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Surface analysis as a method to reconstruct past and recent dynamics of forest ecosystems

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ABSTRACT

The most direct way of deciphering the dynamics of an ecosystem is to examine its biotic and abiotic components based on analysis of living and dead organisms distributed above ground. The surface analysis method presented here provides a centennial to millennial stand-scale composition and disturbance history and is applicable in any wood-dominated ecosystem. A meticulous analysis of living and dead trees, and macroremains (charcoal, leaves and insect) laying above mineral soil was performed in a virgin and an anthropic sugar maple (*Acer saccharum*) forests. Sugar maple ecosystems provide an appropriate setting for testing this method as they are impacted by several natural and human disturbances. The living and dead components in both sites indicate an increase of the species abundance independent of human interventions, although accelerated by logging in the anthropic forest. The stands were affected by recent insect outbreaks and by fire over the last 2000 years. Charcoal remains indicate that a mixed forest occupied both sites with sugar maple as companion species for more than 1000 years. Surface analysis is a direct method for improving our understanding of current, past and future forest dynamics in natural and anthropic conditions, in this case highlighting how a structuring species of eastern North America thrives in different successional states and disturbance regimes. Novel tools that give insight into pre-colonial ecosystems are greatly needed as a proper understanding of species current distributions and behavior relative to allogenic disturbances is of crucial importance for restoration purposes and accurate prediction of future changes.

1. Introduction

Forest ecosystems are either maintained at equilibrium or in transition from one state to another in response to natural disturbances of varying size, frequency and severity (Bormann and Likens, 1979). The frequency of stand disturbances is generally not directly measurable in a human-life span. To compensate for this limitation, one must rely on multiple ecological and paleoecological methods to evaluate the impact of disturbance regimes on ecosystem dynamics and stand succession. Climate change and anthropogenic land-use are other factors that induce changes in forest structure, composition and function (Foster et al., 2003; Nowacki and Abrams, 2015). A better understanding of past forest composition and dynamics is of crucial importance for conservation purposes, resource management, restoration of ecological functions, and prediction of future ecosystem changes (Foster et al., 2003; Jackson and Hobbs, 2009).

Different paleoecological methods can be used to reconstruct portraits of past environments at different, but specific temporal and spatial scales. Palynological studies are dedicated to reconstruction of long-term regional vegetation and fire trends (Carcaillet and Richard, 2000; Jackson et al., 2000), although stratified soils in small forest hollows are well suited for stand-scale to extra-local reconstructions (Calcote, 1995; Colpron-Tremblay and Lavoie, 2010). Stratified lacustrine and peat sediments offer a wide range of continuous, indirect evidence, but studies are limited to the rare environments where such deposits can develop. The botanical identification of radiocarbon-dated soil charcoal is a more widely applicable tool to reconstruct fire history and changes in species composition at the stand scale (Payette et al., 2012), as macrocharcoal fragments are present in every fire-prone forest and deposited in situ. However, data are often incomplete due to the high cost of radiocarbon-dating, absence of information during fire-free periods and degradation or loss of charcoal in certain conditions. Tree-ring analysis is another spatially precise and direct method for reconstructing disturbance history in a variety of forest types (Swetnam et al., 1999; Payette, 2010), although it is limited by tree longevity. Land surveys and aerial photographs allow for precise timewise reconstructions of pre-industrial landscapes. Extensive changes in forest composition are deduced by comparing this type of archival data to

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recent ecological surveys (Whitney, 1994; Foster et al., 1998; Boucher et al., 2006; Dupuis et al., 2011; Laflamme et al., 2016).

The most direct way of accessing recent and past ecosystem structure and composition is to examine its current living and dead components (Henry and Swan, 1974; Linder et al., 1997; Stockland, 2001). Wood remains (hereafter, WR, or coarse woody debris) are a major component of forest ecosystems, with ecological benefits for animal and plant diversity (Drapeau et al., 2009; Stockland, 2012; Dittrich et al., 2014), tree regeneration (Arseneault and Payette, 1992; Robert et al., 2012; Lambert et al., 2016), nutrient cycling and structuring of water streams (Harmon et al., 1986). Botanical identification of logs and stumps has been used to describe WR assemblages (Stone et al., 1998; Rubino and McCarthy, 2003), and sometime used as a tool to evaluate short- and long-term vegetation changes and the impact of past land use (Henry and Swan, 1974; Arseneault and Payette, 1992, 1997; Payette and Delwaide, 2004; Boucher et al., 2006; Woodall and Nagel, 2006; Tanac et al., 2009; Josefsson et al., 2010). Most studies take into account snags and stumps at the surface of the forest floor, while buried wood is usually overlooked (Moroni et al., 2015). As for soil macrocharcoal studies (Payette et al., 2017), we argue that wood anatomy (both macroscopic and microscopic) may be used to identify surface logs and snags as well as well-decomposed WR buried in the organic soil layer. A meticulous analysis of dead wood, including botanical identification of buried wood, will allow reconstruction of a longer, more complete stand-scale composition history. Dead wood not only represents direct evidence of past stand composition, it also has the advantage of being present in most, if not all, forest ecosystems.

In this study, we apply surface analysis of living trees and plant and insect macroremains to reconstruct recent developments of temperate forest ecosystems at the stand scale (Fig. 1). All these biotic ecosystem components are used in this study to gain insights into the disturbance history of two forest sites dominated by sugar maple (*Acer saccharum*), an anthropic stand and a natural stand located at the transition between the mixed-broadleaf and boreal vegetation zones of eastern North America. The forest landscape of the area is currently impacted by an increase of sugar maple induced by logging (Boucher et al., 2009; Dupuis et al., 2011). Conifer forests were transformed into mixed stands, and mixed forests into sugar maple stands (Boucher et al., 2006). Surface analysis of forest ecosystems is used here as a multifaceted method for reconstruction of ecosystem dynamics at the local scale over the last hundreds to thousands of years.

2. Materials and methods

2.1. Forest sites analysed

The forest stands used in the surface analysis are located in the Lower St-Lawrence region (Quebec, Canada), which is characterized by an Appalachian-type landscape composed of undulating, subparallel hills 50–500 m a.s.l. (above sea level). Conifer forests generally dominate on low altitude sites. Eastern white cedar (*Thuja occidentalis* L.) is abundant and often grows in association with balsam fir (*Abies balsamea* (L.) Mill.), red spruce (*Picea rubens* Sargent) and black spruce (*Picea mariana* (Mill.) B.S.P.). Mixed forests, the most abundant forest type in this region, are located on lowland and upland sites. Several tree species grow in these mixed forests, mostly balsam fir, trembling aspen (*Populus tremuloides* Michx.), paper birch (*Betula papyrifera* Marsh.), red maple (*Acer rubrum* L.) and yellow birch (*Betula alleghaniensis* Britton). Sugar maple (*Acer saccharum* Marsh.) forests are generally distributed uphill and on small well-drained summits above *c.* 275 m a.s.l. (Ministère des Forêts et al., 2015). Sugar maple forms monospecific stands, although red maple, yellow birch, white spruce (*Picea glauca* (Moench) Voss) and balsam fir are often present as companion species. The region has been affected by three eastern spruce budworm outbreaks in the 20th century (1975–1992; 1947–1958; 1914–1923) (Boulanger and Arseneault, 2004) and by industrial logging since the end of the 19th century (Boucher et al., 2009).

The first stand analysed is a sugar maple stand in the Nicolas-Riou Seigneury (SNR, 48°12′23″N, 68°39′25″W) that has been preserved in a natural state due to protection from logging. It is located on a south-

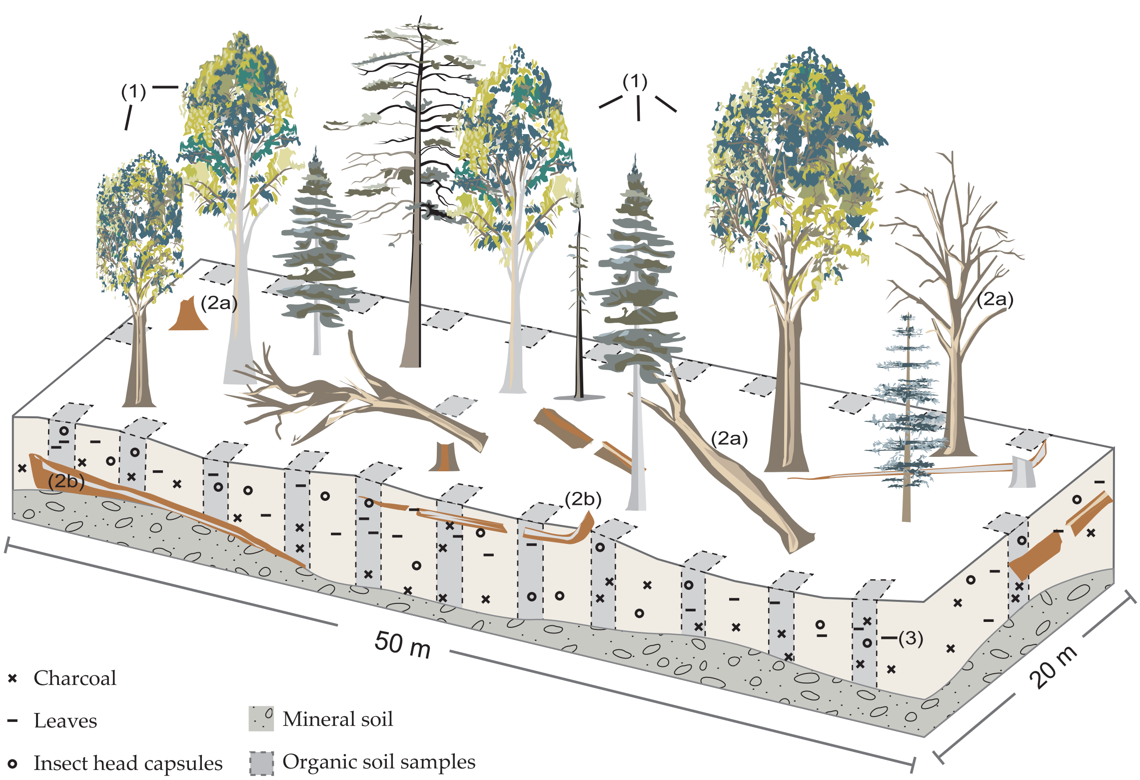

Fig. 1. Diagram illustrating the surface analysis method. The method includes the investigation of the living component (1, canopy trees and regeneration layer), the wood macroremain component (surface (2a) and buried (2b)), and the organic soil component (3, macrocharcoal, leaves, insect head capsules).