

# Is metapopulation size important for the conservation of understory plants and epiphytic lichens?



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## ABSTRACT

For a given species, reducing the extent, connectivity and health status of source populations will diminish the probability of colonizing suitable habitats. In this study, we evaluated if metapopulation size helped predict species presence in suitable habitats, by using boreal understory plants and epiphytic lichens as case studies. We sampled a network of 792 vegetation plots located across a 240,000-km<sup>2</sup> section of pristine boreal forests. Landscape-level species abundance (LLSA), a proxy for metapopulation size, was quantified in a 50 km radius surrounding each plot. The effects of local environmental factors and LLSA on species presence were modelled with general linear models (GLMs). Forty-eight vascular plant species and 8 pendulous epiphytic lichens were abundant enough to be considered in the statistical analyses. Habitat variables explained the presence of 30 vascular plants and 4 lichen species to a relatively strong degree (Tjur's  $R^2 > 0.15$ ). Among these species, 16 vascular plants and 4 lichens were significantly influenced by LLSA, independently of local habitat characteristics. Vascular plant species whose presence was significantly affected by LLSA did not exhibit particular morphological traits or habitat preferences compared with those that were not affected. By contrast, the 4 epiphytic lichen species that were affected by LLSA were all associated with older forests. No species exhibited obvious metapopulation size thresholds below which the probability of species presence in suitable habitats dropped drastically. In terms of conservation, these results suggest that coarse-filter approaches are probably more robust and easy to implement than species-specific threshold approaches in this kind of ecosystem.

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## 1. Introduction

In boreal forests, the stochastic occurrence of large fires results in a shifting forest mosaic of stands of different ages and tree species compositions (Johnson et al., 1998). For the plant and animal species that are present in these ecosystems, this variable environment could favour the emergence of metapopulation dynamics (Hanski and Gilpin, 1997), particularly for those species that exhibit strong habitat preferences and a limited capability to persist in unsuitable habitats (Eriksson, 1996; Freckleton and Watkinson, 2002). When disturbance extent or severity increases, the landscape-level abundance of some habitats will decline, source populations of species associated with these habitats become more fragmented, and the probability that the species can successfully colonize or re-colonize suitable habitats is also expected to decline (Fahrig, 2002). Below a certain threshold of regional-level species abundance, the rate of colonization of new habitats might be insufficient to compensate for local extinctions, and the metapopulation may disappear (Fahrig, 2002; Swift and Hannon, 2010).

These concepts have generated a diversified but relatively theoretical body of work in population ecology. However, they are still relatively seldom tested empirically, particularly for plants (Marini et al., 2012). In boreal forests, understory plants and epiphytic lichens are representative taxa that could be used to examine these effects. Boreal understory plants possess various traits that enable some resilience to disturbances, mostly through robust and diversified regeneration mechanisms (dormancy, vegetative reproduction, fire tolerance, persistent seed banks, etc.) (Eriksson, 1996; Rowe, 1983). In general, these mechanisms can be assumed to allow persistence in unfavorable habitats, which explains why most of these species are thought to conform relatively poorly to classical metapopulation dynamics (Eriksson, 1996; Freckleton and Watkinson, 2002). Still, because some boreal species are strongly associated with particular forest age classes or dominant tree compositions (Aubin et al., 2014; De Grandpré et al., 2003; Rowe, 1983), metapopulation persistence could theoretically be affected by changes in landscape-level habitat abundance (Hanski, 2011).

Epiphytic lichens can be considered to be less resilient to habitat disturbance than understory plants, mostly because they are strictly associated with trees. Indeed, when trees are removed by natural or anthropogenic disturbances, epiphytic organisms cannot persist locally, and will need to recolonize from the surrounding matrix once the forest

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stand regenerates (Sillett and Goslin, 1999; Sillett et al., 2000; Snäll et al., 2003). Moreover, even if lichen spores can disperse across large distances, many epiphytic species colonize primarily through thallus fragments (Dettki et al., 2000; Esseen, 1985), which are presumed to disperse over shorter distances (Johansson and Ehrlén, 2003). Epiphytic lichens population dynamics can thus be expected to conform more closely to a classic metapopulation model compared with understory plants.

Boreal forests are an appropriate ecosystem to test the effect of landscape properties on species distributions, because they present spatial variations in the regional-level proportion of different forest ages or forest composition classes. Since these spatial variations are related to abiotic controls on fire regimes that are likely to have persisted for the last decades or centuries (de Lafontaine and Payette, 2011; Mansuy et al., 2011), it can be assumed that populations have reached some kind of dynamic equilibrium with their environment, and that landscape effects are not masked by extinction debts (Gu et al., 2002; Tilman et al., 1994).

The main objective of this study was to examine if metapopulation size influenced the probability of species presence in suitable habitats. We hypothesized that the epiphytic lichen and understory plant species most strongly affected by metapopulation size (1) have a poor capacity to persist in unsuitable habitats or (2) have limited dispersal capabilities. We also aimed to verify if species-level threshold responses to the spatial gradient in metapopulation size are easily identified in pristine ecosystems, and if this information could be used in a management context.

## 2. Study area

The study area covers 240,000 km<sup>2</sup>, and extends between long. 58°W and 78°W, and lat. 50°N and 53°N (Fig. 1). It is located at the interface between the closed-crown boreal forest (located to the south) and open woodland taiga (to the north). Its characteristics are summarized in Table 1. Soils are mainly dominated by tills left behind during the last glaciations. The Precambrian bedrock is exposed in locations such as hill tops where surficial deposits are thin or absent, and fluvio-glacial and glacio-lacustrine deposits are also common, particularly in valley bottoms and low-elevation areas. Precipitation is more abundant and temperature is colder in the eastern part of the study area (Table 1).

Natural fires are a very important driver of forest dynamics in the study area, with fire recurrences being generally lower in the eastern part (>500 years) compared to the western part (ca. 100 years) (Bouchard et al., 2008; Mansuy et al., 2011). The east–west gradient in fire recurrence is influenced by climate and by variations in landform, as the flat topography in the west tends to be more conducive to large crown fires compared with what is seen in the east (Jobidon et al.,

2015). In addition, an increased presence of well-drained sandy deposits in the central and western parts of the study area probably contribute to higher fire recurrences (Table 1).

Mature forest stands tend to be spatially discontinuous across the study area: they are interspersed with sites with sparse canopy cover, due to the presence of exposed bedrocks or exposition to extreme weather, or to the effect of recurrent fires. When forest vegetation is present, it is overwhelmingly dominated by black spruce, with a lesser presence of stands that comprise other species such as balsam fir (*Abies balsamea* [L.] Mill.), paper birch (*Betula papyrifera* Marsh.), trembling aspen (*Populus tremuloides* Michx.) and jack pine (*Pinus banksiana* Lamb.). Balsam fir, which is mostly present in stands that have not burned for long periods (Bouchard et al., 2008; de Lafontaine and Payette, 2011), is more abundant in the east, whereas jack pine, a fire-adapted species, is more abundant in the west (Table 1).

Direct human influence on natural vegetation is quite limited across this region. Industrial forestry is virtually non-existent, limited to small harvestings in the immediate surroundings of a few villages. There are also important mining and hydroelectric projects in circumscribed areas in this zone, but their effect on the surrounding vegetation can be considered minor and very local (Jobidon et al., 2015).

## 3. Methods

### 3.1. Experimental design and vegetation plots

A total of 792 vegetation plots were established across the study area from 2006 to 2010 (Berger et al., 2008; Jobidon et al., 2015). Site types that were considered unsuitable for forest growth (e.g. exposed bedrock) were not sampled. The sampling intensity of each major forest type was adjusted to its relative abundance across the study area. The plots were distributed randomly within forest types.

Plant species abundances were recorded in 400-m<sup>2</sup> circular plots with a radius of 11.28 m, by assessing the cover of each vascular plant species (Berger et al., 2008). Nomenclature follows Marie-Victorin et al. (2002) for vascular plants. The methodology for sampling pendulous epiphytic lichens is detailed in Berger et al. (2008) and Boudreault et al. (2015). Epiphytic lichens were sampled on the 2 trees (>7 m height) located the nearest to the center of each plot. On each tree, 2 branches >50 cm were selected at a height of 2.5 m from the ground. When no branch was present at this height, the branches >50 cm located the closest to this point were selected and brought back to the laboratory, and pendulous epiphytic species belonging to the genera *Alectoria*, *Bryoria* and *Evernia* were identified to the species level. Nomenclature for the studied species follows Brodo et al. (2001) and Brodo and Hawksworth (1977).

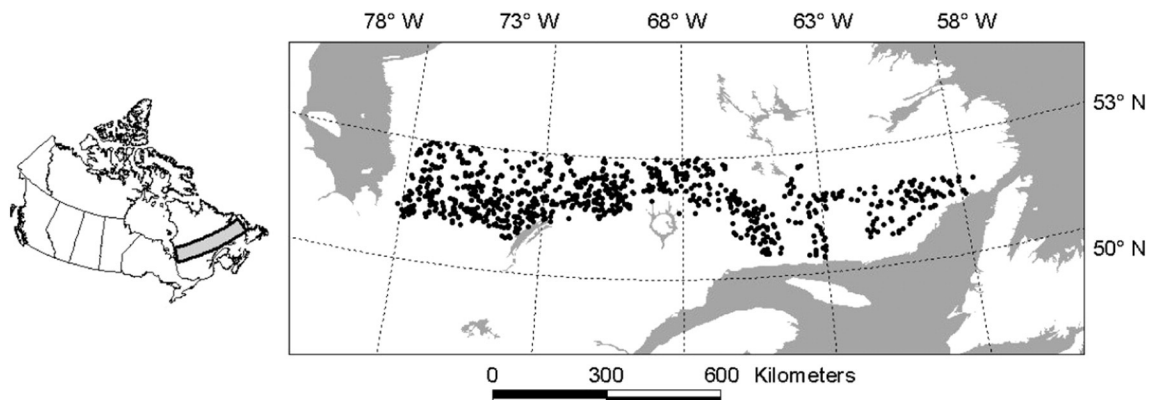


Fig. 1. Study area and location of sample plots in the province of Quebec, Canada.

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