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Bryophyte species assemblages in fire and clear-cut origin boreal forests

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ABSTRACT

Natural and anthropogenic disturbances could have different impacts on understory plant communities. Investigating these differences could help improve silvicultural and management practices in order to better achieve biodiversity protection objectives. Using post-fire (20–90 years) and post-clearcutting (20–70 years) forest chronosequences placed on similar sites, we examined which environmental factors are the main drivers of bryophyte community assembly in eastern Canadian boreal forests, using information on bryophyte life-history strategies (colonist: high reproductive effort but a short potential life span; perennial: low reproductive effort and a long potential life span) to interpret the resulting patterns. The fire origin stands were affected by high-severity fires followed by natural regeneration, whereas the clear-cut stands were regenerated through the advance regeneration present in the understory of the harvested stands. Our results indicate that by killing the existing mosses and baring the mineral soil, fire tends to decrease the cover of perennial species (such as *Pleurozium scherberii*) and increase the presence of colonist species compared with clear-cut. Overall species richness does not increase much in older stands, but some species that have been identified by previous studies as being more sensitive to management activities, such as liverworts, tend to be strongly associated with balsam fir basal area, which is higher in mature clear-cut origin stands. This tree species tends to be heavily affected by partial mortality events after >50 years (insect outbreaks, windthrow), which could accelerate the creation of heterogeneous canopy structure and generate a greater diversity of microhabitats suitable for sensitive bryophyte species. More research needs to be conducted to better understand the underlying functional relationships between overstory tree composition and bryophyte communities.

1. Introduction

In the last decades, the expansion and intensification of forest management activities have led to the replacement of fire by clear-cut logging as the most important disturbance in much of the boreal forest of North America (Cyr et al., 2009; Burton et al., 2010; Bouchard and Pothier, 2011). This represents a major concern from a conservation perspective because some species are suspected to be ill-adapted to maintain healthy populations in anthropogenized environments. Bryophytes, and particularly liverworts, are a good example of a species group that could be negatively affected by forest management (Fenton and Frego, 2005; Hylander et al., 2005; Arseneault et al., 2012; Caners et al., 2013). Bryophytes are a major component of boreal forest ecosystems, and higher bryophyte species richness has been reported in natural forests compared to forests affected by logging (Vanha-Majamaa et al., 2007; Hart and Chen, 2006, 2008; but see Schmalholz et al., 2011). This is often explained by a greater range of environmental conditions in natural forests, which translate in niches for a wider range of specialized organisms (Tilman and Pacala, 1993; Beatty, 2003; Tews et al., 2004). In particular, coarse woody debris (CWD) of variable quality is an important type of microhabitat for bryophyte species (Söderström, 1988; Andersson and Hytteborn, 1991; Rambo and Muir, 1998; Schmalholz et al., 2011), and the

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amount of CWD has been found to be a key factor influencing bryophyte species richness and composition in forest ecosystems (Rydgren et al., 1998; Mills and Macdonald, 2005; Fenton and Bergeron, 2008; Schmalholz et al., 2011).

Forest succession is an important process in natural or managed forest ecosystems, particularly in boreal forests where severe disturbances such as fire and clearcutting are common. Initial post-disturbance microhabitat characteristics and subsequent temporal changes in microhabitat availability are expected to differ following fire or clear-cutting. For example, fire is expected to remove an important part of the organic layer, thus creating a greater quantity of exposed mineral microhabitats compared with clearcutting (Nguyen-Xuan et al., 2000). These conditions favor the recolonization of fire-adapted species through regeneration from seed banks, underground plant structures that may have survived the fire, or from seeds from nearby unburnt stands (Dyrness, 1973). On the other hand, in North-American boreal conditions, clear-cut logging generally causes little direct disturbance to the organic layer outside skidding trails, and the vegetation generally includes a significant number of species that were present prior to disturbance (Timoney et al., 1997; Rees and Juday, 2002; Nguyen-Xuan et al., 2000). Temporal variations in CWD availability are also expected to differ between stand origins: in post-fire stands, CWD will be most abundant during the first few decades after disturbance, but they will decline afterwards and increase again in late successional stage (Brassard and Chen, 2006). By contrast, in clear-cut origin stands, CWD abundance tends to be low initially, and to increase progressively during the subsequent decades (Barrette et al., 2013). The effect of these temporal changes in microhabitat abundance on bryophyte communities has rarely been compared directly thus far, but Schmalholz et al. (2011) found that in mixed-wood forests of eastern Canada, young stands regenerating after natural disturbances were distinctly different from clear-cut origin stands in terms of woody debris flora.

Species life-history strategies are increasingly recognized as good indicators of the functional diversity of an ecosystem. During (1992) has elaborated a classification for bryophytes that integrates reproductive effort, potential life span, size and number of spores. Species from different life-history strategies are expected to be impacted differently by fire and logging. For instance, colonist species with spores well adapted to colonize harsh environments might be more frequent after fire, while perennial species, which have a low reproductive output but long potential life span, could be more abundant in habitats that are relatively stable (see Table S1). By knowing which traits best explain community response to a given environmental modifications, it becomes feasible to expand the results of a study to other regions affected by similar disturbances, or other types of organisms that share similar traits.

In this study, our main objective is to examine bryophyte species assemblages in fire origin and clear-cut origin stands of different ages (ranging from 20 to 90 years), and to examine if these responses are associated with life-history strategies (colonist and perennial). We hypothesize that in young stands, colonist species richness will be higher in fire origin stands (because fire removes organic matter), but perennial species richness will be higher in clear-cut origin stands (because harvests cause little direct disturbance to the organic layer). In older stands, we expect that the closed canopy cover will translate into a higher cover of perennial species and mosses compared with younger stands. We also expect that the differences in species composition between fire origin and clear-cut origin stands will tend to decrease with time as the initial differences in microhabitat characteristics subside. Finally, we expect that coarse woody debris volume will be an important habitat variable to explain species richness and species composition, as suggested by previous studies (Fenton and Bergeron, 2008; Schmalholz et al., 2011; Arseneault et al., 2012).

2. Study area

The study area is located in a section of the boreal forest (49°N–50°N, 68°W–70°W), in the province of Québec, Canada. It is located on the Canadian shield (a granitic, acidic bedrock formation), and surficial deposits are mostly represented by glacial tills of various thicknesses and by fluvioglacial deposits (Bouchard et al., 2008). The study area is located at the interface between two bioclimatic domains, the balsam fir – white birch to the south and black spruce – feathermoss to the north, according to the provincial classification (Morneau and Landry, 2007). Mean annual temperature was 1.5 °C during the 1971–2000 period at the Baie-Comeau weather station, which is located to the south of the study area (Environnement Canada, 2009). Climatic conditions tend to get colder when latitude or elevation increase, approaching 0 °C in average in the northern part of the study region. Average annual rainfall is 684 mm, and average annual snowfall 362 cm (Environnement Canada, 2009). The length of the growing season is between 140 and 160 days, and extends from May to October (Morneau and Landry, 2007).

Large forest fires are an important natural disturbance in this region, with fire return intervals that vary between 250 and 500 years, a fire recurrence that can be considered as relatively long compared with what is generally observed elsewhere in the North American boreal forest (Cyr et al., 2007; Bouchard et al., 2008). The forests are overwhelmingly dominated by the two aforementioned coniferous species, *Picea mariana* (Mill.) (black spruce) and *Abies balsamea* (L.) Mill (balsam fir), with a relatively secondary occurrence of hardwoods such as *Betula papyrifera* (Marsh.) (white birch) and *Populus tremuloides* (Michx.) (trembling aspen), particularly in early successional forests (Bouchard and Pothier, 2011). Forest harvestings have been performed in the region since the 1930s (Bouchard and Pothier, 2011): while they were initially very limited in extent, they increased progressively in importance throughout the 20th century.

Forest stands that originate from two types of stand-origin disturbances were sampled in this study: fires and clearcuts. The fire origin stands that were sampled were affected by high-severity crown fires, regenerated naturally, and were not affected by salvage logging or thinnings during the course of post-fire stand dynamics. Post-clear-cut stands were primarily regenerated through the advanced regeneration (i.e. seedlings or trees <9 cm DBH) that was present in the understory of the harvested stands. Following clearcutting, the sampled stands were not treated with silvicultural treatments such as pre-commercial or commercial thinnings.

3. Methods

3.1. Sampling

A chronosequence of stands originating from fires and from clear-cut logging was established based on disturbance maps available for the study area (Bouchard and Pothier, 2011). These maps were built from the information available from government archives and old aerial photographs, and were validated systematically by using forest inventory plots (Bouchard et al., 2008; Bouchard and Pothier, 2011). The year of stand origin was further validated in this study by taking sample cores of dominant trees in each plot, particularly in older stands for which the year of disturbance was uncertain.