#### Forest Ecology and Management 400 (2017) 485-501



### Forest Ecology and Management

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

# Boreal small mammals show evidence of density-dependent patterns with area-sensitivity



### Emilie E. Chavel<sup>a,\*</sup>, Louis Imbeau<sup>a</sup>, Marc J. Mazerolle<sup>b</sup>, Pierre Drapeau<sup>c</sup>

<sup>a</sup> Centre d'étude de la forêt, Institut de Recherche sur les Forêts (IRF), Université du Québec en Abitibi-Témiscamingue (UQAT), 445 boulevard de l'Université, Rouyn-Noranda, QC J9X 5E4, Canada

<sup>b</sup> Centre d'étude de la forêt, Département des sciences du bois et de la forêt, Université Laval, 2405 rue de la Terrasse, Québec, QC G1V 0A6, Canada <sup>c</sup> Centre d'étude de la forêt, Département des sciences biologiques, Université du Québec à Montréal (UQAM), 141 Avenue Président-Kennedy, Montréal, Québec H2X 1Y4, Canada

#### ARTICLE INFO

Article history: Received 1 March 2017 Received in revised form 13 May 2017 Accepted 5 June 2017

Keywords: Boreal forest Habitat amount Landscape scale Old-growth forest remnants Temporal scale

#### ABSTRACT

In recent years, habitat amount in fragmented landscapes has been shown to positively influence population size, species occurrence, and species diversity. Quantifying how sensitive bioindicator species respond to the amount of habitat in disturbed landscapes (i.e. area-sensitivity) has become a growing research focus to provide robust guidelines for ecosystem-based management. In this study, we modelled the occurrence of North American boreal small mammals in relation with the total amount of forest surrounding remnant forest patches in disturbed landscapes while controlling for local habitat associations. Over the summers of 2013 and 2014, we conducted four trapping sessions in 60 sites located in old forest remnant patches of old forests in both wildfires and aggregated clearcuts, and in continuous old forest blocks within the black spruce forest of northwestern Quebec, Canada. American red squirrels (Tamiasciurus hudsonicus), southern red-backed voles (Myodes gapperi) and masked shrews (Sorex cinereus) represented 85.5% of our total captures. We measured the amount of habitat (percentage of forest cover) within 100 concentric buffers around each capture grid using digital forest cover maps. Buffers varied in radii from 50 m to 5 km. We quantified area-sensitivity using dynamic models of singlespecies occupancy to estimate the probabilities of initial site occupancy, site extinction and site colonisation of each species according to both local habitat variables and surrounding habitat amount. We found no associations between initial site occupancy, site colonisation, or site extinction with local habitat features, possibly in response to habitat structure similarity of our three site types. Species studied had different life histories in terms of population dynamics' and timing of juvenile dispersal, possibly explaining why each species had its individual response to the amount of habitat in the surrounding landscape. For the American red squirrel, we found no evidence of within-year area-sensitivity on initial site occupancy patterns, whereas negative area sensitivity on initial site occupancy between-years was observed for the southern red-backed vole. In contrast, we found positive area-sensitivity on betweenyears site colonisation for this latter species at small spatial scales. For masked shrews, we detected negative area-sensitivity on initial site occupancy within-year. As populations were sampled at low density, we suspect that the sparse distribution of individuals may influence area-sensitivity patterns. Future studies should consider area-sensitivity with regards to both spatial and temporal scales. We encourage long-term monitoring of animal populations at multiple spatial scales to investigate the underlying ecological mechanisms of positive and negative area-sensitivity.

© 2017 Elsevier B.V. All rights reserved.

#### 1. Introduction

Studies identifying habitat characteristics and mechanisms that are critical to maintain vertebrate populations have traditionally been conducted at the local scale (e.g. Dueser and Shugart, 1978; Pough et al., 1987; Dupuis et al., 1995). In recent years, however, spatial heterogeneity at larger scales (i.e. effects of surrounding habitat amount, remnant patch size, and structural connectivity) has been considered to explain patterns of species occurrence that involve underlying biotic processes such as source-sinks dynamics and spatial aggregation of competitor species (Pickett and Cadenasso, 1995; Mazerolle and Villard, 1999; Jones, 2011). The

<sup>\*</sup> Corresponding author at: 7 Avenue Robert Schuman, 6700 Sélestat, France.

*E-mail addresses*: emilie.chavel@uqat.ca (E.E. Chavel), louis.imbeau@uqat.ca (L. Imbeau), marc.mazerolle@sbf.ulaval.ca (M.J. Mazerolle), drapeau.pierre@uqam. ca (P. Drapeau).

proportion of remnant habitat in managed landscapes (habitat amount) and its spatial arrangement (habitat configuration) have been identified as important determinants of the global loss of biodiversity (Czech and Krausman, 1997; Lawler et al., 2002; Kerr and Cihlar, 2004). Habitat loss, rather than fragmentation per se, is generally considered as having the upper hand for explaining population declines (Schmiegelow and Mönkkönen, 2002; Fahrig, 2003; but see Villard et al., 1999 for another perspective). Indeed, habitat area has been shown to have a positive influence on population size, species occurrence, and species diversity (Fahrig, 2003, 2013). As a result, determining the spatial scale of individual species or community responses to habitat area has become a growing research focus (e.g. Holland et al., 2004; Desrochers et al., 2010; Drapeau et al., 2016) with the underlying objective to quantify the sensitivity of species with the amount of habitat in surrounding areas both to fulfil their life cycle and to carry out ecological functions (i.e. species area-sensitivity - Robbins, 1979). In a context of large-scale anthropogenic changes of the environment (e.g. forest management, agriculture) affecting both the availability of habitat and its spatial configuration, empirical studies showing evidence of thresholds of area-sensitivity are required to inform conservation strategies (Linehan et al., 1995; Boutin and Hebert, 2002; Wiens, 2009).

In the eastern Canadian boreal forest, tree harvesting has become the dominant disturbance in several regions, exceeding wildfires in spatial coverage (Drapeau et al., 2009). Tree harvesting has changed the age structure of landscape mosaics with a net decrease in old forest cover types when compared with historical disturbance regimes (Bergeron et al., 2002; Cyr et al., 2009). To mitigate this decline in the proportion of old forest stands, ecologists have proposed ecosystem-based approaches that cast timber harvested landscapes within the range of variation of their natural disturbance regimes (Hunter, 1993; Niemelä, 1999; Bergeron et al., 2007). However, the implementation of this new forest management approach is, in its initial steps, and most of the retention of old-growth forest patches in former and current aggregated clearcuts have not been planned within an ecosystem management framework. Remnant patches of old forests may provide habitat conditions for wildlife. as is the case for fire skips in stand-replacing wildfires (Morissette et al., 2002; Nappi et al., 2010). To better forecast the planning of green retention under the new ecosystem-based approach, there is a need to assess how the current retention strategy of old remnant patches in aggregated clearcuts provides species with habitat conditions that may or may not differ with those in wildfires. Such assessments require going beyond the usual analyses relating species' presence-absence or relative abundance data with stand- and landscape-level habitat explanatory variables (McGarigal and McComb, 1995; Drapeau et al., 2000; Brotons et al., 2003). These assessments should tackle a more in depth analysis on response variables such as initial site occupancy, site colonisation and site extinction rates of species in remnant habitats.

In this study, we used small mammals as a focal species group. Their general biology, habitat associations, and low dispersal capacities suggest that they could be more sensitive to landscape characteristics than anticipated as their response to habitat varies at different scales (Schweiger et al., 1999; Manning and Edge, 2004; Fauteux et al., 2012). To our knowledge, very few studies have considered habitat area to understand small mammal areasensitivity through quantitative analyses of initial site occupancy, site colonisation, and site extinction patterns of small mammals in forest patches (Ritchie et al., 2009). We modelled site occupancy of boreal small mammals in relation to the total amount of forest in the surrounding landscape while controlling for local habitat associations. Specifically, our first objective was to evaluate the importance of remnant patch forest structure for site occupancy by small mammals. We assessed the suitability of remnant patches to pro-

vide habitat conditions comparable to those occurring following wildfires by measuring site occupancy of small mammals in post-fire and post-harvesting remnant stands. Our second objective aimed at measuring the relationship between population parameters (i.e. initial site occupancy, site colonisation, and site extinction) and the amount of forest by using multiple-scale buffers surrounding our sampling sites. Population parameters were estimated from data collected in years of low mammalian density (i.e. when populations are most dependent on critical resources). Evidence supporting area-sensitivity in small mammals would add further value to the reliability of these species as indicators of sustainable forest management (McLaren et al., 1998; Pearce and Venier, 2005; Holloway and Smith, 2011).

According to our objectives, we hypothesised that:

- (1) at the local scale, the occurrence of boreal small mammals would not be explained by patch origin (post-fire vs. postharvest), but rather by forest structure attributes (such as downed woody debris and canopy cover) found in either post-fire or post-harvesting remnant stands (e.g. Orrock and Pagel, 2002; Fauteux et al., 2012; Craig et al., 2014).
- (2) at low density, boreal small mammals are area-sensitive at a spatial scale greater than the local stand scale.

#### 2. Materials and methods

#### 2.1. Study area

The study area covered a total of 8325 km<sup>2</sup> of black sprucefeather moss forest located in northwestern Quebec, Canada (79°29' W, 49°00' N - 75°39' W, 50°22' N - Fig. 1). A subpolar continental climate characterises this boreal region, with mean monthly temperatures ranging from 20 °C to -16 °C and 850 mm of annual precipitation (Blouin and Berger, 2002; Environment Canada, 2015). The forest canopy is dominated by black spruce (Picea mariana). Jack pine (Pinus banksiana) and balsam fir (Abies balsamea) also occur, along with broadleaf species such as paper birch (Betula papyrifera) and trembling aspen (Populus tremuloides). The understory is primarily composed of dwarf ericaceous shrubs (e.g. Rhododendron groenlandicum) and feather mosses (Pleurozium schreberi) forming a dense carpet, replaced by Sphagnum species as drainage conditions deteriorate due to paludification with time since fire (Fenton and Bergeron, 2006). Indeed, the region is also characterised by recurrent and severe wildfires over vast areas (8000 km<sup>2</sup> on average – Payette, 1992; Bergeron et al., 2004; Le Goff et al., 2008), although this major disturbance is increasingly replaced by various forest management and harvesting strategies (Imbeau et al., 2015).

We selected a total of 60 forested sites that were equally distributed among old undisturbed forest (CONTROL – continuous forest over 100-years-old and of more than 200 ha), post-fire remnant patches (POSTFIRE – mean 3.1 ha; range 0.2 – 11.1 ha) left after wildfires that occurred over 20 years ago, green tree retention stands (GREENTREE – mean 0.8 ha; range 0.09 – 1.6 ha) left after recent clear-cuts (< 10 years), and linear cutblock separators (LIN-EARCUT – 60–100 m large, connected to old-growth forests) that separate clearcut areas. Sites were at least 500 m apart. Based on the average movement distance of American red squirrels (*Tamiasciurus hudsonicus*) which are the most vagile species found on our study area (Larsen and Boutin, 1994), this distance of 500 m was sufficient to ensure independence among sites. Details regarding habitat structure and composition in these four site types are found in Appendix A.

Although we initially selected four types of sites, we pooled GREENTREE and LINEARCUT sites together. These two types were pooled to increase species detection in site occupancy models as low species detection reported in GREENTREE sites prevented us



Fig. 1. Location of the study sites in black spruce forest of northwestern Quebec, Canada.

from estimating site occupancy in this site type. Hereafter, we referred to GREENTREE and LINEARCUT sites as harvest retention patches (HARVEST). Habitat structure and composition characterising HARVEST sites are found in Appendix A in comparison to both CONTROL and POSTFIRE sites.

#### 2.2. Small mammal trapping design

Live-trapping was conducted in 2013 from July 23rd to August 15th, as well as from June 1st to August 21st, in 2014. We trapped over three consecutive nights and days, checking the traps twice a

day (early morning and late afternoon) as small mammals are mostly nocturnal except for American red squirrels which start foraging just after sunrise (Merritt, 1981; Whitaker, 2004; Smith, 2012b). Each site was monitored with this trapping regime of three consecutive nights during one session over the summer 2013 (sampling session 1) and three sessions over the summer 2014 (3 nights in each of June – sampling session 2, July – sampling session 3, and August – sampling session 4). Trapping sessions in a given site were separated by 27 days over the summer 2014. Sciurid species were trapped using Tomahawk (Tomahawk Live Trap IIc <sup>®</sup>) live-traps baited with peanut butter and apple pieces, providing food and water to trapped individuals. Cotton batting was also added in each trap to provide shelter. We established one transect line of six live-traps per site with a distance of 10 m between traps. Transects were 50 m long to accommodate our smallest retention and remnant patches. American red squirrels were also sampled using point and playback counts. These consisted of first listening for squirrels for 10 min after having checked traps and released any trapped individuals. Then, we called individuals using recorded red squirrels calls over a period of 10 min and noted any response to these playback calls (Chavel et al., 2017). Cricetine species were trapped using Sherman (H.B. Sherman Traps, Inc. <sup>®</sup>) live-traps supplied with peanut butter, apple pieces, and cotton batting. At each site, we established a trapping grid of  $4 \times 4$  traps with a distance of 5 m between traps. We observed incidental captures of amphibians and lethal captures of small mammals in pitfall traps deployed to sample arthropods (i.e. environmental data - see below), which allowed us to include soricids in subsequent analyses. We used 26 cl pitfall traps half-filled with salty water in which odourless soap was dissolved. Four pitfall traps were placed in each site, forming a 20 m-long square grid. In 2013, pitfall traps were checked the morning after three consecutive trapping nights. During the 2014 trapping sessions, pitfall traps were checked on three consecutive mornings. Trapping grids and transect lines were centred on each site (Fig. 2).

Individuals captured alive were pit-tagged (Biomark ®), identified to sex and age using visual characteristics. All live individuals were subsequently released. Dead individuals were stored in a sealed plastic bag to confirm species identification according to tooth patterns and other cranial characteristics (Lupien, 2001, 2002; Fauteux et al., 2014). Shrews captured in Sherman livetraps were excluded from our analyses for two main reasons. First, most soricid species potentially found in the study area are too light to trigger the traps. Only heavier individuals could be caught which means that we could only sample a portion of the population. Secondly, identifying some species such as masked shrews (Sorex cinereus) and pygmy shrews (S. hoyi) is often impossible unless measuring tooth pattern and other cranial characteristics (Nagorsen, 1996). We considered each Sherman and Tomahawk trap as providing an effort of one trap night, except traps which were accidentally sprung and were consequently noted as providing an effort of 0.5 trap night (Nelson and Clark, 1973). Likewise, all pitfall traps were considered as providing an effort of one trap night, unless dug out. All manipulations adhered to the Canadian Council on Animal Care Guidelines and were approved by the Institutional Animal Care Review Committee, Université du Québec en Abitibi-Témiscamingue (UQAT, permit No. permit No. 2013-04-02).

#### 2.3. Environmental data

#### 2.3.1. Stand scale microhabitat associations

Microhabitats were characterised at the level of the Sherman grid ( $15 \times 15$  m). All sampling plots were centred on a single point (Fig. 2), from where all weather variables were also recorded. Stand age (AGE) was obtained by coring ten of the largest live trees located within a plot 30 m in diameter. Core samples were extracted with a  $400 \times 5.15 \text{ mm}$  increment borer and stand age was measured by counting growth rings on sanded samples through an Olympus SZX12 binocular (90-fold magnification). Canopy cover (CANCOV) was measured on hemispherical photographs taken with a camera Nikon CoolPix 990 with a fisheye lens FC-E8 and using the "Threshold" tool on Adobe Photoshop Element 2.0 (Adobe Systems, 2002). Nine photographs were taken per site, one in the grid centre, four at each grid corner, and four 10 m away from each grid side. Photographs were taken at both 20 and 150 cm off the ground (CANCOV20 and CANCOV150) as we expected sciurid species to be more impacted by the tree canopy,



**Fig. 2.** Schematic representation of a sampling site. The black cross (+) represents the centre of all sampling plots where all weather variables were recorded. White circles  $(\bigcirc)$  represent one Tomahawk live-trap, grey circles  $(\bigcirc)$  represent one Sherman live-trap, black circles  $(\bullet)$  represent one arthropod pitfall trap, the dotted square represents the quadrat in which tree and snag densities were recorded as well as volumes of downed woody debris, while the dotted circle represents one plot in which canopy cover and tree stand age were recorded. The presence of deciduous trees was assessed from the grid centre as well as 4 other points 15 m away from the grid centre and located at each cardinal point.

whereas we expected other small mammals to react to both tree and understory canopy. Both canopy covers were expressed in percentages (%). We identified all tree species observed from the site centre as well as from four other points located 15 m away from it and facing each cardinal point. This measure was primarily taken to record the presence of deciduous trees (DECID – binary variable).

We counted all large standing trees (live and dead) within a  $15 \times 15$  m quadrat. We defined large trees and snags as those with a diameter at breast height (dbh) equal or larger than 10 cm (Déry and Leblanc, 2005). All snags shorter than 1.2 m were excluded from the count. We then obtained the total density of large live trees (TREEDENS) and the density of large snags (SNAGDENS). All values were expressed as a number of stems per hectare (stems. ha<sup>-1</sup>). The volume of downed woody debris (DWD) was inventoried in a 15 m-sided triangle (Harvey and Brais, 2007), following the methods and the decay classes described in Fauteux et al. (2012). Volumes of logs were calculated using the conicparaboloid formula (Fraver et al., 2002) and were expressed in cubic meters per hectare (m<sup>3</sup>.ha<sup>-1</sup>).

Night temperatures were measured at each site by setting data loggers (Hydrochron iButton<sup>®</sup>, Maxim Integrated, San Jose, CA, USA) 1 m off the ground, in a shaded area, protected from the wind. Data loggers were set to record temperatures (°C) every 4 h. Temperatures were recorded for every trapping session except for June 2014 due to technical problems. We only considered mean night temperatures that were obtained by separating night time

from daytime temperatures according to the sunrise and sunset times (http://www.sunrise-and-sunset.com). Mean night temperature was then calculated for each trapping night. Night rainfall (mm) was measured daily using rain gauges. Moon illumination, expressed as the percentage of visible moon, was determined according to the lunar calendar found on http://time.unitarium.com/moon/where.html, and by setting the UTC time at one hour after sunset on the day when traps were set (i.e. when nocturnal small mammals are most active).

# 2.3.2. Landscape association with the amount of forest at different scales

Species encountered at our study sites have been reported in different forest cover types, even though some of the species prefer old-growth or coniferous forests (Merritt, 1981; Whitaker, 2004; Smith, 2012b). As a consequence, we focused on the total amount of forest located around capture grids, regardless of forest composition and tree density. Forest cover was obtained using an ArcGIS layer updated in 2013 produced by the Ministère du Développement durable, de l'Environnement et de la Lutte contre les changements climatiques (MDDELCC) (Bissonnette and Lavoie, 2015). Forested areas were defined as patches of trees with a minimum area of 0.1 ha, a canopy cover  $\geq 10\%$ , a stand height  $\geq 2$  m, and a stand age  $\geq 20$  years-old.

Percent area covered by forest was measured in a total of 100 concentric buffers defined around the centre of each capture grid, using all radii with increments of 50 m, from 50 m up to 5 km. We chose a maximal radius of 5 km because the two most vagile species encountered in our study sites (i.e. northern flying squirrels – *Glaucomys sabrinus* – and American red squirrels) may be impacted by landscape disturbances both within and beyond their home range (Larsen and Boutin, 1994; Bowman et al., 2002; Ritchie et al., 2009). Grid resolution of the map (30 X 30 m) was kept constant among radii.

#### 2.4. Statistical analyses

#### 2.4.1. Stand scale microhabitat associations

We used dynamic single-species occupancy models to estimate the probabilities of initial site occupancy ( $\psi$ ), site extinction ( $\varepsilon$ ), site colonisation ( $\gamma$ ), and detection (p) of each species (MacKenzie et al., 2003). We considered the populations of small mammals to be open because 1) cricetine juveniles are usually weaned and independent at about three weeks (Merritt, 1981), and 2) juvenile American red squirrels begin to disperse within the first month after leaving the family den (Larsen and Boutin, 1994; Steele, 1998). All parameters were estimated with maximum likelihood using the *unmarked* package (Fiske and Chandler, 2011) in R (version 3.0.1, R Development Core Team, 2015).

We considered two time frames to analyse data, each one consisting of two primary periods. The first time frame accounts for between-years variations, and included data collected in late July-August 2013 (sampling session 1) and during August 2014 (sampling session 4). The second time frame accounts for within-year variations, and included data collected in July 2014 (sampling session 3) and again in August 2014 (sampling session 4). Data obtained in June 2014 (sampling session 2) were excluded as detections of most species were too low to obtain a reliable estimate of initial occupancy. In any of these two time frames, we considered a total of 67 models (Appendix B). The probabilities of initial site occupancy, site colonisation, and site extinction were allowed to vary, one at a time, according to a set of seven hypotheses, and the detection probability was allowed to vary with one of three scenarios (Table 1).

We used an information-theoretic approach based on Akaike's Information Criterion for small samples (AIC<sub>c</sub>) to compare candidate models (Burnham and Anderson, 2002). The goodness-of-fit of occupancy models was tested by performing 10 000 bootstraps on the most global model using an extension of the MacKenzie and Bailey (2004) goodness-of-fit test for occupancy models, which was implemented in the *AICcmodavg* package (Mazerolle, 2015). Slight overdispersion was suggested for all sets of analyses ( $\hat{c} = [1.16; 2.04]$ ) but one (i.e. *M. gapperi*, within-year analyses –  $\hat{c} = 0.89$ ). Multimodel inference was conducted on each variable that was contained in the top models to compute 95% unconditional confidence intervals and model-averaged predictions based on the entire set of candidate models.

## 2.4.2. Landscape association with the amount of forest at different scales

We evaluated the relationship between species occurrence and forested areas (i.e. level of area-sensitivity) at the spatial scale used to measure habitat availability. Three parameters of species occurrence, namely initial site occupancy, site colonisation, and site extinction probabilities, were successively and independently evaluated. We used top-ranking models defined for each species in the first set of analyses (stand scale microhabitat associations - see above) to build on the following landscape modelling. We allowed initial site occupancy ( $\psi$ ), site colonisation ( $\gamma$ ), and site extinction  $(\varepsilon)$  to vary with the amount of forested areas measured in each concentric buffers around capture grids. Each of these three parameters was analysed by varying the amount of forested area in concentric buffers while holding the other parameters constant. To quantify the response to forested areas (area sensitivity), we extracted the  $\beta$  estimates associated with the amount of forested area for each parameter ( $\psi$ ,  $\gamma$ ,  $\varepsilon$ ), from each dynamic model. For each parameter, we used the βestimates of the amount of forested area in four candidate models (see below). To avoid correlations among consecutive measures of forested areas, we selected a series of  $\beta$  estimates, starting at the  $\beta$  estimates associated with the amount of forested area in the two smallest radii (0.050 and 0.100 km). We then selected  $\beta$  estimates associated with the amount of forested area in each radius that was the sum of the two preceding radii, i.e. radii of 0.150 km, 0.250 km, 0.400 km, 0.650 km, 1.050 km, 1.700 km, 2.750 km, and 4.450 km. We used this series of ten  $\beta$  estimates to in four candidate linear regressions.

The first regression allowed the dependent variable to be constant, and this model tested whether  $\beta$  estimates associated with the amount of forested area were independent of the radii of the concentric circles where forested area was measured. The second regression tested whether there was a linear relationship between β estimates and circle radii. The third regression tested a quadratic relationship, assuming an optimal radius for patterns of area sensitivity. Finally, a logarithmic relationship between the dependent variable and the circle radii was tested according to a fourth regression using the log of circle radii and hypothesising that  $\beta$ estimates become more stable at larger scales. Parameters of the regressions were estimated by maximum likelihood using generalised least squares with an autoregressive first-order correlation structure using the nlme package (Pinheiro et al. 2014). We conducted model selection and multimodel inference based on Akaike's Information Criterion for small samples (AIC<sub>c</sub>) to compare these four candidate models (Burnham and Anderson 2002).

#### 3. Results

#### 3.1. Small mammal surveys

We captured a total of 676 small mammals (280 rodents and 396 shrews – Appendix C.1) during the trapping sessions of 2013 and 2014 with a total effort of 11055 Sherman trap-nights,

#### Table 1

List of hypotheses tested with 67 dynamic single-species occupancy models to analyse detection data of American red squirrel (*Tamiasciurus hudsonicus*), southern red-backed vole (*Myodes gapperi*), and masked shrew (*Sorex cinereus*), sampled in black spruce forest of northwestern Quebec.

Model structure	Predictions	References
Scenarios applied independently on	either one of the parameters of initial site occupancy ( $\psi$ ), site o	colonisation ( $\gamma$ ), and site extinction ( $\epsilon$ )
(.)	Probabilities of site occupancy, site colonisation,	N/A
	and site extinction are constant.	
(туре)	No differences in either initial site occupancy or site colonisation probabilities among site types.	Green-tree retention patches should act as refuges and sources of dispersers (Leblanc and Pouliot, 2011; Robinson et al. 2013)
(EARLYDWD + LATEDWD)	Probabilities of site occupancy and site colonisation increase with increasing volumes of downed woody debris.	Small mammals use woody debris as cover, feeding grounds, and even as structures facilitating their movements (Moseley et al., 2008; Sullivan and Sullivan, 2012; Craig et al., 2014).
(CAN: LATEDWD)	Canopy cover mitigates the effects of late- decayed woody debris on probabilities of initial	Mammalian association with late-decayed downed woody debris can be partially released depending on the canopy
(decid)	Probabilities of initial site coolinsation. Probabilities of initial site occupancy and site colonisation increase with the presence of broadleaf trees.	Some hypogeous fungi are related to the presence of broadleaf trees (Crites and Dale, 1998). Boreal small mammals either have a diet primarily composed of hypogeous fungi (Orrock and Pagel, 2002) or opportunis- tically feed on them (Currah et al., 2000; Pyare and Longland 2001)
(can)	Probabilities of initial site occupancy and site colonisation increase with canopy cover.	Small mammals in our study sites are associated to features of old-growth forests (McLaren et al., 1998; Pearce and Venier, 2005; Smith, 2012a).
(can2)	Probabilities of initial site occupancy and site colonisation increase with canopy cover up to an optimal value, and then decrease.	Old-growth forests are characterised by canopy openings favourable for small mammals (Crête et al., 1995).
(treedens + snagdens)	Probabilities of initial site occupancy and site colonisation increase with the presence of large trees and snags.	Sciurid species benefit from the presence of large snags as well as large live trees (Carey, 1995; Darveau and Desrochers, 2001; Vanderwel et al., 2010).
Set of scenarios applied on the dete	ction parameter (p)	
(.)	Detection probabilities are constant.	N/A
(Session + method)*	For cricetine species only, detection probabilities increase from 2013 to 2014. Within-year (from July to August 2014), detection of all species (except sciurids) increases. Detection probabilities of American red squirrels are not affected by the sampling technique.	With an increasing density during a breeding season, there is a greater chance to detect at least one individual. Some cricetine species also cycle over four years (e.g. red-backed voles, Fauteux et al., 2015). We sampled individuals during the low and increasing phases of this cycle. Cyclicity in sciurids and soricids is unknown, but sciurids show no within-year change in their detection probability (Chavel et al., 2017). Detection of American red squirrels is similar using either live-trapping, playback or point counts (Chavel et al., 2017).
(rain + temp + moon)**	Detection probabilities increase with rainfall. Detection probabilities of cricetine and soricid species increase with average night temperature up to 20 °C.Detection probabilities of cricetine and soricid species decrease with increasing moon illumination.	Some small mammals are more active during rainy and warm nights (Vickery and Bider, 1981).Small mammals benefit from positive ambient temperature below 20 °C, i.e. temperatures when body water loss becomes a severe issue (Getz, 1961; McManus, 1974; Cherry and Verner, 1975).Nocturnal small mammals are more likely to be predated during bright nights (Clarke, 1983; Orrock et al., 2004).
(arthro + mollusc)	Detection probabilities (especially of insectivorous soricids) increase with the amount (weight) of ground-dwelling arthropods and to a lower extent, to the amount of molluscs.	Small mammals are either insectivorous or feed opportunistically on invertebrates (Whitaker and French, 1984; Bellocq and Smith, 1994; Pretzlaw et al., 2006).

Notes: Covariate acronyms: ARTHRO, weight of ground-dwelling arthropods; CANCOV, canopy cover taken either 150 cm off the ground to analyse squirrel data or 20 cm off the ground to analyse data from all other species (linear form); CANCOV2, canopy cover (quadratic form); DECID, presence of deciduous trees; EARLYDWD, early decayed downed woody debris; IATEDWD, late decayed downed woody debris; METHOD, methods used to detect individuals (live-trapping, live-trapping + playback count, live-trapping + point count + playback count; MOLLUSC, weight of terrestrial molluscs; MOON, percentage of moon illumination during each trapping night; RAIN, rainfall measured after each trapping night; session, trapping session (i.e. primary period – August 2013, July 2014, August 2014); SNAGDENS, density of snags with a dbh larger than 10 cm; TYPE, site type (control, post-fire remnant patch, harvest retention patch). Parameters followed by (.) indicate that they are constant.

METHOD was only used to analyse detection data of American red squirrels (*Tamiasciurus hudsonicus*).

\*\* MOON was not used to analyse detection of American red squirrels.

4229.5 Tomahawk trap-nights, and 2828.5 pitfall trap-nights. Three species represented 85.5% of our total captures: masked shrew (*S. cinereus* – 52.4%), southern red-backed vole (*M. gapperi* – 23.1%), and American red squirrel (*T. hudsonicus* – 10.0%). Other species that were sporadically trapped included, in decreasing abundance, pygmy shrew (*S. hoyi*), deer mouse (*P. maniculatus*),

northern flying squirrel (*G. sabrinus*), eastern heather vole (*Phenac-omys ungava*), Arctic shrew (*S. arcticus*), northern short-tailed shrew (*Blarina brevicauda*), field vole (*Microtus pennsylvanicus*), and smoky shrew (*S. fumeus*). We captured twice as many small mammals in August 2014 as compared to August 2013 (number of individuals per 100 trap nights: No/100TN<sub>session1</sub> = 3.11,

No/100TN<sub>session4</sub> = 7.08). More individuals were also caught from June to August 2014 (No/100TN<sub>session2</sub> = 0.63, No/100TN<sub>session3</sub> = 4.09, No/100TN<sub>session4</sub> = 7.08). We present species-specific detection results in Appendix C.1. A similar pattern could be observed for the number of sites occupied by small mammals (i.e., model-averaged site occupancy  $[\psi]$  \* number of sites) with an estimated 17 sites occupied in session 2, 52 sites occupied in session 3, and 56 occupied in session 4.This pattern was consistent among site types (Appendix C.2).

#### 3.2. Stand-scale microhabitat association

Detection data were too scarce for the algorithms to converge, except for three species, namely *T. hudsonicus*, *M. gapperi*, and *S. cinereus*. Moreover, between-years (August 2013, August 2014) and within-year (July 2014, August 2014) analyses could only be conducted for *M. gapperi*. Only within-year analyses could be carried out on both *T. hudsonicus* and *S. cinereus*.

For southern red-backed voles, detection probability varied with explanatory variables, but none of the variables were related to microhabitat. This held true in both analyses conducted on this species (i.e., between-years and within-year). The top-ranked model for between-year data had an Akaike weight of 0.31, and the model allowed the initial site occupancy probability to vary with the interaction between the canopy cover taken at 20 cm

off the ground and the volume of LATEDWD (Table 2). In this model, the detection probability was allowed to vary with the trapping session. This latter variable produced the only effect on detection probability, with an increase from August 2013 to August 2014 (model-averaged effect size on logit scale: 2.12, 95% CI: [0.85, 3.39]; Fig. 3).

The top-ranked model for within-year data allowed the initial site occupancy probability to vary with site type, whereas the detection probability included the effect of moon illumination, rain that fell within 24 h prior to sampling, and average night temperature. This model had 77% of the weight (Table 2). Multimodel inference showed that all covariates had only marginal support, except for the average night temperature. Indeed, detection probability of southern red-backed voles decreased with increasing average night temperature (model-averaged effect size on logit scale: -1.90, 95% CI: [-3.59, -0.22]; Fig. 4a). Detection probability marginally decreased with moon illumination (model-averaged effect size on logit scale: -1.09, 95% CI: [-2.29, 0.11]; Fig. 4b) and marginally increased with rainfall (model-averaged effect size on logit scale: 1.22, 95% CI: [-0.28, 2.71]; Fig. 4c). Finally, southern red-backed voles occurred as often in control sites as in post-fire retention patches (model-averaged effect size of POSTFIRE compared to CONTROL on logit scale: -0.06, 95% CI: [-1.71, 1.59]). The species occurred marginally less often in green-tree retention patches (model-averaged effect size of HARVEST compared to CONTROL on logit scale: -1.89, 95% CI: [-4.24, 0.45]; Fig. 4d).

#### Table 2

Ranking of dynamic single-species occupancy models for each of the three small mammal species based on their relative support ( $w_i$ ). Two data sets (between-years and with-year) were analysed for southern red-backed voles (*Myodes gapperi*). Only models with a  $\Delta < 4$  are included in this table.

Candidate models	К	QAIC <sub>c</sub>	Δ	Weight ( $\omega$ )
M. gapperi – Between-year variations (August 2013, Augus	st 2014)			
$\psi$ (latedwd: cancov) $\gamma$ (.) $\epsilon$ (.) $p$ (session)	9	231.18	0.00	0.31
$\psi(.)\gamma(\text{treedens} + \text{snagdens})\varepsilon(.)p(\text{Session})$	8	232.20	1.02	0.19
$\psi(\text{earlydwd} + \text{latedwd})\gamma(.)\varepsilon(.)p(\text{Session})$	8	232.65	1.47	0.15
$\psi(.)\gamma(.)\varepsilon(.)p(Session)$	6	233.32	2.14	0.11
$\psi(.)\gamma(\text{earlydwd} + \text{latedwd})\varepsilon(.)p(\text{Session})$	8	235.04	3.86	0.05
M. gapperi – Within-year variations (July 2014, August 201	14)			
$\psi(\text{type})\gamma(.)\varepsilon(.)p(\text{temp} + \text{rain} + \text{moon})$	9	303.79	0.00	0.77
S. cinereus – Within-year variations (July 2014, August 201	4)			
$\psi(Cancov)\gamma(.)\varepsilon(.)p(arthro + mollusc)$	8	352.60	0.00	0.21
$\psi(.)\gamma(.)\varepsilon(.)p(.)$	5	353.37	0.77	0.14
$\psi(CANCOV)\gamma(.)\varepsilon(.)p(SESSION)$	7	353.62	1.02	0.13
$\psi(.)\gamma(\text{Earlydwd} + \text{Latedwd})\varepsilon(.)p(\text{Arthro} + \text{Mollusc})$	9	355.35	2.75	0.05
$\psi(.)\gamma(.)\varepsilon(.)p(Session)$	6	355.75	3.15	0.04
$\psi$ (treedens + snagdens) $\gamma$ (.) $\varepsilon$ (.) $p$ (Session)	8	355.82	3.225	0.04
$\psi$ (treedens + snagdens) $\gamma(.)\varepsilon(.)p(arthro + mollusc)$	9	355.83	3.24	0.04
T. hudsonicus – Within-year variations (July 2014, August	2014)			
$\psi(.)\gamma(.)\varepsilon(.)p(.)$	5	165.49	0.00	0.24
$\psi(.)\gamma(CANCOV)\varepsilon(.)p(ARTHRO + MOLLUSC)$	8	166.16	0.67	0.08
$\psi(Cancov)\gamma(.)\varepsilon(.)p(arthro + mollusc)$	8	166.29	0.80	0.08
$\psi(CANCOV^2)\gamma(.)\varepsilon(.)p(ARTHRO + MOLLUSC)$	8	166.36	0.87	0.07
$\psi(.)\gamma(.)\varepsilon(Cancov)p(arthro + mollusc)$	8	166.62	1.13	0.06
$\psi(CANCOV)\gamma(.)\varepsilon(.)p(Session + Method)$	8	167.13	1.64	0.05
$\psi(.)\gamma(\text{decid})\varepsilon(.)p(\text{arthro} + \text{mollusc})$	8	167.31	1.82	0.05
$\psi(.)\gamma(.)\varepsilon(Cancov^2)p(arthro + mollusc)$	8	167.54	2.05	0.4
$\psi(\text{decid})\gamma(.)\varepsilon(.)p(\text{arthro} + \text{mollusc})$	8	167.78	2.29	0.04
$\psi(.)\gamma(.)\varepsilon(CANCOV)p(Session + METHOD)$	8	167.87	2.37	0.03
$\psi(.)\gamma(CANCOV)\varepsilon(.)p(Session + METHOD)$	8	167.88	2.39	0.03
$\psi(\text{decid})\gamma(.)\varepsilon(.)p(\text{Session} + \text{Method})$	8	168.19	2.70	0.03
$\psi(.)\gamma(CANCOV)\varepsilon(.)p(RAIN + TEMP)$	8	168.43	2.94	0.03

**Note:** Covariate acronyms: ARTHRO, weight of ground-dwelling arthropods; CANCOV, canopy cover taken either 150 cm off the ground to analyse squirrel data or 20 cm off the ground to analyse data from all other species (linear form); CANCOV, canopy cover (quadratic form); DECID, presence of deciduous trees; EARLYDWD, early decayed downed woody debris; IATEDWD, late decayed downed woody debris; METHOD, methods used to detect American red squirrels (live-trapping, live-trapping + playback count, live-trapping + point count, live-trapping + point count, live-trapping period - August 2013, July 2014, August 2014); SNAGDENS, density of snags with a dbh larger than 10 cm; TEMP, average night temperatures for each trapping night; TREEDENS, density of live trees with a dbh larger than 10 cm; TYPE, site type (control, post-fire remnant patch, harvest retention patch). Parameters followed by (.) indicate that they are constant.

Indicates that overdispersion did not occur (c-hat < 1) and that we relied on the AIC<sub>c</sub> instead of the QAIC<sub>c</sub>.



**Fig. 3.** Between-year detection probabilities of southern red-backed voles (*Myodes gapperi*) over the trapping sessions in August 2013 and August 2014 based on multimodel inference. Error bars represent 95% unconditional confidence intervals.

The top-ranked model for the within-year data of masked shrews accounted for 21% of the weight, and it allowed the initial site occupancy probability to vary with the canopy cover taken 20 cm above the ground (Table 2). However, the null model followed this model closely. Unsurprisingly, multimodel inference revealed that none of the covariates had any support. Finally, the null model ranked highest for the within-year data of American red squirrels (Table 2), indicating that none of the variables influenced any of the parameters.

#### 3.3. Landscape association with the amount of forest at different scales

At a local scale, the amount of forest rapidly dropped from 63% to 40%, then slowly rose to plateau at 56%. The remaining 44% included disturbed habitat, different bodies of water and human infrastructures such as roads and mines (Fig. 5).

A total of 1 200 species-radius dynamic models ((3 parameters  $[\psi, \gamma, \text{ or } \epsilon] \times 100 \text{ radii} \times 3$  species captured within a year) + (3 parameters  $\times 100 \text{ radii} \times 1$  species captured between-years)) were built to observe changes in occupancy according to the spatial scale



**Fig. 5.** Percentage of forest around capture grids (n = 60) in concentric circular areas, with a radius varying from 0.05 to 5 km. Dotted lines represent 95% confidence intervals around the average values.

used to measure forested area. All models that allowed the probability of occupancy or the probability of site colonisation to vary with the amount of forest converged. In contrast, out of 400 models allowing site extinction to vary with forested areas, 83 models (12 and 71 models for T. hudsonicus and S. cinereus, respectively) produced unstable beta estimates with large SE, likely due to the scarcity of site extinction events for these two species (Fig. 6). By considering a 90% CI (instead of the more conservative 95% CI), a marginal negative area-sensitivity was observed for the initial site occupancy patterns of both masked shrews (relatively constant at all radii, within-year) and southern red-backed voles (at radii greater than 1 km, between-year only; Figs. 6 and 7). Although we found no evidence of an effect of area-sensitivity on site extinction for red-backed voles, we found evidence (using a 90% CI) of marginal positive area-sensitivity in site colonisation for this species at small scales (between-years).

The top-ranked regression of beta estimates for between-year initial site occupancy by southern red-backed voles assumed a logarithmic relationship of area-sensitivity (90% of the weight). Multimodel inference indicated beta estimates increased with decreasing radii (model-averaged effect size on probability scale:



**Fig. 4.** Within-year detection probabilities of southern red-backed voles (*Myodes gapperi*) fordifferent scenarios; nightly average temperature (a), rainfall (b), and moon illumination (c) based on multimodel inference. Dotted lines represent 95% unconditional confidence intervals. Within-year initial site occupancy probabilities of southern red-backed voles in old-growth forests (CONTROL), post-fire remnant patches (POSTFIRE), and both linear cutblock separators and green-tree retention stands pooled together (HARVEST) (d). Bars represent 95% unconditional confidence intervals.



**Fig. 6.** Detailed patterns of area-sensitivity by four small mammals species measured in concentric circles extending from 1 to 5 km centred on trapping grids. Betas estimates for the amount of forested area contained in concentric circles were extracted from dynamic single species occupancy models where each parameter (initial site occupancy  $\psi$ , site colonisation  $\gamma$ , and site extinction  $\varepsilon$ ) was in turn allowed to vary with the amount of forested area. Shaded area corresponds to the 95% confidence intervals around beta estimates. Acronyms: MYOGAP, southern red-backed vole (*Myodes gapperi*); SORCIN, masked shrew (*Sorex cinereus*); TAMHUD, American red squirrel (*Tamiasciurus hudsonicus*); N/A, non-applicable.



Fig. 7. Schematic patterns of area-sensitivity by two small mammals species (southern red-backed vole – *Myodes gapperi* – and masked shrews – *Sorex cinereus*), measured in concentric circles extending from 1 to 5 km centred on trapping grids.

1.27, 95% CI: [0.29, 2.25], Figs. 6 and 7). On the other hand, the top-ranked regression for within-year initial site occupancy by masked shrews allowed a quadratic relationship (74% of the weight), but

this relationship was only marginally supported and the effect itself was very low (model-averaged effect size on probability scale: 0.22, 95% CI: [-0.10, 0.54], Figs. 6 and 7).

#### 4. Discussion

The aim of the present study was to model initial site occupancy, site colonisation and site extinction of North American boreal small mammals as a function of the total amount of forest present in the surrounding landscape while controlling for local habitat conditions. The importance of both local and landscape scales in predicting species occurrence in boreal forest landscapes is being increasingly documented (Drapeau et al. 2000, 2016; Brotons et al., 2003; Mönkkönen et al., 2014). However, to our best knowledge, this study is the first to examine possible relationships between area-sensitivity and demographic parameters such as site colonisation and site extinction. To do so, we used an innovative statistical approach that accounts for imperfect detection probability. Furthermore, by highlighting a negative rather than a positive area-sensitivity pattern on a vertebrate, this study strongly suggests that a bottom-up process hierarchically structured around local scale density-dependence and landscape scale habitat amount can drive small mammals area-sensitivity in disturbed boreal landscapes.

#### 4.1. Stand scale microhabitat associations

New clear-cutting strategies have been proposed over the past years in an attempt to better emulate the structures left by wildfires at both the stand and landscape scales (Niemelä, 1999; Bergeron et al., 2007). According to ecosystem-based management, all the vegetation structure features and legacies critical for the occurrence of small mammals should be encountered within the same range of variability in all types of our study sites (Bergeron et al., 2007). Moreover, some small mammal species such as voles remain relatively unaffected by patch geometry as they have been reported to use patch-cut interior and are edge-tolerant species (Harper et al., 1993; Hayward et al., 1999; Tallmon and Mills, 2004). We first hypothesised that at the local scale, the occurrence of North American boreal small mammals in remnant patches would mainly respond to their structural attributes rather than to site disturbance origin (wildfire vs. harvesting). Despite some minor differences, we found several similarities in the vegetation structure between old post-fire forest remnants and post-harvest green-tree retention patches. Accordingly, initial site occupancy patterns of small mammals did not vary with the landscape origin in which these remnants were embedded despite a marginally lower initial site occupancy in post-harvest patches (HARVEST) for the southern red-backed vole. Unlike past studies that found associations of small mammals with habitat elements, occupancy patterns did not strongly vary with stand-level habitat variables most likely due to the limited range of variation of the vegetation structure in our study sites (Moseley et al., 2008; Sullivan and Sullivan, 2012; Craig et al., 2014). Top-models highlighted the importance of environmental variables on detection probability. Indeed, the detection probability of southern red-backed voles varied mainly with climatic and light conditions propitious to nocturnal activities (e.g. foraging, searching for mates) as it was previously shown to a lower extent by other studies (McManus, 1974; Vickery and Bider, 1981).

#### 4.2. Cyclicity of small mammals

Populations of some small mammal species show cyclic patterns (Boonstra and Krebs, 2012; Krebs, 2013), and in our study sites, populations of southern red-backed voles cycle over an average of four years (Cheveau et al., 2004; Fauteux et al., 2015). According to Fauteux et al. (2015), the years of 2013 and 2014 corresponded to the low phase of the population cycle and the phase of increase, respectively. The increase in the total number of all small mammals over the late-summer trapping session of these two consecutive years, from 2013 to 2014, suggests continuation of these previously documented small mammal cycles.

Sampling southern red-backed voles during the low and the increasing phases of the cycle implies that: (1) patterns of initial site occupancy might reveal local conditions critical for the species because at low densities, individuals will remain where the most needed resources occur (Fretwell and Lucas, 1969; Hayward et al., 1999; Andreassen and Ims, 2001), (2) patterns of site colonisation might get more obvious by the summer of the increasing phase, i.e. when populations have had time to build up to reach high densities and favour dispersal (van Horne, 1983; Bondrup-Nielsen and Karlsson, 1985), (3) site extinction might not be favoured. Indeed, sites with required resources are not yet overcrowded, and therefore individuals are not forced to leave such sites due to competition.

#### 4.3. Area-sensitivity and small mammals

In a context of large-scale anthropogenic changes to forests (i.e. tree harvesting), testing whether small mammals are areasensitive becomes critical, especially if they are considered reliable indicators of sustainable forest management (McLaren et al., 1998; Pearce and Venier, 2005; Holloway and Smith, 2011). Research on area-sensitivity has initially focused on presence-absence data of various species (mainly birds - Robbins, 1979; Walk and Warner, 1999; Desrochers et al., 2010) to later shift to species richness, density, and reproductive success (Donovan and Lamberson, 2001; Davis, 2004; Smith et al., 2011). These studies led us to hypothesise that small mammals could display scale-dependent areasensitivity at spatial scales even greater than the one of their home range. In our study, we used an innovative approach to address the question of area-sensitivity of small mammals by using dynamic occupancy analyses to account for imperfect detection probability. Five main results emerge from our study: (1) both masked shrews and southern red-backed voles were marginally area-sensitive. whereas American red squirrel was not area-sensitive, regardless of the scale, (2) the main response was observed on initial site occupancy, whereas we found no patterns of area-sensitivity for site extinction, and only a slight response was observed on site colonisation patterns, (3) at all spatial scales, initial site occupancy decreased with an increase in the amount of available forest habitat, (4) responses observed on initial site occupancy of masked shrews were constant at all spatial scales whereas initial site occupancy of southern red-backed voles decreased with an increase in the buffer radius considered around the trapping grids and rapidly reached a plateau, and 5) there was a difference in the response depending on whether the analyses included between-years data or within-year data (i.e., analyses of southern red-backed vole data).

To our knowledge, most studies found area-sensitivity to arise as a positive relationship between habitat amount and species abundance or between habitat amount and species occurrence. Indeed, positive area-sensitivity has been recorded in butterflies (Fred and Brommer, 2003; Baunerfeind et al., 2009), in amphibians and reptiles (Knutson et al., 1999; Guerry and Hunter, 2002), in grassland birds (Walk and Warner, 1999; Davis, 2004), and in forest birds (Trzcinski et al., 1999; Lee et al., 2002; Desrochers et al., 2010). Our study is one of the first to record negative areasensitivity, i.e. species probability of occurrence at a site decreases with an increasing area of suitable habitat in the surrounding landscape. We believe that to interpret such an unexpected trend we have to consider area-sensitivity as being both a scale and density-dependent pattern. First, we considered red-backed voles which have been reported to cycle over a period of four years in sites located a few kilometres south of our study sites, and we sampled this species during the low and increasing phases of its abundance cycle (Fauteux et al., 2015). On the other hand, we also considered shrews for which there is generally no strong evidence of cyclicity, except maybe for common shrew (Sorex araneus) (Korpimäki et al., 2005, but see Henttonen et al., 1989 for another perspective). Long-term data on masked shrews are scarce (e.g. Fryxell et al., 1998). However, there are few reports showing masked shrews' abundance fluctuating with prey abundance (e.g. Innes et al., 1990; McCay and Storm, 1997). We also observed such fluctuations in our study sites with 50% between-year and nearly 100% within-year population increases. Moreover, shrew abundance has often been reported to vary jointly with rodent abundance, although not as strong (e.g. Henttonen et al., 1989; Zub et al., 2012 in common shrews; Fryxell et al., 1998 in masked shrews). These observations concur with our own. Based on these two previous statements, we believe that the masked shrew populations we sampled were not as densely populated as they could have been. As a consequence, we considered fluctuating populations of red-backed voles sampled at low density, and potentially sparse shrew populations whereas all previous area-sensitivity studies carried out until now focused on species with relatively stable populations. We suggest that the negative trends we observed in the occupancy of both southern red-backed voles and masked shrews might be linked to the spatial distribution of individuals when local populations are at low density.

At low densities, individuals will first occupy the most suitable areas (Fretwell and Lucas, 1969; Hayward et al., 1999; Andreassen and Ims, 2001). Resources may be found where sampling grids are set, but with an increasing amount of suitable habitat in the surrounding landscape, the chance of detecting individuals at low density in such a grid decreases. As density increases, individuals disperse. All suitable areas become increasingly occupied, and successful sampling of species does no longer rely on chance. We hypothesise that the analysis of data covering the increasing phase and the peak of the cycle may reveal a weaker relationship between species' site occupancy and the amount of forested area. At the peak of the cycle of small mammal populations, we expect that the relationship between the initial site occupancy of a species and the amount of forested area would disappear, although this should be tested empirically. Both southern red-backed voles and masked shrews use disturbed and regenerating matrices around forested areas (Hayward et al., 1999; Fisher and Wilkinson, 2005; Zwolak, 2009). These environments will be more likely to be used when population size goes above the carrying capacity of a forested site. Thus, the amount of forest would no longer have an effect on their occurrence.

Although the disturbed and regenerating matrix around remnant forest sites can provide shelter to southern red-backed voles, forested areas hold habitat elements favoured by the species. Indeed, the between-year initial site occupancy pattern was negative for this species. Their between-year site colonisation pattern was positive at a local scale (radii under 500 m): the probability of individuals to disperse between the low phase and the buildup phase of their population cycle increases with a greater amount of forest in the surrounding landscape. We believe that this result highlights the importance of large amounts of forested areas within dispersal distance for southern red-backed voles when populations are building up and individuals are dispersing toward new sites. However, this result also shows that area-sensitivity cannot be studied by exclusively focusing on the effect of the habitat amount on the abundance or occurrence of a species.

Past studies have attempted to link species' life-history and strength of area-sensitivity (e.g. Henle et al., 2004; Desrochers et al., 2010; Öckinger et al., 2010), with limited results as most of these reports did not account for the scale- and density-

dependence of area-sensitivity. Moreover, it is interesting to note that the three species studied had a different life-history in terms of population cycle and dispersal timing, possibly explaining why each species had its own response to the amount of habitat in the surrounding landscape. Populations of American red squirrels are not reported to fluctuate between years and individuals mostly start dispersing by the end of summer (Wauters and Dhondt, 1993; Larsen and Boutin, 1994; Steele, 1998). For this species, we found no evidence of within-year area-sensitivity on initial site occupancy patterns. In contrast, populations of southern red-backed voles fluctuate between years and individuals start dispersing in late summer (Bondrup-Nielsen and Karlsson, 1985). For southern red-backed voles, we observed between-years negative areasensitivity on initial site occupancy but not within-year areasensitivity. In contrast, area sensitivity was positive at small scales for between-year site colonisation. Finally, populations of masked shrews could fluctuate but masked shrews do not show any peak for dispersal during the season (Whitaker, 2004). For this last group, we detected within-year negative area-sensitivity on initial site occupancy. Given these interspecific differences and responses in terms of area-sensitivity, we recommend sampling small mammals over one complete population cycle to better understand the trends described for American red squirrels, masked shrews, and southern red-backed voles. This would include sampling these species over four consecutive years from the beginning of June to the end of October in order to compare area-sensitivity during all four phases of a population cycle as well as when individuals are dispersing.

#### 5. Conclusions

By comparing small mammal occurrence in green-tree retention, post-fire remnant patches and old-growth forests, our study showed that old forest patches in harvested landscapes acted as refuges and sources of dispersers for small mammals to a degree similar to what occurs in post-fire remnant patches (Leblanc and Pouliot, 2011; Robinson et al., 2013). Retention patches in conventional clear-cut agglomerations are thus playing a functional role for small mammal populations in human-disturbed landscapes which can be improved by ecosystem-based management through planning for the amount and spatial arrangement of old forest habitats at levels that better reflect the regional natural disturbance regimes (Drapeau et al., 2016).

We encourage long-term monitoring of populations of animals at multiple spatial scales to investigate ecological mechanisms behind positive and negative area-sensitivity patterns (Desrochers et al., 2010). Indeed, we found that area-sensitivity could be density-dependent for populations characterised by cyclic abundance patterns, such as the southern red-backed vole which is particularly interesting as it shows cyclic patterns in some parts of its range (Boonstra and Krebs, 2012; Krebs, 2013; Fauteux et al., 2015). However, further studies are required to investigate the relationship between occurrence of small mammals and habitat amount during the peak of their cycle.

#### Acknowledgements

This study was funded by fellowships from the Fonds de Recherche du Quebec – Nature et Technologies, Canada (FRQNT), the *Natural Sciences and Engineering Research Council of Canada* (NSERC), and the Université du Québec en Abitibi-Témiscamingue, Canada (UQAT). The authors thank all of our field assistants, especially Michaël Paquin, Juliette Duranleau, Antoine Juigner, Hélène Dion-Phénix and Francis Bordeleau-Martin, who provided invaluable assistance.

#### Appendix A

Habitat structure and composition encountered in the 60 sampling sites used to investigate the occurrence of small mammals in black spruce forests of northwestern Quebec.

#### A.1. Site selection

We selected a total of 60 forested sites that were equally distributed among old undisturbed forest (CONTROL - continuous forest over 100-years-old), post-fire remnant patches (POSTFIRE mean 3.1 ha; range 0.2–11.1 ha) left after wildfires that occurred over 20 years ago, green tree retention stands (GREENTREE – mean 0.8 ha; range 0.09 – 1.6 ha) left after recent clear-cuts (<10 years), and linear cutblock separators (LINEARCUT – 60–100 m large, connected to old-growth forests) that separate clearcut areas.

#### A.2. Statistical analyses

We first investigated potential relationships between numeric habitat variables and site type (CONTROL, POSTFIRE, GREENTREE

and LINEARCUT) using one-way ANOVA. We subsequently conducted multiple comparisons with a Tukey contrast matrix to observe potential differences among sites and regarding each of the continuous habitat variables considered.

In the study, we pooled GREENTREE and LINEARCUT sites together to increase species detection in site occupancy models (low species detection reported in GREENTREE sites prevented us from accurately analysing site occupancy in this site type). The resulting site type was named HARVEST. We then conducted a second set of one-way ANOVA analyses, coupled with multiple comparisons with a Tukey contrast matrix, to compare the three remaining site types to one another.

All analyses were conducted in R (version 3.0.1, R Development Core Team, 2015).

#### A.3. Results

Some differences among measured habitat variables were identified in each site type but the most noticeable difference concerned site age (Table A.3.1). Residual patches left after logging

#### Table A.3.1

Mean values (±sd) of site age as well as all site covariates introduced in models, according to site types (CONTROL, POSTFIRE, GREENTREE, LINEARCUT).

Variable	Control	Postfire	Greentree	Linearcut
AGE				
(years)	158.9 ± 55.6 (a)	168.5 ± 65.8 (a)	104.1 ± 43.6 (b)	108.3 ± 33.9 (b)
CANCOV20				
(%)	74.0 ± 13.8 (a)	82.9 ± 7.7 (ab)	80.4 ± 11.0 (ab)	85.0 ± 6.3 (b)
CANCOV150				
(%)	59.3 ± 22.6 (a)	70.0 ± 18.0 (ab)	69.1 ± 16.5 (ab)	78.1 ± 12.3 (b)
TREEDENS				
(no. trees. ha <sup>-1</sup> )	838.5 ± 619.0 (ab)	826.7 ± 499.7 (a)	583.7 ± 568.4 (a)	1407.4 ± 738.5 (b)
SNAGDENS				
(no. snags. ha <sup>-1</sup> )	83.0 ± 71.0 (a)	284.4 ± 428.2 (a)	71.1 ± 101.9 (a)	165.9 ± 108.2 (a)
EARLYDWD $(m^3.ha^{-1})$	35.7 ± 42.2 (a)	144.2 ± 264.5 (a)	25.6 ± 52.1 (a)	121.8 ± 157.8 (a)
LATEDWD (m <sup>3</sup> .ha <sup>-1</sup> )	10.7 ± 21.2 (ab)	29.72v43.1 (a)	4.05 ± 9.2 (b)	15.69 ± 19.8 (ab)

Note: Site type acronyms: CONTROL, control (old-growth forest); GREETREE, green-tree retention stand; LINEARCUT, linear cutblock separator; POSTFIRE, post-fire remnant patch. Variable acronyms: AGE, stand age; CANCOV20, canopy cover measured 20 cm off the ground; CANCOV150, canopy cover measured 150 cm off the ground; EAR-LYDWD, volume of early decayed down woody debris; SNAGDENS, density of large snags; TREEDENS, density of large live trees. Values with same letters are not statistically different.



**Fig. A.3.1.** Median values and dispersion of all site covariates introduced in models, according to site types: CONTROL, control (old-growth forest); POSTFIRE, post-fire remnant patch; GREENTREE, green-tree retention patch which includes both linear cutblock separators (LINEARCUT) and green tree retention stands (GREENTREE). Variable acronyms: CANCOV20, canopy cover measured 20 cm off the ground; CANCOV150, canopy cover measured 150 cm off the ground; EARLYDWD, volume of early decayed down woody debris; LATEDWD, volume of late decayed down woody debris; SNACDENS, density of large snags; TREEDENS, density of large live trees.

were younger than control and post-fire remnant patches, and lacked some structural attributes found in old-growth stands.

GREENTREE sites were characterised by dense monospecific forests of smaller diameter and shorter black spruces than all other sites. GREENTREE sites also had few large trees (dbh > 10 cm), low volumes of LATEDWD, and small snags, mainly of early decay classes. LINEARCUT sites were characterised by the largest live trees and snags belonging to both coniferous and deciduous trees. Overstory cover were the greatest (no canopy openings) unlike understory covers which were reduced and not as rich in ericaceous shrubs as other site types. POSTFIRE sites were composed of old-growth forests as were CONTROL sites, which presented canopy openings (as shown by a smaller basal area and less important overstory covers) as well as species-rich understory. Large live trees and snags could be encountered although their density was lower than the density of large live trees and large snags found in either LINEARCUT or POSTFIRE.

Finally, HARVEST sites were similar to CONTROL and POSTFIRE sites across all habitat variables (Fig. A.3.1).

#### Appendix B

List of 67 dynamic occupancy models used to assess site occupancy ( $\psi$ ) of small mammals in black spruce forests as well as site colonisation ( $\gamma$ ) and local extinction ( $\epsilon$ ).

Candidate models	Occupancy	Colonisation	Local Extinction	Detection	К
M0	ψ(.)	$\gamma(.)$	ε(.)	<i>p</i> (.)	4
M1	$\psi(.)$	γ(.)	ε(.)	$p(R_{AIN} + T_{EMP} + M_{OON})$	7
M2	$\psi(.)$	γ(.)	ε(.)	p(Session + Method)	7
M3	$\psi(.)$	γ(.)	ε(.)	p(Arthro + Mollusc)	6
Occupancy models	with weather variables on	the detection parameter			
M4	$\psi(T_{YPE})$	γ(.)	ε(.)	p(Rain + Temp + Moon)	9
M5	$\psi$ (EarlyDwd + LateDwd)	γ(.)	ε(.)	p(RAIN + TEMP + MOON)	9
M6	$\psi$ (LateDwd : CanCov)	γ(.)	ε(.)	p(RAIN + TEMP + MOON)	10
M7	$\psi(\text{Decid})$	γ(.)	ε(.)	p(RAIN + TEMP + MOON)	10
M8	$\psi$ (CanCov)	γ(.)	ε(.)	p(RAIN + TEMP + MOON)	8
M9	$\psi$ (CanCov <sup>2</sup> )	γ(.)	ε(.)	p(Rain + Temp + Moon)	8
M10	$\psi$ (TreeDens + SnagDens)	$\gamma(.)$	ε(.)	$p(R_{AIN} + T_{EMP} + M_{OON})$	9
Occupancy models	with trapping variables on	the detection parameter			
M11	$\Psi(T_{YPE})$	γ(.)	ε(.)	p(Session + Method)	9
M12	$\Psi(\text{EarlyDwd} + \text{LateDwd})$	$\gamma(.)$	ε(.)	p(Session + Method)	9
M13	$\Psi$ (LATEDWD : CANCOV)	$\gamma(.)$	ε(.)	p(Session + Method)	10
M14	$\Psi(\text{Decid})$	$\gamma(.)$	ε(.)	p(Session + Method)	10
M15	$\Psi(CANCOV)$	$\gamma(.)$	ε(.)	p(Session + Method)	8
M16	$\sqrt{(CanCov^2)}$	$\gamma(.)$	s(.)	p(Session + Method)	8
M17	$\sqrt{(\text{TreeDens} + \text{SnacDens})}$	$\gamma(.)$	ε(.)	p(Session + Method)	9
Occupancy models	with invertebrates variable	es on the detection param	eter	p(obsider married)	U
M18	W(Type)	γ(.)	s(.)	p(ARTHRO + MOLLUSC)	8
M19	$\sqrt{(EarryDwd + LateDwd)}$	$\gamma(.)$	ε(.)	p(ARTHRO + MOLLISC)	8
M20	$\psi(\text{LATEDWD} : \text{CANCOV})$	$\gamma(.)$	ε(.)	p(ARTHRO + MOLLISC)	9
M20 M21	$\psi(\mathbf{D}_{\text{FCID}})$	$\gamma(\cdot)$	ε( )	p(ARTHRO + MOLLOSC)	9
M22	$\psi(CANCOV)$	$\gamma(\cdot)$	ε( )	n(Arthro + Mollisc)	7
M23	$\psi(CanCov^2)$	$\gamma(\cdot)$	ε( )	p(ARTHRO + MOLLOSC)	, 7
M23	$\psi(\text{CREEDENS} + \text{SNACDENS})$	$\gamma(\cdot)$	ε( )	n(Arthro + Mollisc)	8
Colonisation models	$\varphi(\text{IREEDENS} + \text{Similables})$	n the detection narameter		p(rikiliko · Mollosc)	0
M25	y()	v(Type)	F( )	$p(R_{AIN} + T_{EMP} + M_{OON})$	9
M26	$\psi(.)$	$\gamma(FARLYDWD + LATEDWD)$	ε( )	$p(R_{AIN} + T_{EMP} + M_{OON})$	9
M23	$\psi(.)$	$\gamma(\text{LATEDWD} \cdot \text{CANCOV})$	ε( )	$p(R_{AIN} + T_{EMP} + M_{OON})$	10
M28	$\psi(\cdot)$	$\gamma(\mathbf{D}_{\text{FCID}})$	$\varepsilon(.)$	$p(R_{AIN} + T_{EMR} + M_{OON})$	10
M20 M29	$\psi(\cdot)$	$\gamma(C_{AN}C_{OV})$	$\varepsilon(.)$	$p(R_{AIN} + T_{EMR} + M_{OON})$	8
M20	$\Psi(\cdot)$	$\gamma(CANCOV)^2$	c(.)	p(RAIN + TEMP + MOON)	8
M31	$\Psi(\cdot)$	$\gamma$ (TreeDens + SnacDens)	c(.)	p(RAIN + TEMP + MOON)	Q
Colonisation models	$\Psi(\cdot)$ with tranning variables of	r the detection narameter	r (.)	$p(\mathbf{RAIN} + \mathbf{IEMP} + \mathbf{MOON})$	5
M32	y(1)	$\gamma(T_{VDE})$	c( )	n(Session + METHOD)	Q
M33	$\Psi(\cdot)$	$\gamma(TTP)$ $\gamma(FARLYDIARD + LATEDIARD)$	c(.)	p(Session + Method)	g
M34	$\Psi(.)$	$\gamma(LAREDWD + LATEDWD)$ $\gamma(LATEDWD + CANCOV)$	c(.)	p(Session + Method)	10
M25	$\Psi(.)$	$\gamma(\text{Drop})$	c(.)	p(Session + Method)	10
M36	$\Psi(\cdot)$	$\gamma(DECID)$	c(.)	p(Session + Method)	20 Q
M27	$\Psi(\cdot)$	$\gamma(CANCOV)$	c(.)	p(SESSION + IVIETHOD)	0
1010/ M20	$\Psi(\cdot)$	Y(CANCOV)	ε(.) ε(.)	p(SESSION + IVIETHOD)	0
δςινι	Ψ(.)	$\gamma$ (TREEDENS + SNAGDENS)	દ(.)	p(SESSION + IMETHOD)	9

(continued on next page)

#### Appendix B (continued)

Candidate models	Occupancy	Colonisation	Local Extinction	Detection	К			
Colonisation models with invertebrate variables on the detection parameter								
M39	ψ(.)	γ(Type)	ε(.)	p(Arthro + Mollusc)	8			
M40	ψ(.)	$\gamma$ (EarlyDwd + LateDwd)	ε(.)	p(Arthro + Mollusc)	8			
M41	ψ(.)	$\gamma$ (LateDwd : CanCov)	ε(.)	p(Arthro + Mollusc)	9			
M42	ψ(.)	$\gamma(D_{ECID})$	ε(.)	p(Arthro + Mollusc)	9			
M43	ψ(.)	γ(CanCov)	ε(.)	p(Arthro + Mollusc)	7			
M44	ψ(.)	$\gamma$ (CanCov <sup>2</sup> )	ε(.)	p(Arthro + Mollusc)	7			
M45	ψ(.)	$\gamma$ (TreeDens + SnagDens)	ε(.)	p(Arthro + Mollusc)	8			
Extinction models	with weather variables on	the detection parameter						
M46	ψ(.)	γ(.)	ε(Type)	p(RAIN + TEMP + MOON)	9			
M47	ψ(.)	γ(.)	$\varepsilon$ (EarlyDwd + LateDwd)	p(RAIN + TEMP + MOON)	9			
M48	ψ(.)	γ(.)	ε(LateDwd : CanCov)	p(RAIN + TEMP + MOON)	10			
M49	ψ(.)	γ(.)	$\epsilon(D_{ECID})$	p(RAIN + TEMP + MOON)	10			
M50	ψ(.)	γ(.)	ε(CanCov)	p(RAIN + TEMP + MOON)	8			
M51	ψ(.)	γ(.)	ε(CanCov <sup>2</sup> )	p(RAIN + TEMP + MOON)	8			
M52	ψ(.)	γ(.)	$\epsilon$ (TreeDens + SnagDens)	p(RAIN + TEMP + MOON)	9			
Extinction models	with trapping variables on	the detection parameter						
M53	ψ(.)	γ(.)	ε(Type)	p(Session + Method)	9			
M54	ψ(.)	γ(.)	$\varepsilon$ (EarlyDwd + LateDwd)	p(Session + Method)	9			
M55	ψ(.)	γ(.)	ε(LateDwd : CanCov)	p(Session + Method)	10			
M56	ψ(.)	γ(.)	$\epsilon(\text{Decid})$	p(Session + Method)	10			
M57	ψ(.)	γ(.)	ε(CanCov)	p(Session + MethodSession + Method)	8			
M58	ψ(.)	γ(.)	ε(CanCov <sup>2</sup> )	p(Session + Method)	8			
M59	ψ(.)	γ(.)	ε(TreeDens + SnagDens)	p(Session + Method)	9			
Extinction models	with invertebrate variable:	s on the detection parame	ter					
M60	ψ(.)	γ(.)	ε(Type)	p(Arthro + Mollusc)	8			
M61	ψ(.)	γ(.)	$\varepsilon$ (EarlyDwd + LateDwd)	p(Arthro + Mollusc)	8			
M62	ψ(.)	γ(.)	ε(LateDwd : CanCov)	p(Arthro + Mollusc)	9			
M63	ψ(.)	γ(.)	$\epsilon(\text{Decid})$	p(Arthro + Mollusc)	9			
M64	ψ(.)	γ(.)	ε(CanCov)	p(Arthro + Mollusc)	7			
M65	ψ(.)	γ(.)	$\varepsilon$ (CanCov <sup>2</sup> )	p(Arthro + Mollusc)	7			
M66	ψ(.)	γ(.)	ε(TreeDens + SnagDens)	p(Arthro + Mollusc)	8			

**Note1:** Covariate acronyms: ARTHRO, weight of ground-dwelling arthropods; CANCov, canopy cover taken either 150 cm off the ground to analyse squirrel data or 20 cm off the ground to analyse data from all other species (linear form); CANCov<sup>2</sup>, canopy cover (quadratic form); DECID, presence of deciduous trees; EARLYDWD, early decayed downed woody debris; LATEDWD, late decayed downed woody debris; METHOD\*, methods used to detect individuals (live-trapping, live-trapping + playback count, live-trapping + point count, live-trapping + point count + playback count); MOLLUSC, weight of terrestrial molluscs; MOON\*\*, percentage of moon illuminated during each trapping night; RAIN, rainfall measured after each trapping night; SESSION, trapping session (August 2013, July 2014, August 2014); SNACDENS, density of snags with a dbh larger than 10 cm; TEMP, average night temperatures for each trapping night; TREEDENS, density of live trees with a dbh larger than 10 cm; TYPE, site type (control, post-fire remnant patch, green-tree retention patch). Parameters followed by (.) indicate that they are constant.

**Note2:** \* Different methods were only used to detect squirrels; \*\* Moon illumination was not used to analyse squirrel data.

#### Appendix C

#### C.1. Appendix

Number of individuals caught, by species, by trap type and by trapping session. Trapping session 1 corresponds to August 2013, trapping session 3 to July 2014 and trapping session 4 to August 2014.

Mammalian species	August 2013 (Session 1)			July 2014 (Session 3)			August 2014 (Session 4)		
	Sherman	Tomahawk	Pitfall	Sherman	Tamahawk	Pitfall	Sherman	Tomahawk	Pitfall
Glaucomys sabrinus	1	0	0	0	0	0	6	10	0
Tamiasciurus hudsonicus	0	3	0	0	24	0	2	36	0
Myodes gapperi	16	0	0	54	0	0	72	0	0
Microtus pennsylvanicus	0	0	0	0	0	0	1	0	0

#### Appendix C (continued)

Mammalian species	August 2013 (Session 1)			July 2014	July 2014 (Session 3)			August 2014 (Session 4)		
	Sherman	Tomahawk	Pitfall	Sherman	Tamahawk	Pitfall	Sherman	Tomahawk	Pitfall	
Peromyscus maniculatus	5	0	0	10	0	0	11	0	0	
Phenacomys ungava	0	0	0	8	0	1	4	0	0	
Blarina brevicauda	2	0	1	0	0	0	0	0	0	
Sorex cinereus	0	0	101	5	0	82	12	0	151	
Sorex hoyi	0	0	13	1	0	6	0	0	7	
Sorex arcticus	0	0	1	0	0	3	0	0	4	
Sorex fumeus	0	0	0	0	0	0	0	0	1	

#### C.2. Appendix

Number of sites reported with at least one detection, regardless of the small mammal species, given by site type and trapping session. Trapping session 1 corresponds to August 2013, trapping session 3 to July 2014 and trapping session 4 to August 2014.

Site type (/no of sites sampled)	Trapping session 1	Trapping session 2	Trapping session 3
CONTROL (/15)	3	10	10
POSTFIRE (/15)	7	9	11
GREENTREE (/15)	3	8	9
LINEARCUT (/15)	5	8	12
TOTAL (/60)	18	35	42

**Note:** Site type acronyms: CONTROL, control (old-growth forest); GREENTREE, green-tree retention patch; LINEARCUT, linear cutblock separator; POSTFIRE, post-fire remnant patch.

#### References

- Adobe Systems, 2002. Adobe Photoshop Elements 2.0. Adobe Systems Incorporated, San Jose, United States of America.
- Andreassen, H.P., Ims, R.A., 2001. Dispersal in patchy vole populations: role of patch configuration, density dependence, and demography. Ecology 82, 2911–2926.
- Baunerfeind, S.S., Theisen, A., Fischer, K., 2009. Patch occupancy in the endangered butterfly Lycaena helle in a fragmented landscape: effects of habitat quality, patch size and isolation. J. Insect. Conserv. 13, 271–277.
- Bellocq, I., Smith, S.M., 1994. Arthropods preferred as food by Sorex cinereus (masked shrew) and Peromyscus maniculatus (deer mouse): an experimental approach. Mammalia 58, 391–396.
- Bergeron, Y., Leduc, A., Harvey, B.H., Gauthier, S., 2002. Natural fire regime: a guide for sustainable management of the Canadian boreal forest. Silva Fenn. 36, 81–95.
- Bergeron, Y., Gauthier, S., Flannigan, M., Kafka, V., 2004. Fire regimes at the transition between mixedwood and coniferous boreal forest in northwestern Québec. Ecology 85, 1916–1932.
  Bergeron, Y., Drapeau, P., Gauthier, S., Lecomte, N., 2007. Using knowledge of
- Bergeron, Y., Drapeau, P., Gauthier, S., Lecomte, N., 2007. Using knowledge of natural disturbances to support sustainable forest management in the northern Clay Belt. Forest. Chron. 83, 326–337.
- Bissonnette, J., Lavoie, S., 2015. Utilisation du territoire\_ Méthodologie et description de la couche d'information géographique. Version 1.2. Gouvernement du Québec, Ministère du Développement durable, de l'Environnement et de la Lutte contre les changements climatiques (MDDELCC).
- Blouin, J., Berger, J.P., 2002. Guide de reconnaissance des types écologiques-Région écologique 5a Plaines de l'Abtibi. Ministère des Ressources Naturelles et de la Faune, Direction des Inventaires Forestiers, Division de la classification écologique et productivité des stations, Québec (Canada). Rep. no 2002–3072.
- Bondrup-Nielsen, S., Karlsson, F., 1985. Movements and spatial patterns on populations of *Clethrionomys* species: a review. Ann. Zool. Fennici. 22, 385–392. Boonstra, R., Krebs, C.J., 2012. Population dynamics of red-backed voles (*Myodes*) in
- North America. Oecologia 168, 601–620. Boutin, S., Hebert, D., 2002. Landscape ecology and forest management: developing
- an effective partnership. Ecol. Appl. 12, 390–397.
- Bowman, J., Jaeger, J.A.G., Fahrig, L., 2002. Dispersal distance of mammals is proportional to home range size. Ecology 83, 2049–2055.
- Brotons, L., Mönkkönen, M., Huhta, E., Nikula, A., Rajasärkkä, A., 2003. Effects of landscape structure and forest reserve location on old-growth forest bird species in Northern Finland. Landsc. Ecol. 18, 377–393.
- Burnham, K.P., Anderson, D.R., 2002. Model Selection and Multimodel Inference: a Practical Information-Theoretic Approach. Springer-Verlag, New York, USA.

Carey, A.B., 1995. Sciurids in Pacific Northwest managed and old-growth forests. Ecol. Appl. 5, 648–661.

- Cheveau, M., Drapeau, P., Imbeau, L., Bergeron, Y., 2004. Owl winter irruptions as an indicator of small mammal population cycles in the boreal forest of eastern North America. Oikos 107, 190–198.
- Chavel, E.E., Mazerolle, M.J., Imbeau, L., Drapeau, P., 2017. Comparative evaluation of three sampling methods to estimate detection probability of American red squirrels (*Tamiasciurus hudsonicus*). Mamm. Biol. 83, 1–9.
- Cherry, R.H., Verner, L., 1975. Seasonal acclimatization to temperature in the Prairie vole, Microtus ochrogaster. Am. Midl. Nat. 94, 354–360.
- Clarke, J.A., 1983. Moonlight's influence on predator/prey interactions between short-eared owls (Asio flammeus) and deermice (Peromyscus maniculatus). Behav. Ecol. Sociobiol. 13, 205–209.
- Craig, V.J., Klenner, W., Feller, M.C., Sullivan, T.P., 2014. Population dynamics of redbacked voles (*Myodes gapperi*) and their relationship to downed wood in management forests of Southern British Columbia. Can. Wildl. Biol. Manage. 3, 93–108.
- Crête, M., Drolet, B., Huot, J., Fortin, M.J., Doucet, G.J., 1995. Chronoséquence après feu de la diversité de mammifères et d'oiseaux au nord de la forêt boréale québécoise. Can. J. For. Res. 25, 1509–1518.
- Crites, S., Dale, M.R., 1998. Diversity and abundance of bryophytes, lichens, and fungi in relation to woody substrate and successional stage in aspen mixedwood boreal forests. Can. J. Bot. 76, 641–651.
- Currah, R.S., Smreciu, E.A., Lehesvirta, T., Niemi, M., Larsen, K.W., 2000. Fungi in the winter diets of northern flying squirrels and red squirrels in the boreal mixedwood forest of Northeastern Alberta. Can. J. Bot. 78, 1514–1520.
- Cyr, D., Gauthier, S., Bergeron, Y., Carcaillet, C., 2009. Forest management is driving the eastern North American boreal forest outside its natural range of variability. Front. Ecol. Environ. 7, 519–524.
- Czech, B., Krausman, P.R., 1997. Distribution and causation of species endangerment in the United States. Science 277, 1116–1117.
- Darveau, M., Desrochers, A., 2001. Le bois mort et la faune vertébrée État des connaissances au Québec. Québec, Ministère des Ressources naturelles, Direction de l'environnement forestier (DEF 0199).
- Davis, S.K., 2004. Area sensitivity in grassland passerines: effects of patch size, patch shape, and vegetation structure on bird abundance and occurrence in southern Saskatchewan. Auk 121, 1130–1145.
- Déry, S., Leblanc, M., 2005. Lignes directrices pour l'utilisation des pratiques sylvicoles adaptées rattachées à l'objectif sur le maintien de forêts mûres et surannées, Québec, gouvernement du Québec, ministère des Ressources naturelles et de la Faune, Direction de l'environnement forestier.
- Desrochers, A., Renaud, C., Hochachka, W.M., Cadman, M., 2010. Area-sensitivity by forest songbirds: theoretical and practical implications of scale-dependency. Ecography 33, 921–931.
- Donovan, T.M., Lamberson, R.H., 2001. Area-sensitive distributions counteract negative effects of habitat fragmentation on breeding birds. Ecology 82, 1170– 1179.
- Drapeau, P., Villard, M.-A., Leduc, A., Hannon, S., 2016. Natural disturbance regimes as templates for the response of bird species assemblages to contemporary forest management. Divers. Distrib. 22, 385–399.
- Drapeau, P., Leduc, A., Giroux, J.-F., Savard, J.-P., Bergeron, Y., Vickery, W., 2000. Landscape-scale disturbances and changes in bird communities of boreal mixed-wood forests. Ecol. Monogr. 70, 423–444.

Drapeau, P., Leduc, A., Bergeron, Y., 2009. Bridging ecosystem and multiple species approaches for setting conservation targets in managed boreal landscapes. In: Villard, M.-A., Jonsson, B.-G. (Eds.), Setting Conservation Targets in Managed Forest Landscapes. Cambridge University Press, New York, USA, pp. 129–160.

- Dueser, R.D., Shugart, H.H., 1978. Microhabitats in a forest-floor small mammal fauna. Ecology 59, 89–98.
- Dupuis, L.A., Smith, J.N., Bunnell, F., 1995. Relation of terrestrial-breeding amphibian abundance to tree-stand age. Conserv. Biol. 9, 645–653.
- Environment Canada, 2015. Canadian climate normals 1981–2010 Station data http://climate.weather.gc.ca/climate\_normals/results\_1981\_2010\_e.html? stnID=6051&lang=e&StationName=Lebel+sur+Quevillon&SearchType= Contains&stnNameSubmit=go&dCode=5&dispBack=1. accessed 08.11.15.
- Fahrig, L., 2003. Effects of habitat fragmentation on biodiversity. Annu. Rev. Ecol. Evol. Syst. 34, 487–515.

Fahrig, L., 2013. Rethinking patch size and isolation effects: the habitat amount hypothesis. J. Biogeogr. 40, 1649-1663.

- Fauteux, D., Imbeau, L., Drapeau, P., Mazerolle, M.J., 2012. Small mammal response to coarse woody debris distribution at different spatial scales in managed and unmanaged boreal forests. Forest. Ecol. Manage. 266, 194-205.
- Fauteux, D., Lupien, G., Fabianek, F., Gagnon, J., Séguy, M., Imbeau, L., 2014. An illustrated key to the mandibles of small mammals of Eastern Canada. Can. Field. Nat. 128, 25-37.
- Fauteux, D., Cheveau, M., Imbeau, L., Drapeau, P., 2015. Cyclic dynamics of a boreal southern red-backed vole population in Northwestern Quebec. J. Mammal. 96, 573-578.
- Fenton, N.J., Bergeron, Y., 2006. Facilitative succession in a boreal bryophyte community driven by changes in available moisture and light. J. Veg. Sci. 17, 65 - 76
- Fisher, J.T., Wilkinson, L., 2005. The response of mammals to forest fire and timber harvest in the North American boreal forest. Mamm. Rev. 35, 51-81.
- Fiske, I., Chandler, R., 2011. Unmarked: an R package for the fitting hierarchical models of wildlife occurrence and abundance. J. Stat. Softw. 43, 1-23.
- Fraver, S., Wagner, R.G., Day, M., 2002. Dynamics of coarse woody debris following gap harvesting in the Acadian forest of central Maine, USA. Can. J. For. Res. 32, 2094-2105.
- Fred, M.S., Brommer, J.E., 2003. Influence of habitat quality and patch size on occupancy and persistence in two populations of the Apollo butterfly (Parnassius apollo). J. Insect. Conserv. 7, 85-98.
- Fretwell, S.D., Lucas Jr., H.L., 1969. On territorial behavior and other factors influencing habitat distribution in birds. I. Theoretical development. Acta. Biotheor. 19, 16-36.
- Fryxell, J.M., Falls, J.B., Falls, J.A., Brooks, R.J., 1998. Long-term dynamics of smallmammal populations in Ontario. Ecology 79, 213-225.
- Getz, L.L., 1961. Responses of small mammals to live-traps and weather conditions. Am. Midl. Nat. 66, 160–170.
- Guerry, A.D., Hunter Jr., M.L., 2002. Amphibian distributions in a landscape of forests and agriculture: an examination of landscape composition and configuration. Conserv. Biol. 16, 745-754.
- Harper, S.J., Bollinger, E.K., Barrett, G.W., 1993. Effects of habitat patch shape on population dynamics of meadow voles (Microtus pennsylvanicus). J. Mammal. 74. 1045-1055.
- Harvey, B.D., Brais, S., 2007. Partial cutting as an analogue to stem exclusion and dieback in trembling aspen (Populus tremuloides) dominated boreal mixedwoods: implications for deadwood dynamics. Can. J. Forest. Res. 37, 1525-1533.
- Hayward, G.D., Henry, S.H., Ruggiero, L.F., 1999. Response of red-backed voles to recent patch cutting in subalpine forest. Conserv. Biol. 13, 168-176.
- Henle, K., Davies, K.F., Klever, M., Margules, C., Settele, J., 2004. Predictors of species sensitivity to fragmentation. Biodiv. Conserv. 13, 207–251.
- Henttonen, H., Haukisalmi, V., Kaikusalo, A., Korpimäki, E., Norrdahl, K., Skarén, U.A. P., 1989. Long-term population dynamics of the common shrew *Sorex araneus* in Finland. Ann. Zool. Fenn. 26, 349-355.
- Holland, J.D., Bert, D.G., Fahrig, L., 2004. Determining the spatial scale of species' response to habitat. Bioscience 54, 227-233.
- Holloway, G.I., Smith, W.P., 2011. A meta-analysis of forest age and structure effects
- on northern flying squirrel densities. J. Wildlife. Manage. 75, 668–674. Hunter, M., 1993. Natural fire regimes as spatial models for managing boreal forests. Biol. Conserv. 65, 115-120.
- Imbeau, L., St-Laurent, M.H., Marzell, L., Brodeur, V., 2015. Current capacity to conduct ecologically sustainable forest management in Northeastern Canada reveals challenges for conservation of biodiversity. Can. J. For. Res. 45, 567-578.
- Innes, D.G.L., Bendell, J.F., Naylor, B.J., Smith, B.A., 1990. High densities of the masked shrew, Sorex cinereus, in jack pine plantation in Northern Ontario. Am. Midl. Nat. 124, 330–341. Jones, J.P.G., 2011. Monitoring species abundance and distribution at the landscape
- scale. J. Appl. Ecol. 48, 9–13.
- Kerr, J.T., Cihlar, J., 2004. Patterns and causes of species endangerment in Canada. Ecol. Appl. 14, 743–753.
- Knutson, M.G., Sauer, J.R., Olsen, D.A., Mossman, M.J., Hemesath, L.M., Lannoo, M.J. 1999. Effects of landscape composition and wetland fragmentation on frog and toad abundance and species richness in Iowa and Wisconsin, USA. Conserv. Biol. 13. 1437-1446.
- Korpimäki, E., Norrdahl, K., Huitu, O., Klemola, T., 2005. Predator-induced synchrony in population oscillations of coexisting small mammal species. Proc. R. Soc. Lond. [Biol] 272, 193-202.
- Krebs, C.J., 2013. Population Fluctuations in Rodents. The University of Chicago Press, Chicago, USA.
- Larsen, K.W., Boutin, S., 1994. Movements, survival, and settlement of red squirrel (Tamiasciurus hudsonicus) offspring. Ecology 75, 214-223.
- Lawler, J.J., Campbell, S.P., Guerry, A.D., Kolozsvary, M.B., O'Connor, R.J., Seward, L.C., 2002. The scope and treatment of threats in endangered species recovery plans. Ecol. Appl. 12, 663-667.
- Leblanc, M., and Pouliot, B., 2011. La coupe avec protection de la régénération et des sols avec rétention de bouquets - Fondements et exécution opérationnelle, Québec, gouvernement du Québec, ministère des Ressources naturelles et de la Faune
- Lee, M., Fahrig, L., Freemark, K., Currie, D.J., 2002. Importance of patch scale vs landscape scale on selected forest birds. Oikos 96, 110-118.
- Le Goff, H., Flannigan, M.D., Bergeron, Y., Leduc, A., Gauthier, S., Logan, K., 2008. Des solutions d'aménagement pour faire face aux changements climatiques,

l'exemple des feux de forêt. In: Gauthier, S., Vaillancourt, M.-A., Leduc, A., De Grandpré, L., Kneeshaw, D., Morin, H., Drapeau, P., Bergeron, Y. (Eds.), Aménagement écosystémique en forêt boréale. Presses de l'Université du Québec, Québec, Canada, pp. 109-135.

- Linehan, J., Gross, M., Finn, J., 1995. Greenway planning: developing a landscape ecological network approach. Landscape Urban. Plan. 33, 179-193.
- Lupien, G., 2001. Recueil photographique des caractéristiques morphologiques servant à l'identification des micromammifères du Québec: volume I insectivores. Société de la Faune et des Parcs du Québec, Jonquière.
- Lupien, G., 2002. Recueil photographique des caractéristiques morphologiques servant à l'identification des micromammifères du Québec: volume II rongeurs. Société de la Faune et des Parcs du Québec, Jonquière.
- MacKenzie, D.I., Nichols, J.D., Hines, J.E., Knutson, M.G., Franklin, A.B., 2003. Estimating site occupancy, colonization and local extinction when a species is detected imperfectly. Ecology 84, 2200-2207.
- MacKenzie, D.I., Bailey, L.L., 2004. Assessing the fit of site-occupancy models. J. Agric. Biol. Environ. Statist. 9, 300-318.
- Manning, J.A., Edge, W.D., 2004. Small mammal survival and downed wood at multiple scales in managed forests. J. Mammal. 85, 87-96.
- Mazerolle, M.J., 2015. AICcmodavg: Model selection and multimodel inference based on (Q)AIC(c). R package version 2.0-3.
- Mazerolle, M.J., Villard, M.-A., 1999. Patch characteristics and landscape context as predictors of species presence and abundance: a review. Écoscience 6, 117-124.
- McCay, T.S., Storm, G.L., 1997. Masked shrew (Sorex cinereus) abundance, diet and prey selection in an irrigated forest. Am. Midl. Nat. 138, 268-275.
- McGarigal, K., McComb, W.C., 1995. Relationships between landscape structure and breeding birds in the Oregon coast range. Ecol. Monogr. 65, 235-260.
- McLaren, M.A., Thompson, I.D., Baker, J.A., 1998. Selection of vertebrate wildlife indicators for monitoring sustainable forest management in Ontario. Forest. Chron. 74, 241–248.
- McManus, J.J., 1974. Bioenergetics and water requirements of the redback vole, Clethrionomys gapperi. J. Mammal. 55, 30-44.
- Merritt, J.F., 1981. Clethrionomys gapperi. Mammalian Species 146, 1–9.
- Mönkkönen, M., Rajasärkkä, A., Lampila, P., 2014. Isolation, patch size and matrix effects on bird assemblages in forest reserves. Biodivers. Conserv. 23, 3287-3300.
- Morissette, J.L., Cobb, T.P., Brigham, R.M., James, P.C., 2002. The response of boreal forest songbird communities to fire and post-fire harvesting. Can. J. For. Res. 32, 2169-2183
- Moseley, K.R., Owens, A.K., Castleberry, S.B., Ford, M.W., Kilgo, J.C., McCay, T.S., 2008. Soricid response to coarse woody debris manipulations in coastal plain loblolly pine forests. Forest Ecol. Manage. 255, 2306–2311.
- Nappi, A., Drapeau, P., Angers, V.-A., Saint-Germain, M., 2010. Effect of fire severity on long-term occupancy of burned boreal conifer forests by saproxylic insects and wood-foraging birds. Int. J. Wildl. Fire 19, 500-511.
- Nelson Jr., L., Clark, F.W., 1973. Correction for sprung traps in catch/effort calculations of trapping results. J. Mammal. 54, 295-298.
- Niemelä, J., 1999. Management in relation to disturbance in the boreal forest. Forest Ecol. Manage. 115, 127-134.
- Nagorsen, D.W., 1996. Opossums, Shrews and Moles of British Columbia. The Mammals of British Columbia, Vol. 2. UBC Press, Vancouver, B.C., Canada, Öckinger, E., Schweiger, O., Crist, T.O., Debinski, D.M., Krauss, J., Kuussaari, M.,
- Petersen, J.D., Pöyry, J., Settele, J., Summerville, K.S., Bommarco, R., 2010. Lifehistory traits predict species responses to habitat area and isolation: a crosscontinental synthesis. Ecol. Lett. 13, 969-979.
- Orrock, J.L., Pagel, J.F., 2002. Fungus consumption by the southern red-backed vole (Clethrionomys gapperi) in the Southern Appalachians. Am. Midi. Nat. 147, 413-418
- Orrock, J.L., Danielson, B.J., Brinkerhoff, J.R., 2004. Rodent foraging is affected by indirect, but not by direct, cues of predation risk. Behav. Ecol. 15, 433-437.
- Payette, S., 1992. Fire as a controlling process in the North American boreal forest. In: Shugart, H.H., Leemans, R., Bonan, G.B. (Eds.), A System Analysis of the Global Terrestrial Boreal Forest. Cambridge University Press, New York, USA, pp. 144-169.
- Pearce, J., Venier, L., 2005. Small mammals as bioindicators of sustainable boreal forest management. For. Ecol. Manage. 208, 153-175.
- Pickett, S.T.A., Cadenasso, M.L., 1995. Landscape ecology: spatial heterogeneity in ecological systems. Science 269, 331–334.
- Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D., Heisterkamp, S., Van Willigen, B., 2014. nlme: linear and nonlinear mixed effects models. R package version 3.1-117.
- Pough, F.H., Smith, E.M., Rhodes, D.H., Collazo, A., 1987. The abundance of salamanders in forest stands with different histories of disturbance. Forest Ecol. Manage. 20, 1-9.
- Pretzlaw, T., Trudeau, C., Humphries, M.M., LaMontagne, J.M., Boutin, S., 2006. Red squirrels (Tamiasciurus hudsonicus) feeding on spruce bark beetles (Dendroctonus rufipennis): energetic and ecological implications. J. Mammal. 87.909-914.
- Pyare, S., Longland, W.S., 2001. Patterns of ectomycorrhizal-fungi consumption by small mammals in remnant old-growth forests of the Sierra Nevada. J. Mammal. 82 681-689
- R Development Core Team, 2015. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.
- Ritchie, L.E., Betts, M.G., Forbes, G., Vernes, K., 2009. Effects of landscape composition and configuration on northern flying squirrels in a forest mosaic. Forest Ecol. Manag. 257, 1920-1929.

- Robbins, C.S., 1979. Effect of forest fragmentation on bird populations. In: DeGraaf, R.M., Evans, R.E. (Eds.), Management of North Central and Northeastern Forests for Nongame Birds Proceedings of the Workshop, General Technical Report NC-51. U.S. Forest Service, Minneapolis, USA, pp. 198–212.
- Robinson, N.M., Leonard, S.W.J., Ritchie, E.G., Bassett, M., Chia, E.K., Buckingham, S., Gibb, H., Bennett, A.F., Clarke, M.F., 2013. Refuges for fauna in fire-prone landscapes: their ecological function and importance. J. Appl. Ecol. 50, 1321– 1329.
- Schmiegelow, F.K.A., Mönkkönen, M., 2002. Habitat loss and fragmentation in dynamic landscapes: avian perspectives from the boreal forest. Ecol. Appl. 12, 375–389.
- Schweiger, E.W., Diffendorfer, J.E., Pierotti, R., Holt, R.D., 1999. The relative importance of small-scale and landscape-level heterogeneity in structuring small mammal distributions. In: Barret, G.W., Peles, J.D. (Eds.), Landscape Ecology of Small Mammals. Springer, New York, New York, USA, pp. 175–207.
- Smith, W.P., 2012a. Sentinels of ecological processes: the case of the northern flying squirrel. Bioscience 62, 950–961.
- Smith, W.P., 2012b. Flying squirrel demography varies between island communities with and without red squirrels. Northwest Sci. 86, 27–38.
- Smith, A.C., Fahrig, L., Francis, C.M., 2011. Landscape size affects the relative importance of habitat amount, habitat fragmentation, and matrix quality on forest birds. Ecography 34, 103–113.
- Steele, M.A., 1998. Tamiasciurus hudsonicus. Mamm. Species 586, 1-9.
- Sullivan, T.P., Sullivan, D.S., 2012. Woody debris, voles, and trees: influence of habitat structures (piles and windrows) on long-tailed vole populations and feeding damage. Forest Ecol. Manage. 263, 189–198.
- Tallmon, D.A., Mills, S., 2004. Edge effects and isolation: red-backed voles revisited. Conserv. Biol. 18, 1658–1664.

- Trzcinski, M.K., Fahrig, L., Merriam, G., 1999. Independent effects of forest cover and fragmentation on the distribution of forest breeding birds. Ecol. Appl. 9, 586– 593.
- Vanderwel, M.C., Malcolm, J.R., Caspersen, J.P., Newman, M.A., 2010. Fine-scale habitat associations of red-backed voles in boreal mixedwood stands. J. Wildl. Manage. 74, 1492–1501.
- van Horne, B., 1983. Density as a misleading indicator of habitat quality. J. Wildl. Manage. 47, 893–901.
- Vickery, W.L., Bider, J.R., 1981. The influence of weather on rodent activity. J. Mammal. 62, 140–145.
- Villard, M.-A., Trzcinski, M.K., Merriam, G., 1999. Fragmentation effects on forest birds: relative influence of woodland cover and con- figuration on landscape occupancy. Conserv. Biol. 13, 774–783.
- Walk, J.W., Warner, R.E., 1999. Effects of habitat area on the occurrence of grassland birds in Illinois. Am. Midl. Nat. 141, 339–344.
- Wauters, L., Dhondt, A.A., 1993. Immigration pattern and success in red squirrels. Behav. Ecol. Sociobiol. 33, 159–167.
- Whitaker Jr., J.O., 2004. Sorex cinereus. Mamm. Species 743, 1-9.
- Whitaker Jr., J.O., French, T.W., 1984. Foods of six species of sympatric shrews from New Brunswick. Can. J. Zool. 62, 622–626.
- Wiens, J.A., 2009. Landscape ecology as a foundation for sustainable conservation. Landsc. Ecol. 24, 1053–1065.
- Zub, K., Jedrzejewska, B., Jedrzejewski, W., Bartón, K.A., 2012. Cyclic voles and shrews and non-cyclic mice in a marginal grassland within European temperate forest. Acta Theriol. 57, 205–216.
- Zwolak, R., 2009. A meta-analysis of the effects of wildfire, clearcutting, and partial harvest on the abundance of North American small mammals. Forest Ecol. Manage. 258, 539–545.