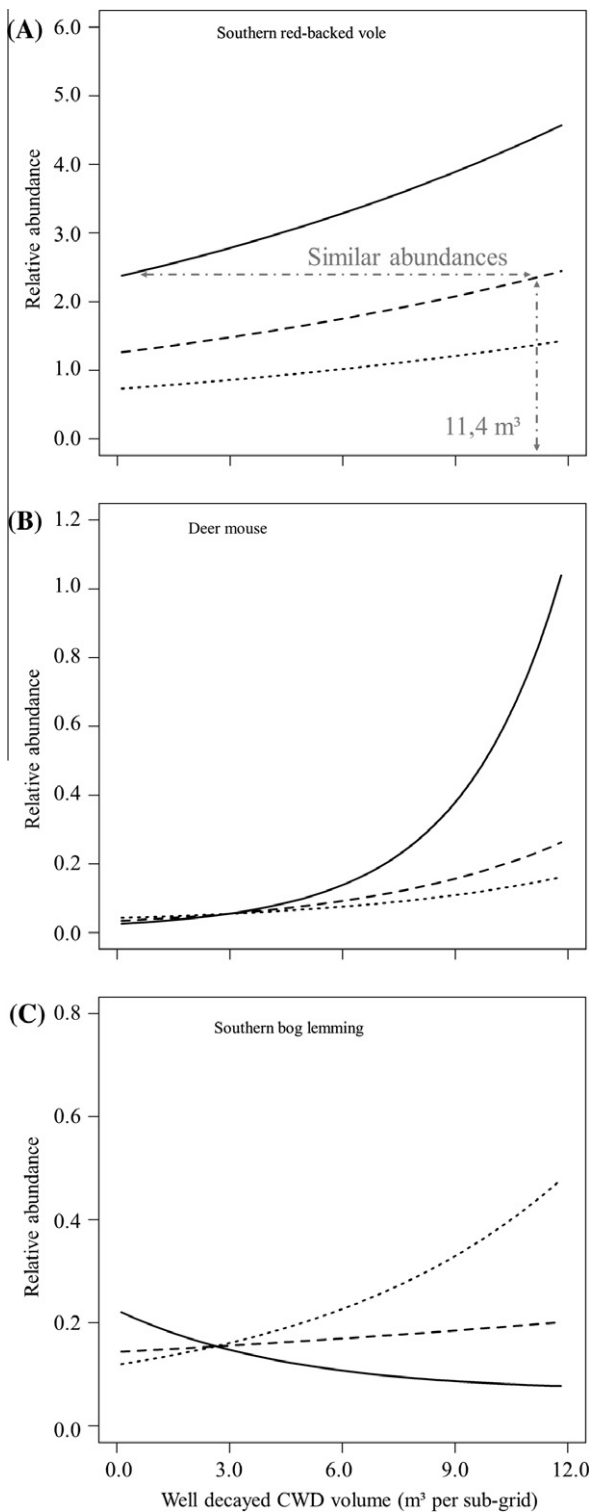


Fig. 3. Model-based predictions of relative abundances at the sub-grid-level (100 trap-nights; fine-scale analyses) of red-backed voles (A), deer mice (B), and southern bog lemmings (C) on a late decay class log volume gradient in clearcuts, partial cuts and controls. Patches of partial cuts composed of high volumes of well decayed logs presented similar abundances of red-backed voles compared to patches of controls (uncut) with few logs. For southern bog lemmings (B), the effects of well decayed log volumes differ between treatments.

are well decayed, have the potential to offer moister conditions compared to open grounds (Brannon, 2000; Fraver et al., 2002; Rittenhouse et al., 2008). Chambers are components of these microhabitats and they are often found in large and well decayed

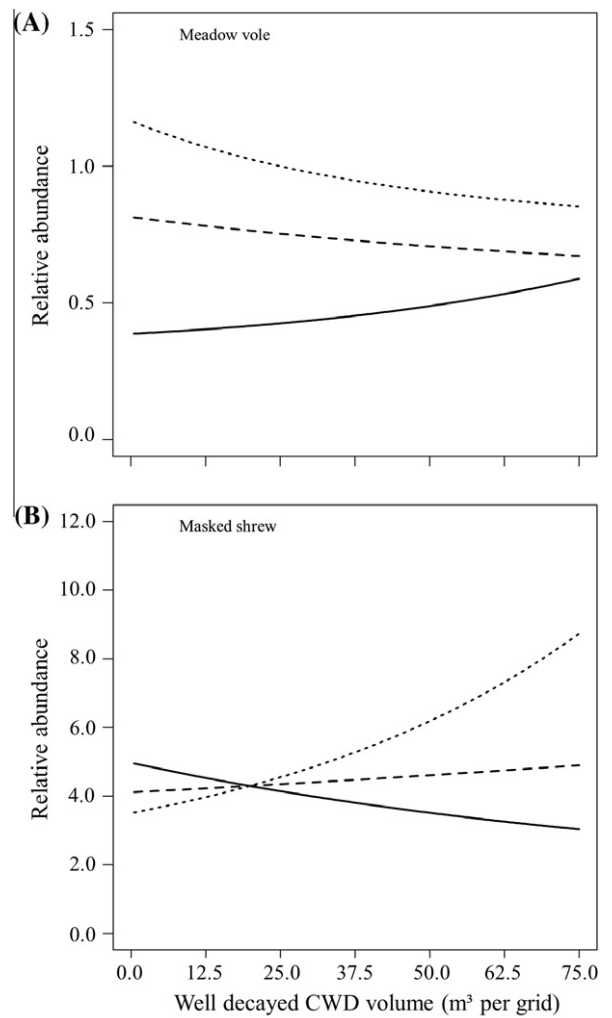


Fig. 4. Model-based predictions of relative abundances at the grid-level (100 trap-nights; stand-scale analyses) of meadow voles (A) and masked shrews (B) on a late decay class log volume gradient in clearcuts, partial cuts and controls. Effects of well decayed CWD on meadow vole and masked shrew abundances differ between treatments.

logs (Maser et al., 1979; Barry and Francq, 1980). Individuals using these chambers often benefit from moist environments and are further protected against predators by reducing their visibility.

Stumps in late decay classes were also important for red-backed voles and masked shrews, which corroborates the observations of Brannon (2000). According to previous studies (Gunderson, 1959; Yahner, 1983), red-backed voles can use these structures as nest sites and refuges in a variety of habitats. Shrews and other insectivores may also benefit from stumps as a source of saproxylic insects (Lassauce et al., 2011).

4.2. CWD as a mitigating factor for tree removal

Our second prediction (2) stated that strong positive responses of small mammals to high volumes of CWD in all treatments, considering both spatial scales, may indicate that this resource may act as a mitigating factor for tree removal. This prediction was partly supported since meadow vole abundance was positively associated with CWD in controls, but not in harvested stands, as indicated by the interaction term between well decayed CWD volume and live tree basal area. Meadow voles were positively associated with high volumes of well decayed logs in controls alongside

with early decay class logs. These sites may have been important to meadow voles for cover and food normally offered by herbaceous cover, which was low in our study area and especially in controls due to heavy paludification in the Clay Belt region of eastern North America (Reich, 1981; Bescond et al., 2011).

In contrast with meadow voles, red-backed vole and deer mouse abundances were positively associated with well decayed CWD in all treatments and masked shrews as well as southern bog lemmings were associated with well decayed logs in more open sites. Soils of clearcuts are exposed to drier conditions because of extended exposure to sunlight. Small mammals that are found in clearcuts are exposed to high predation risk due to exposure to avian predators, but CWD might reduce this risk by providing visual protection against avian predators. By effectively retaining humidity, well decayed CWD may have provided a good substrate for fungi and good habitat for insects, which are food for small mammals (Amaranthus et al., 1994; Clarkson and Mills, 1994; Claridge et al., 1999). Moist environments are also very important for many species of small mammals (Getz, 1961a,b).

Small rodents are subject to spatial segregation due to direct resource use and density-dependent factors, such as interspecific competition. Red-backed voles have the potential to displace meadow voles and deer mice from forest habitats to more open ones, probably because of their competitive behavior (Morris and Grant, 1972; Crowell and Pimm, 1976; Merritt, 1981). In contrast, other studies reported that meadow voles and deer mice may also affect red-backed voles because of their competitive behaviors (Iverson and Turner, 1972; Lemaitre et al., 2010). Such spatial dynamics over short distances were probably affecting the spatial distribution of small rodents in our sites. Although we cannot infer on which mechanism best explained the distribution of small mammals, our results suggest that red-backed vole, meadow vole, and deer mouse abundances were all positively associated with high volumes of CWD in controls. During our surveys, we often observed more than one species that were captured in a single sub-grid. Thus, microhabitat preferences of these three species may have been more important to explain spatial distribution than competitive interactions.

We did not observe a positive response of deer mice abundance to tree removal, a pattern reported in many studies (Carey and Johnson, 1995; Steventon et al., 1998; Moses and Boutin, 2001; Etcheverry et al., 2005). This is contrary to results obtained by Sullivan et al. (2008) and Le Blanc et al. (2010) for this species regarding variable green-tree retention in partial cuts. The highest abundance of deer mice observed in our study was in partial cuts, which may indicate that fine-scale disturbances are the most beneficial for this species. We found that southern bog lemmings inhabit a broad spectrum of habitats and were not strongly affected by tree removal, which concurs with the observations of Kirkland (1977) and Linzey (1983). Nevertheless, CWD legacies, and probably other old growth forest features contributing to the complexity of the forest floor, may be beneficial for this species.

Red-backed voles are often less abundant in harvested stands (Fisher and Wilkinson, 2005), but predictions from our models indicate that patches of partial cuts with high volumes of well decayed CWD (11.4 m³ per 0.03 ha) have the potential to maintain numbers similar to those in unharvested controls (Fig. 3A). This indicates that the abundance of CWD in late decay classes may, in part, mitigate the impacts of tree removal. Thus, similar abundances of red-backed voles in harvested and uncut stands may occur due to the presence of abundant forest floor resources such as CWD, as reported in other studies (Potvin et al., 1999; Etcheverry et al., 2005; Klenner and Sullivan, 2009). In addition to volumes, the stage of decay is also important for assessing the responses of boreal small mammals to CWD. An important issue is that well decayed CWD are hardly found in stands that have been cut several times and in which no significant input of dead wood has been al-

lowed for several silvicultural interventions. Thus, high volumes of CWD may have the potential of mitigating the impacts of tree removal but only if late decay classes are found *in situ* prior to harvesting. We also found that the southern red-backed vole abundance was positively associated with high volumes of CWD in early decay, which suggests that felled trees left on site after harvest might have an immediate positive effect on this species. Leaving recently felled trees on site should also be considered to ensure new input of decaying wood.

We sampled small mammals in one forest block 3 years post-harvest and in three forest blocks 7 years post-harvest. Relationships between southern red-backed vole, meadow vole and deer mice abundance with CWD may not change during subsequent years because we observed positive associations to CWD in clearcuts, as well as in mature forests. However, southern bog lemmings and masked shrews may stop responding to CWD volumes in later stages of forest succession because they responded to CWD mainly in open areas. The closure of the canopy as the forest gets older may reduce the importance of CWD for protection against predators and consequently, may reduce its importance for southern bog lemmings and masked shrews.

4.3. The effects of scale on microhabitat associations

Our second hypothesis was that small mammal microhabitat associations may depend on the spatial scale. In accordance with our third prediction (3), red-backed vole, southern bog lemming, and deer mouse abundances were positively associated with microhabitat features at the fine-scale. However, we also found positive associations between well decayed CWD and abundances of meadow vole, deer mouse, southern bog lemming, and masked shrew at the stand-scale (*i.e.*, between large trapping grids). Our results substantiate the existence of spatial structures at different scales for small mammals (Orrock et al., 2000; Bowman et al., 2001; Manning and Edge, 2004). Furthermore, the scales that we used allowed us to assess the effects of CWD on spatial structures of small mammals inside the area of a regular home range for boreal small mammals and inside forest stands; which respectively relate to the second order and third order habitat selection described in Johnson (1980). Red-backed voles, deer mice, southern bog lemmings and masked shrews were all associated with microhabitat features mainly at the fine-scale (*i.e.*, inside their home range). High quality patches were probably hosting more individuals than low quality microhabitats by having high carrying capacities, which may have reduced the effects of competition due to abundant resources. As a result, it created a strong spatial structure inside our trapping grids (0.25 ha). Similarly, Thompson et al. (2009) reported that western red-backed vole core areas (*i.e.*, centers of activity in home ranges) included more CWD than their surroundings.

Red-backed vole abundance was positively associated with high volumes of CWD exclusively at the fine-scale. Interestingly, other studies also reported that red-backed voles, deer mice, and white-footed mice abundances did not change with CWD volumes between stands composed of similar residual live tree densities (Moses and Boutin, 2001; Etcheverry et al., 2005; Le Blanc et al., 2010). Therefore, it is possible that red-backed voles were affected by a dynamic process caused by density-dependent factors such as extinction and re-colonization at the stand-scale (Bowman et al., 2001). Predation may have limited southern red-backed vole population growth in control stands with high volumes of CWD because American martens (*Martes americana*) have also been positively associated with CWD in the boreal forest (Godbout and Ouellet, 2010). Strong effects of predation and other density-dependent factors might have affected southern red-backed vole abundance in trapping grids, which could have prevented us from

finding microhabitat associations at the stand-scale. We also found that the abundance of masked shrews, the most abundant species in our study area, was positively associated with well decayed stumps, shrubs, and trees exclusively at the fine-scale. This species has often been documented as a generalist because it can subsist in a large range of environmental and habitat conditions (Yahner, 1986; Pearce and Venier, 2005). However, our results suggest that masked shrews may be opportunistic and benefit from abundant stumps, shrubs, and trees in boreal forests when available without a strong impact at the population level.

We observed other relationships between boreal small mammal abundances and CWD volumes that depended on the spatial scale. Deer mice abundance was positively associated with high volumes of well decayed CWD at fine- and stand-scales. Lee (2004) found that deer mice populations in sites with high volumes of CWD were more stable, had a higher survivorship, recruitment, and mean residency time than in sites with few CWD. These positive population dynamics probably led to high abundances locally and at larger spatial scales (Manning and Edge, 2004). Red-backed voles were positively associated with well decayed stumps exclusively at the stand-scale. To our knowledge, there is no previous study showing empirical evidence of the positive association of stumps with red-backed vole abundance. Our results suggest that these structures had a positive effect on red-backed vole abundance, probably because stumps were used as refuges against predators and nest sites (Gunderson, 1959; Merritt, 1981). Masked shrews on the other hand, were more abundant in stands with more well decayed logs than in those with fewer logs, but this pattern was restricted to clearcuts. Even though masked shrew abundance was associated with high CWD volumes at the fine-scale, the benefits CWD can provide such as humidity and cover against predators may have helped increase the quality and carrying capacity of the stand for shrews.

Meadow voles, for their part, were not associated with CWD at the fine-scale. Since meadow voles responded positively to CWD at the stand-scale, the lack of associations at the fine-scale that we observed may have been caused by several factors. An overriding regulatory factor (Krohne and Burgin, 1990), the lack of predation as well as other density-dependent factors such as intraspecific competition (Turner and Iverson, 1973; Oatway and Morris, 2007; Morris and MacEachern, 2010) may have had a significant impact on the local distribution of meadow voles.

5. Management implications

In this study, we found positive effects of CWD (logs and stumps) on red-backed voles and deer mice in clearcuts, partial cuts, and controls, with mean residual live tree basal areas of 1, 8, and 21 m² ha⁻¹, respectively. The abundance of red-backed voles in patches of partial cuts with high volumes (11 m³ 0.03 ha⁻¹) of well decayed CWD were comparable to the abundance in controls with low volumes of CWD. Interestingly, similar CWD volumes were recommended in Oregon as they indicated that 2 m³ 0.01 ha⁻¹ ha were maximizing deer mice survival in Douglas-fir forests (Manning and Edge, 2004). Red-backed voles have been previously identified as an indicator of sustainable forest management (Pearce and Venier, 2005) and should be considered while planning timber harvest.

To maintain high abundances of southern red-backed voles in black spruce-feather moss forests, our results suggest that the total volume of well decayed CWD in partial cuts should be above 44 m³ ha⁻¹. Indeed, we found that the southern red-backed vole abundance was positively associated with sub-grids (0.03 ha) with high volumes of well decayed CWD (11 m³ ha⁻¹) within our trapping grids that covered an area of 0.25 ha. Thus, this volume (44 m³ ha⁻¹) could be dispersed throughout the stand with small (0.03 ha) con-

centrated piles (i.e., ≥ 11 m³ of ≥ 9 cm diameter logs, based on results obtained at the sub-grid level). A recent study conducted in British Columbia also showed that the accumulation of CWD in piles or windrows maintained higher abundances of southern red-backed voles than uniformly dispersed CWD (Sullivan et al., 2011). Smaller volumes of CWD should also be left outside patches of high volumes of CWD to ensure certain connectivity between patches.

In order to reach 30% retention of cover in managed stands, which has been suggested by Sullivan and Sullivan (2001) to maintain small mammal populations, patches of high volumes of well decayed CWD should be larger instead of more numerous. Red-backed voles are rarely found near edges (Mills, 1995; Menzel et al., 1999) and increasing the size of patches would reduce the perimeter to area ratio.

Our results indicate that most small mammal abundance was positively associated with high volumes of well decayed CWD considering both spatial scales. Thus, our study supports the idea that in addition to volumes, the stage of decay is an important factor for assessing the responses of boreal small mammals to CWD. High volumes of well decayed CWD were found in our study area because our sites, prior to harvesting, were old-growth forests (>150 years). Thus, partial cuts should be employed in old forests where CWD cover a wide range of decay stages *in situ*. Finally, partial cuts retain more undisturbed forest floor microhabitat components as well as mature trees, ensuring a continuous input of snags and logs (Drapeau et al., 2009).

Acknowledgements

We thank the Natural Sciences and Engineering Research Council of Canada and the Fonds québécois de la recherche sur la nature et les technologies (FQRNT) for their financial support through a FQRNT grant (Work and collaborators) and a FQRNT-Équipe grant (Drapeau and collaborators). We are also very grateful for the academic, logistic, and technical support provided by the Centre for Forest Research and the NSERC-UQAT-UQAM Industrial Chair in Sustainable Forest Management. This study would not have been possible without the contribution of R. Julien, D. Charron, H. Bescond, M.-H. Longpré, G. Brochu, F. Boucher-Boisclair, G. Duchesne, A. Ousmane-Dia, R. Elferjani, J. Arseneault, A. Yasuda and P. Fauteux. Special thanks to late A. Duchesne for his special contribution to the field work.

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