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# Temporal changes in habitat use by snowshoe hares and red squirrels during post-fire and post-logging forest succession

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ABSTRACT

Ecosystem-based management has taken a central role in the conservation of animal populations in managed landscapes. A fundamental assumption of ecosystem-based management by the emulation of natural disturbances is that logging practices would protect biodiversity by maintaining key ecosystem properties. The hypothesis, however, needs to be tested on a broad range of organisms. We assessed the relative influence of natural and anthropogenic disturbances on habitat use by snowshoe hare (*Lepus americanus*) and red squirrel (*Tamiasciurus hudsonicus*). We compared the intensity of habitat use by the two species along a chronosequence of succession after fire (20–200 years) and clear-cutting (20–80 years) in boreal landscapes dominated by old-growth forest stands. We also characterised temporal changes in vegetation along both chronosequences. We found that snowshoe hare preferentially uses cutting-origin stands and that the peak of habitat use by red squirrels occurs about 20 years earlier after cutting than after fire. Higher tree density and earlier balsam fir (*Abies balsamea*) regeneration after clear-cutting than after fire partly explained these differences in animal response to the type of disturbance. As a result, forest fires cannot be simply reproduced by clear-cutting, and ecosystem-based management should take these differences into account whenever the management objective is to alleviate the long-term impact of forestry on forest ecosystems.



## 1. Introduction

Human disturbances can cause large changes in the structure and functioning of forest ecosystems. Ecosystem-based management has subsequently emerged as a promising avenue for alleviating human impacts on ecosystem properties by preserving some key forest attributes at the stand- and landscape-levels (Gauthier et al., 2009). Ecosystem-based management strategies generally involve harvesting techniques that attempt to emulate natural disturbances (Bergeron and Harvey, 1997), because the forest biota should be adapted to the periodic occurrence of these disturbances.

Fire is a dominant natural disturbance agent in the boreal forest that creates mosaics of stands, which vary in composition, structure and age. Some effects of forest fires are generally emulated by clear-cutting because the latter disturbance produces a similar degree of overstorey removal over wide areas (Hart and Chen, 2006). Yet, short-term differences are apparent between fire and clear-cutting. For example, clear-cutting tends to preserve a thicker humus layer (Rees and Juday, 2002) and a large part of the understorey vegetation (Ruel and Huot, 1993), whereas stand-replacing fires frequently destroy advance regeneration and the tree seedbank, which is present in the upper organic layer (Johnson and Fryer, 1996).

Differences in vegetational composition and development between post-fire and post-logging stands (Bouchard and Pothier, 2011; Franklin et al., 2002) may create differences in the availability of food and shelter for some animal species, thereby affecting local wildlife communities (e.g., Buddle et al., 2006; Schieck and Song, 2006). Small mammals are considered to be valuable bioindicators of sustainable boreal forest management (e.g., Koprowski, 2005; Pearce and Venier, 2005). Thus, our study focuses on the effects that post-disturbance vegetation may impose on populations of snowshoe hare (*Lepus americanus* Erxleben) and red squirrel (*Tamiasciurus hudsonicus* L.), two species that are typical of the boreal forest and which are known to be strongly affected by

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clear-cutting (e.g., Ferron et al., 1998; Holloway and Malcolm, 2006). They are also key prey species influencing the abundance and distribution of many predators, including lynx (*Lynx canadensis* Kerr), marten (*Martes americana* Turton), and predatory birds (Boutin et al., 1995; Krebs, 2011; Sherburne, 1993; Thompson and Colgan, 1987; Thompson et al., 1989). Recommendations for habitat management of red squirrels and snowshoe hares, therefore, should have concurrent implications for the management of forest predators (e.g., Carey, 1995).

Patterns of abundance and distribution of snowshoe hares are positively correlated with the abundance of the understorey vegetation (e.g., Hodges et al., 2009; Litvaitis et al., 1985; Wirsing et al., 2002). For hares, shrubs and saplings provide food and lateral protective cover, two vegetation attributes that are found primarily in early to mid-successional stands (e.g., Hodson et al., 2011; Newbury and Simon, 2005). Accordingly, snowshoe hare populations generally peak in 15- to 30-year-old regenerating stands (Fisher and Wilkinson, 2005; Hodges, 2000; Newbury and Simon, 2005; Sullivan et al., 2012). Red squirrels are mainly conifer seed specialists (Yahner, 2003), and their abundance increases with increasing density of large conifer trees, and increased cone and conifer seed production (Fisher and Bradbury, 2006; Holloway and Malcolm, 2006; Russell et al., 2010; Wheatley et al., 2002). Both of these habitat components are abundant in mature forests, with the consequence that red squirrels tend to be more numerous in old-growth forests than in early seral stands (Roy et al., 1995; Thompson et al., 1989).

To date, most of our knowledge regarding long-term changes (>60 years) in hare and red squirrel abundances during forest succession is derived from post-harvest stands (e.g., Newbury and Simon, 2005; Thompson and Curran, 1995). The effects of fire on these two species have been mostly investigated along short forest successional gradients (but see Crête et al., 1995; Hodson et al., 2011; Roy et al., 1995). Consequently, very few studies have compared the abundance of each species over decadal-scales (up to 80 years) of post-fire and post-logging succession (Fisher and Wilkinson, 2005; Hodson et al., 2011). Collection of information over long gradients of forest succession is essential, however, to gain a greater overall understanding of long-term disturbance effects. Hodson et al. (2011) used chronosequences to simultaneously compare changes in hare abundance during the first 80 years of post-fire and post-logging successions in boreal forest, but to our knowledge, such long-term comparisons are lacking for red squirrel. Their study showed that variations in annual hare abundances were similar after logging and fire during this period, suggesting that fire and clear-cutting create comparable habitat conditions for hares. However, hare mortality tends to be highest in winter, mainly due to predation (Murray, 2003; Trostel et al., 1987). During this season, hares have limited access to food and cover, which strongly influences their survival (Litvaitis et al., 1985). Because logging activities affect both of these resources, the response of hare to disturbance during winter (instead of the entire year) should clearly reveal the role of factors limiting the distribution and abundance of the species. We thus estimated patterns of hare distribution along chronosequences using browsing intensity on hardwood saplings (following Hodson et al., 2012). Hares consume woody browse mainly in winter and, therefore, browse surveys can inform on spatial patterns in the intensity of winter habitat use (Pease et al., 1979). Hares can use both coniferous and deciduous species as browse and cover. In winter, however, deciduous species are preferred as browse, whereas coniferous species provide higher lateral cover (Litvaitis et al., 1985; Pease et al., 1979).

We studied red squirrel and snowshoe hare because the former is considered a late-seral stage species, whereas the latter is an early to mid-successional species (Fisher and Wilkinson, 2005; Hodson et al., 2011). Studying these two species should thus provide general insights regarding the effects of plant succession after fire and logging on wildlife habitats, and the similarity in their response to natural and anthropogenic disturbances should inform on the legitimacy of a fundamental assumption of ecosystem-based management.

Our objectives were: (1) to characterise successional changes in forest structure and composition after fire and clear-cutting in the boreal forest, (2) to determine whether, as expected, the intensity of habitat use by snowshoe hare and red squirrel peaks, respectively, during early to mid-successional and late-seral stages of forest succession, and (3) to identify differences in the intensity of habitat use by these two species between forest successions originating from fire and clear-cutting, in the black spruce boreal forest of northeastern Quebec, Canada.

## 2. Methods

### 2.1. Study area

The study area (Fig. 1) was located north of Baie Comeau (49°07′N, 68°10′W), Québec, Canada, in the black spruce–feather moss bioclimatic subdomain (Robitaille and Saucier, 1998). The climate is boreal humid according to the closest meteorological station (Baie Comeau). Mean annual temperature (1971–2000) is 1.5 °C, with 1014 mm of annual precipitation (Environment Canada 2011; available at http://www.climat.meteo.gc.ca/climate_normals/results_f.html). Thirty-five percent of annual precipitation falls as snow, and air temperature is above 6 °C for about 155 days per year.

Fire is the dominant, broad-scale natural disturbance in the region. The long fire cycle (270 years, Bouchard et al., 2008) has led

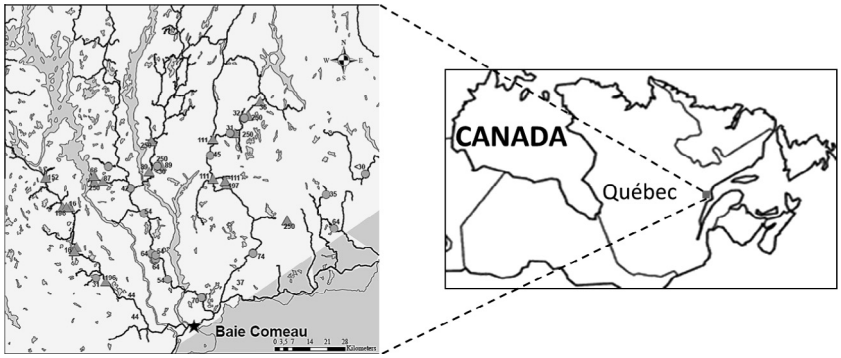


**Fig. 1.** Locations of the black spruce stands surveyed in the Côte-Nord region of eastern Québec, Canada. Triangles indicate fire-origin stands and circles, those of harvest-origin. Numbers are the ages of the stands.