Forest Ecology and Management 400 (2017) 485–501

Contents lists available at ScienceDirect

Forest Ecology and Management

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

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

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ARTICLE INFO

Article history:
Received 1 March 2017
Received in revised form 13 May 2017
Accepted 5 June 2017
Available online 26 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 single-species 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 between-years 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.

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

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http://dx.doi.org/10.1016/j.foreco.2017.06.008
0378-1127/

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 area-sensitivity 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 provide 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. post-harvest), 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^2 of black spruce-feather 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^2 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 (LINEARCUT – 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