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Structural diversity and dynamics of boreal old-growth forests case study in Eastern Canada

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ABSTRACT

Old-growth stands are considered as key components of boreal forest diversity and their preservation is largely integrated into management plans. However, while the differences between old-growth and young forests have largely been studied, little is known about the diversity of boreal old-growth forests. In managed landscapes, the efficacy of old-growth conservation plans may be reduced depending on how these old-growth forests are considered: as a single, homogeneous and steady-state forest type or as multiple, diverse and dynamic forest types. To fulfil this gap, our objectives were: (1) to create a typology of old-growth boreal structures; (2) to observe how these structures are influenced by environmental and temporal parameters; and (3) to elaborate a succession model of old-growth structural dynamics along temporal and environmental gradients. Seventy-one mature and overmature stands were sampled within a 2200 km^2 territory situated in Eastern Canada. Cluster analysis divided the sampled stands into two even-aged types, three transition old-growth types and six true old-growth types. Slope, minimum time since last fire and organic horizon depth were the three environmental and temporal parameters influencing the old-growth structures. Paludification-related productivity decline was present in only one old-growth forest type, while the other sites remained productive. These results allowed the creation of three succession models of the dynamics of old-growth stands in the boreal forest of eastern Canada. Boreal stands can undergo numerous structural changes once the old-growth succession process is initiated. An increase in structural diversity when the true old-growth stage is reached, coupled with a variety of secondary disturbance characteristics, favours multiple pathways of structural evolution of these ecosystems over time. Therefore, forest management planning should incorporate this complexity to improve the preservation of old-growth forests in managed territories.

1. Introduction

In forest ecosystems, the old-growth stage can mainly be defined as stands driven by gap-dynamics, with tree mortality caused by secondary disturbances (Hilbert and Wiensczyk, 2007; Wirth et al., 2009; Shorohova et al., 2011). In the boreal biome, old-growth forests represent a significant proportion of the natural landscape, regardless of the differences in disturbance dynamic and species traits among the boreal regions (Östlund et al., 1997; Cyr et al., 2009; Shorohova et al., 2009). Even in territories characterized by short fire cycles, old-growth forests are present due to the random distribution of fire (Bergeron et al., 2002; Bouchard et al., 2008; Cyr et al., 2009). These ecosystems are considered as key habitats of the boreal biome because of their specific structural attributes and their relative stability in comparison to younger stands driven by stand-replacing disturbances (Esseen et al., 1997; Kimmins, 2003; Fenton and Bergeron, 2011). In managed territories, the choice of harvesting system tends to be determined by the system's short-term profitability and its capacity to generate the maximum possible volume (Haeussler and Kneeshaw, 2003), leading to an upper limit of forest rotation, which is generally earlier than the initiation of gap dynamics (Östlund et al., 1997; Bergeron et al., 2002). Furthermore, in some boreal regions, natural disturbances such as fire, windthrow or insect outbreak still occur and compound the impacts of forest harvesting (Armstrong, 1999; Bergeron et al., 2006). Consequently, many boreal landscapes are now rejuvenated, simplified and fragmented (Östlund et al., 1997; Etheridge et al., 2006; Boucher et al., 2015). As a result, in heavily managed boreal territories, a significant portion of the erosion of forest biodiversity is linked to the rejuvenation of the forest landscape (Berg et al., 1994; Esseen et al., 1997; Siitonen 2001). In territories where forests are mainly harvested for the first time and where the knowledge about local biodiversity is still scarce, similar losses are expected (Cyr et al., 2009).

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Old-growth forests consequently represent an important issue in forest management, with different planning processes aimed at minimizing the loss of old-growth forests and reducing the impacts when it is harvested (Mosseler et al., 2003; Le Goff et al., 2010). Emphasis has been placed on management models based on the natural disturbance regime (Kuuluvainen 2002; Gauthier et al., 2009) or on the imitation of stand scale natural processes (Vanha-Majamaa et al., 2007; Kuuluvainen 2009). However, these models require a complete understanding of boreal forest natural dynamics at all temporal and spatial scales to be efficient (Kneeshaw and Gauthier, 2003; Kuuluvainen, 2009; Halme et al., 2013). Each boreal region presents specific characteristics because of particular combinations of climatic factors, disturbance dynamics and species traits (Kneeshaw et al., 2011; Shorohova et al., 2011). Hence, a fine scale understanding of the old-growth dynamics in each boreal region is necessary for efficient management.

Eastern Canada boreal forests fall into this paradigm and a more detailed understanding of old-growth forests is needed. Indeed, most management strategies in this territory consider old-growth forests as a homogeneous group, contrasted uniquely to even-aged stands (Brassard and Chen, 2006; Bergeron and Harper, 2009). Studies about their diversity and dynamics have focused on the transition processes from even-aged to old-growth forest, typically defined by canopy break-up, the presence of gap dynamics and the progressive replacement of the first cohort (Bergeron and Harper, 2009). Once this transition is complete, old-growth forests tend to be viewed as structurally undifferentiated (Nguyen, 2002; Harvey et al., 2002). Structural evolution has been observed, however, in boreal old-growth forests undergoing paludification (Lecomte et al., 2006; Bergeron and Harper 2009), a process that is associated with certain soil types and climatic conditions (Lavoie et al., 2005). However, when other soil types and climates are examined, more complex dynamics of old-growth boreal stands can be expected (De Grandpré et al., 2008; Gauthier et al., 2010), as productivity declines due to paludification are associated with specific abiotic conditions (Pollock and Payette 2010; Girard et al., 2014; Ward et al., 2014).

Therefore, the analysis of Eastern Canadian boreal old-growth forest structural diversity and the factors explaining its distribution across the landscape is a pertinent case study of a common old-growth forest management problem. A management strategy that aims to maintain old-growth forests, yet which considers them as homogeneous entities, cannot preserve all types of old-growth forest. This recurring issue can be expressed as follows: in a given ecological context, are the old-growth forests a homogeneous and steady-state forest type or multiple, diverse and dynamic forest types? Our study aims to fill this knowledge gap for Eastern Canada by identifying the diversity of old-growth forest structures and their dynamics across a boreal landscape. Specifically, our objectives are: (1) to define a typology of boreal old-growth forests based on their structural attributes; (2) to observe whether the groups created by the typology can be related to specific environmental characteristics; and (3) to create a succession model of old-growth structural dynamics along both temporal and environmental gradients.

2. Methods

2.1. Study territory

The study site covers a 2200 km^2 area of public land along the southern edge of Lake Mistassini (72°52′36″ W, 50°18′50″ N) (Fig. 1). The area is crossed by the Mistassini, the Ouasiemsca and the Nestaocano rivers. The study site is part of the western subdomain of the black spruce (*Picea mariana* (Mill.))–feather moss bioclimatic domain and belongs to the physiographic region of the Nestaocano River Hills. The topography is essentially characterized by gentle hills and an altitude range from 350 to 750 m. Thick glacial tills are the dominant surface deposits. Rivers and streams are often surrounded by sand deposits or vast bogs. Mean annual temperature ranges from −2.5 to 0.0 °C, annual rainfall (rain and snow) from 700 to 1000 mm and growing season length from 120 to 155 days. Black spruce and balsam fir (*Abies balsamea* (L.) Mill.) are the dominant tree species, and they are sometimes found with jack pine, *(Pinus banksiana* (Lamb.), white spruce (*Picea glauca* (Moench) Voss), paper birch (*Betula papyrifera* Marsh.) and trembling aspen (*Populus tremuloides*) (Bergeron et al., 1998). Timber exploitation in the region began in 1992 and continued at a relatively low level until 2000 when harvest levels increased. This region was chosen for study because it encompasses the spectrum of environmental diversity of the western black spruce–feather moss bioclimatic domain, from poorly-drained valley bottoms situated on organic deposits to well-drained till slopes.

2.2. Sampling

Based on the Québec's Ministry of Forests, Wildlife and Parks (MFWP) ecological classification, this territory can be divided into 19 environmental types; six of these represent over 72% of the total area. They can be defined by the following Potential vegetation/Slope/Deposit/Drainage associations: Balsam fir – white birch/Medium/Till/Mesic; Black spruce – balsam fir/Medium/Till/Mesic; Black spruce – feather moss (BSFM)/Low/Sand/Mesic; BSFM/Low/Till/Mesic; BSFM/Low/Till/Subhydric; BSFM/Low/Organic/Hydric (Blouin and Berger, 2004). Because they cover the environmental diversity of the study territory, we selected sites within these six environmental types, with an objective of each having equal sampling intensity. According to Oliver and Larson (1996), old-growth forests can be divided into two stages: transition old-growth (gap dynamics have started, however the stand is still dominated by first cohort trees) and true old-growth (all the trees from the first cohort have disappeared). Following this definition, we attempted to sample the complete successional sequence from mature stands (stands approaching the age of canopy break-up) to true old-growth forests. However, we faced limitations during our site selection. The first limitation is that the dominant boreal tree species in the study area are relatively short-lived (Burns and Honkala, 1990), making it impossible to estimate stand ages older than 200 years without using radiocarbon dating (Fenton and Bergeron, 2011; Garet et al., 2012). The second is the absence of clear and constant age thresholds between the transition processes, making it impossible to define age classes based on a single transition process. Therefore based on the literature (Uhlig et al., 2001; Bergeron and Harper, 2009; Gauthier et al., 2010), we decided to divide our sample stands into three age groups, each one dominated by a single transition process: 80–100 years (maturing), 100–200 years (canopy break-up and beginning of the gap dynamic), > 200 years (first cohort disappearance).

A first survey was realized in order to assess the age of the site, through core sampling of five dominant and codominant trees per sites. Then, seventy-one sites were sampled based on stratified random sampling of forest inventory environmental type and stand age, depending on accessibility. As the study territory is a managed area, the 80–100 years class was the least abundant (12 sites sampled, with at least one site per environmental type), as this class is the most often harvested (Bouchard and Garet, 2014). However, gap-dynamics do not start exactly 100 years after the fire (Bouchard et al., 2008; Lecomte et al., 2006), so we assumed that numerous sites in the 100–200 years class were still even-aged, compensating the lack of sites in the 80–100 years class.

At each site, the centre of the plot was systematically placed 125 m beyond the stand edge in order to limit edge effects and to avoid bias. Soil and topographic parameters were determined by digging a soil profile at the plot centre and measuring topographic variables with a clinometer. Living trees having a diameter at breast height (dbh) ≥ 9 cm (merchantable trees) were sampled in a 400 m^2 square plot (20 × 20 m), the standard plot size in the Québec forest survey (MFFP, 2016). For each individual tree, we noted dbh, vitality (alive, senescent or dead) and position in the canopy (dominant, codominant,