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Pre-industrial landscape composition patterns and post-industrial changes at the temperate–boreal forest interface in western Quebec, Canada

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Keywords
Abies balsamea; Historical forest ecology; Land-use legacies; Naturalness; *Picea mariana*; *Pinus strobus*; *Populus tremuloides*; Spatially constrained clustering; *Thuja occidentalis*

Nomenclature
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Abstract

Questions: What were the pre-industrial forest landscape composition patterns? Which factors had structured the pre-industrial landscape patterns? How have pre-industrial landscape patterns and post-industrial disturbances controlled composition changes?

Location: An area of 4175 km^2 at the temperate–boreal forest interface of southwest Quebec, Canada.

Methods: Reconstruction of the pre-industrial composition is based on an original early land survey data set (1874–1935). Composition changes were computed by comparing historical data with modern forest inventories. Landscape-scale patterns and composition changes were assessed through spatially constrained clustering analysis.

Results: Pre-industrial forest composition was structured across the landscape by the combination of environmental gradients (topography, deposits, drainage, etc.) and recurrence of fire. Frequency and intensity of fires were most likely the main drivers of forest dynamics and composition across the landscape. Black spruce (*Picea mariana*) and balsam fir (*Abies balsamea*) dominated hilly areas affected by former fires; aspen (*Populus tremuloides*) dominated lowlands following recent fire. White cedar (*Thuja occidentatlis*) and pines (*Pinus* spp.) dominated areas probably affected by small surface fires. New disturbance regimes that were subsequently incurred by human activities have shifted the pre-industrial landscape mosaic and have led to the current landscapes. Composition changes included a replacement of conifers by early successional species within settled or burned areas, and the maintenance of conifers and an increase in cedar dominance in areas affected by partial disturbance.

Conclusions: Post-industrial composition changes must be perceived as complex interactions between pre-industrial landscape patterns and natural and human disturbances. Such land-use legacies could be important drivers of future landscape change and should be investigated and considered when predicting future climate-induced ecological changes.

Introduction

Since thousands of years before the industrial era, human populations have altered the forest naturalness through their use of lands and resources from northern boreal forest (Johnson & Miyanishi 2012) to rain forest (Willis et al. 2004). During the last few centuries, industrialization and land-use intensification has dramatically transformed the global forest cover (Houghton 1994; Foley 2005; Ellis et al. 2010). In northeastern America, native populations have modified the pre-settlement forest landscape through use of fire, forest clearing, wild plants and animal population management (Day 1953; Denevan 1992, 2011; Delcourt & Delcourt 2004; Abrams & Nowacki 2008). Thereafter, European colonial settlement contributed to major transformation of forest landscape characteristics,

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which are generally considered as younger and more fragmented than pre-industrial landscape (Mladenoff et al. 1993; Whitney 1994; Foster et al. 1998; Lorimer 2001).

Composition changes that have been observed since pre-industrial times in eastern North America are mainly the result of human activities (Thompson et al. 2013; Nowacki & Abrams 2015). Yet, significant climate change has also occurred between the pre-industrial period and the present time in North America (Mann & Jones 2003; Moberg et al. 2005; Gennaretti et al. 2014), and the relative importance of land-use and climate effects on vegetation changes over the last several centuries remains a lively debate (Pederson et al. 2014; Abrams & Nowacki 2015; Nowacki & Abrams 2015). Biogeographic transition zones also appear to be especially sensitive to climate change (Parmesan et al. 2005; Beckage et al. 2008), such as the temperate–boreal forest interface (Fisichelli et al. 2014; Reich et al. 2015).

Understanding the development of current forest landscapes under disturbance regimes that have been modified by human activities is fundamental to anticipating how present-day forests will evolve in a global change context (Foster et al. 2003; Schrott et al. 2005; Rhemtulla & Mladenoff 2007; Gillson 2009; Ewers et al. 2013). Many studies have used historical land survey records to reconstruct pre-industrial forest composition (Whitney 1994), and some have developed methodological tools to map and interpret these data at the landscape scale (Manies & Mladenoff 2000; Schulte et al. 2002; He et al. 2006; Rhemtulla et al. 2007; Dupuis et al. 2011). At the landscape scale, pre-industrial forest composition was commonly structured by the combination of environmental gradients and disturbance history (Lewis & Ferguson 1988; White & Mladenoff 1994; Lorimer 2001; Schulte et al. 2002, 2007; Abrams & Nowacki 2008; Boucher et al. 2009; Josefsson et al. 2010). Different land-use conditions subsequently may have led to different dynamic trajectories across the landscape (Wallin et al. 1994; Bellemare et al. 2002; Turner et al. 2003; Hermy & Verheyen 2007; Boucher & Grondin 2012; Boucher et al. 2014; Grondin et al. 2014). Accordingly, to understand current landscapes, ecologists should consider interactions between (1) pre-industrial landscapes patterns, (2) environmental gradients and (3) natural and human disturbances.

In this study we reconstruct pre-industrial forest composition at the temperate–boreal forest interface, based on an original data set of early land survey records. Our aims were to highlight both regional changes and the existence of distinct pre-industrial landscapes. We discuss three questions: (1) which factors had structured the pre-industrial landscape patterns; (2) how was the pre-industrial landscape modified by native populations; and (3) how have interactions between pre-industrial patterns and 20th century disturbances controlled composition changes to produce present-day forest landscape patterns?

Study area

The study area covers 4175 km^2 in the Témiscamingue region, which is located in southwestern Quebec (47°30′ N, 79°00′ W; Fig. 1a). Mixed forests in the region represent the transition zone between northern temperate hardwood and southern boreal conifer-dominated forests (Rowe 1972), and which corresponds to the balsam fir–yellow birch bioclimatic domain according to the provincial classification system (Robitaille & Saucier 1998). Surface deposits are mainly divided between clays deposited by the pro-glacial Barlow Lake in lowland areas (Vincent & Hardy 1977) and glacial till along with rocky outcrops in upland areas. According to data averaged from four weather stations in the study area, mean annual temperature is 2.7 °C and mean annual precipitation is 888 mm (1981–2010 time period).

In this region, the topographic gradient is linked to factors that influence the establishment and growth of different tree species, such as drainage, nutrient availability, soil depth, microclimate (Fraser 1954; MacHattie & McCormack 1961; Brown 1981) and disturbances. The natural fire rotation period has been estimated to be about 200-yrs long in the region (Grenier et al. 2005), and spruce budworm (*Choristoneura fumiferana*) outbreaks have also been identified as an important disturbance of natural forest dynamics over the last several centuries (Bouchard et al. 2005, 2006a,b).

Native populations have occupied the study area for at least 5000 yrs (Riopel 2002). The Algonquin/Anishinaabe tribes were nomadic hunter-gatherers, and totalled from about 800 to a few thousand individuals (Couture 1983; Riopel 2002), but their impact on the forest remains unknown. From the 18th century, the region was frequented by Euro-Americans, who were engaged in the fur trade. Logging did not begin until 1840, and was mainly focused on selective cutting of tall pine trees until 1917 (Riopel 2002). From 1917 until the end of the 20th century, partial cutting of spruces (*Picea* spp.) and balsam fir (*Abies balsamea*) for wood pulp became the main logging activity following the construction of a paper mill in the city of Témiscaming (Lienert 1966). Clear-cutting practices emerged with the mechanization of forestry in the 1970s. European settlement evolved in parallel with the forest industry, and the Euro-American population grew from a few hundred people in 1890 to nearly 30 000 in 1950 (Riopel 2002).

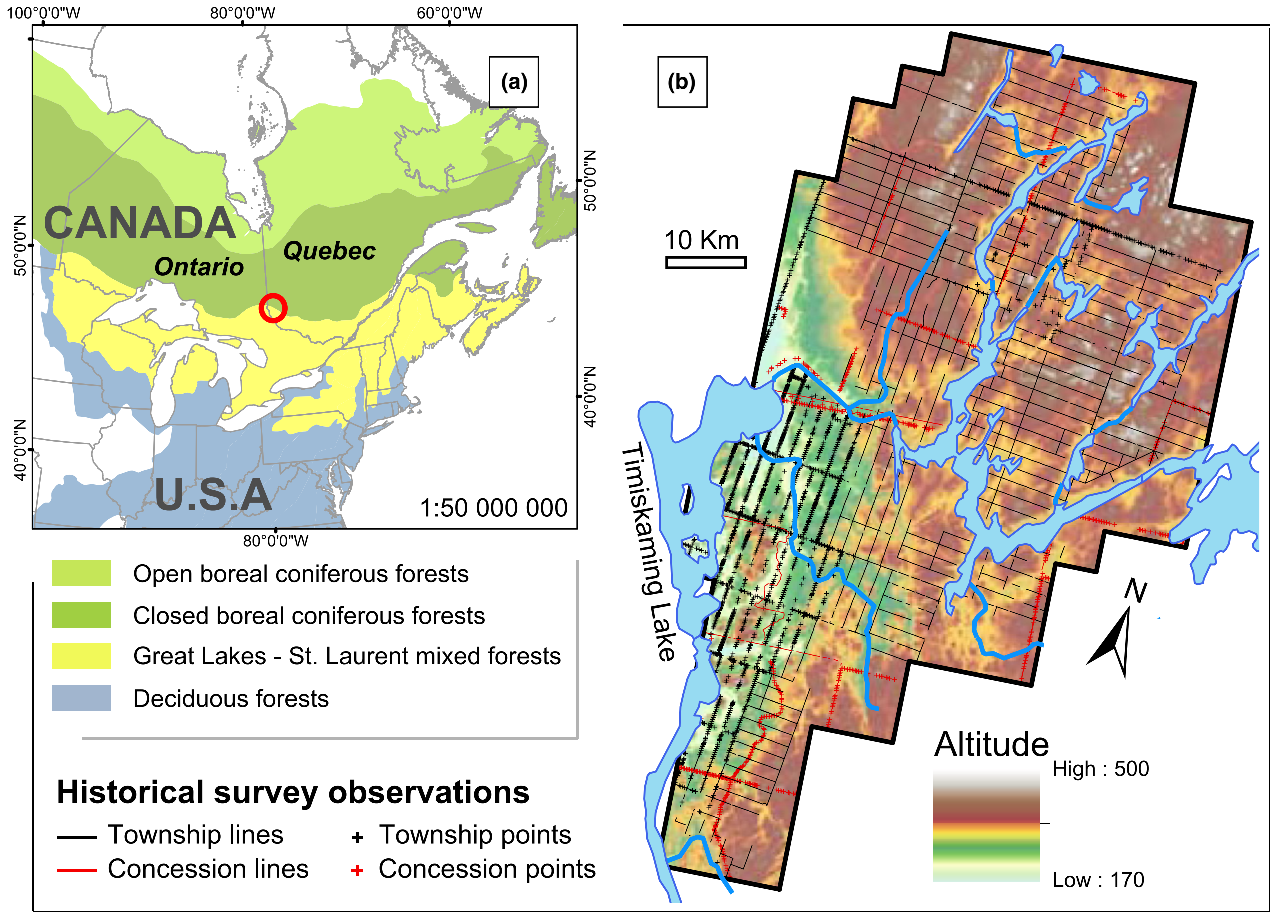

Fig. 1. (**a**) Location of the study area. (**b**) Study area and distribution of historical survey data.

Methods

Database construction

This study is based on 36 logbooks from the surveys of 16 townships and ten forest concessions by 16 different surveyors between 1874 and 1935. In the province of Quebec, public lands were divided into townships of about 16 km × 16 km (10 miles × 10 miles) and further subdivided into parallel ranges that were 1.6-km wide. Surveys were conducted along the boundaries of the township and range lines. Forest concessions varied in size, but only their boundaries were surveyed. Three observation types concerning forests are found in these archives: taxon lists (e.g. pine, spruce, white birch and a few maples), forest cover types (e.g. hardwood, softwood, etc.) and disturbance observations (e.g. burned, windthrow, etc.). In this study, only observations that mentioned taxa were selected.

The historical database comprises 5207 observations that are unevenly spread across the study area (Fig. 1b), and which mention at least one tree taxon. Observations are divided into two geometric types: (1) line descriptions that clearly indicate a beginning and an end, and (2) regularly or irregularly distributed point observations along the surveyed lines. In order to incorporate these two observation types into the same database, point observations were weighted, based on their mean spacing (mean of distances to the previous and next observations), while the weight of each line description corresponded to its lengths (Dupuis et al. 2011). For all observations, a rank was assigned to each taxon listed according to its position in the taxon list, assuming that this position reflects their relative basal area (Terrail et al. 2014). These data were then precisely georeferenced as lines or points with modern cadastral maps built from these early land surveys.

To assess changes between pre-industrial and modern composition, data from the historical survey records were compared with the Quebec government's forest inventories from the last three decades (1980, 1990 and 2000). These inventories are based on 0.04-ha plots that are distributed proportionally according to the surface area of different types of productive forest stands (capable of producing at least 30 $m^3 \cdot ha^{-1}$ timber in <120 yrs). Within

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the plots, all stems >2 cm DBH (1.3 m) of each species are measured and inventoried, and used here to calculate basal area ($m^2 \cdot ha^{-1}$) by species. Finally, a rank was assigned to each taxon according to its relative basal area within modern plots. Some species (spruces, maples, pines, poplars) within the modern database were grouped at the genus level to match the taxa mentioned by surveyors. Taxa mentioned in less than 5% of taxon lists of both historical and modern databases were grouped as 'others'.

Data analysis

Three different composition indices were computed for both historical and modern databases. First, an overall prevalence index was computed as the percentage occurrence of each taxon in all taxon lists, regardless of its rank in those lists. Second, a frequency index (F_{ir}) was computed for each taxon occurring in the first four ranks of enumeration in the taxon lists (i.e. r = 1, 2, 3, 4; Scull & Richardson 2007) using the formula:

$$F_{ir} = (N_{ir}/M_r) \times 100$$

where N_{ir} is the number of times taxon i is ranked at position r, and M_r is the total number of observations that include at least r taxa. Third, the dominance index represents the frequency of occurrence of each taxon i at the first ranking position (i.e. r = 1).

To compare pre-industrial and modern compositions at the landscape scale, the study area was divided into 25-km^2 cells (5 km × 5 km). Prevalence and dominance indices were computed for each epoch and each cell with at least five observations. This resulted in two grids, respectively containing 129 and 155 cells for the pre-industrial and modern periods (modern inventories were more uniformly spread, allowing a larger number of cells to be retained).

Spatially constrained clustering (Legendre & Fortin 1989; Legendre & Legendre 2012) was then used to determine geographically homogeneous areas of pre-industrial and modern composition. The test determines agglomerative clusters, with a spatial contiguity constraint, for a distance matrix that is calculated from multivariate data (Legendre 2011; Legendre & Legendre 2012). Prevalence and dominance index values of each taxon and each cell were converted to a Euclidean distance matrix. Clustering was then computed on the basis of this matrix, constrained by a geographic distance matrix between cells. Optimal numbers of groups were chosen by cross-validation to minimize residual error. Within each group, prevalence and dominance indices were recomputed and expressed as diagrams attached to the results maps (Fig. 2a,c).

Spatially constrained clustering was used with 11 environmental and historical variables. The 11 variables represent three types of surface deposits (lacustrine clay, glacial till and rocky deposits), three types of drainage, four variables related to settlement (agricultural land, urban land, paved roads and secondary roads) and one variable representing burned areas during the 20th century (geo-referenced data from aerial photographs and remote sensing data dated from 1924 to 2011; SOPFEU database). The vast majority of burned areas dated from the period 1930–1950, and mainly from the 1930s. Apart from paved and secondary roads, which were expressed in kilometres, all other variables were expressed as percentages of land area per cell. This data matrix was standardized and then converted to a Euclidean distance matrix prior to spatially constrained clustering. All clustering analysis were performed with the 'const.clust' package (v 1.2; http://numericalecology.com/rcode) included in the R freeware (v 3.1.2; R Foundation for Statistical Computing, Vienna, AT; http://www.r-project.org/.).

Results

In the pre-industrial era (Table 1), spruces (*Picea* spp.), balsam fir (*Abies balsamea*) and paper birch (*Betula papyrifera*) were the most frequently mentioned taxa (78.1–65.7% of all taxa lists). Pines (*Pinus* spp.), poplars (*Populus* spp.), white cedar (*Thuja occidentalis*) and yellow birch (*Betula alleghaniensis*) were also common (31.5–14.2%). The most dominant taxa (listed as rank 1) were spruces and fir (46.5% and 20.8%, respectively). Spruces were more frequently mentioned at rank of 1 than ranks 2–4, indicating that they tended to dominate the canopy when present.

Comparison of pre-industrial and modern forest composition highlights significant changes at the regional scale (Table 1). Maples (*Acer* spp.) and poplars have experienced the largest prevalence increases (+47.0% and +38.5%, respectively). With regard to dominance, poplars and paper birch increased by +19.9% and +8.1%, while spruce and fir decreased by −27.6% and −7.8%.

At the landscape scale, spatially constrained clustering highlights a strong pattern within the composition of the pre-industrial forests (Fig. 2a). In group 1a the most frequent and dominant taxa were spruces, fir and paper birch. Group 2a differed from the first group by its stronger balsam fir dominance. Dominated by white cedar, pines and poplars, Group 3a clearly stood out from the rest of the study area. Group 4a covered the southern portion of the study area and was dominated by poplars, spruce and paper birch. In contrast, the modern era (Fig. 2c) comprises five groups dominated by conifers, mainly spruces

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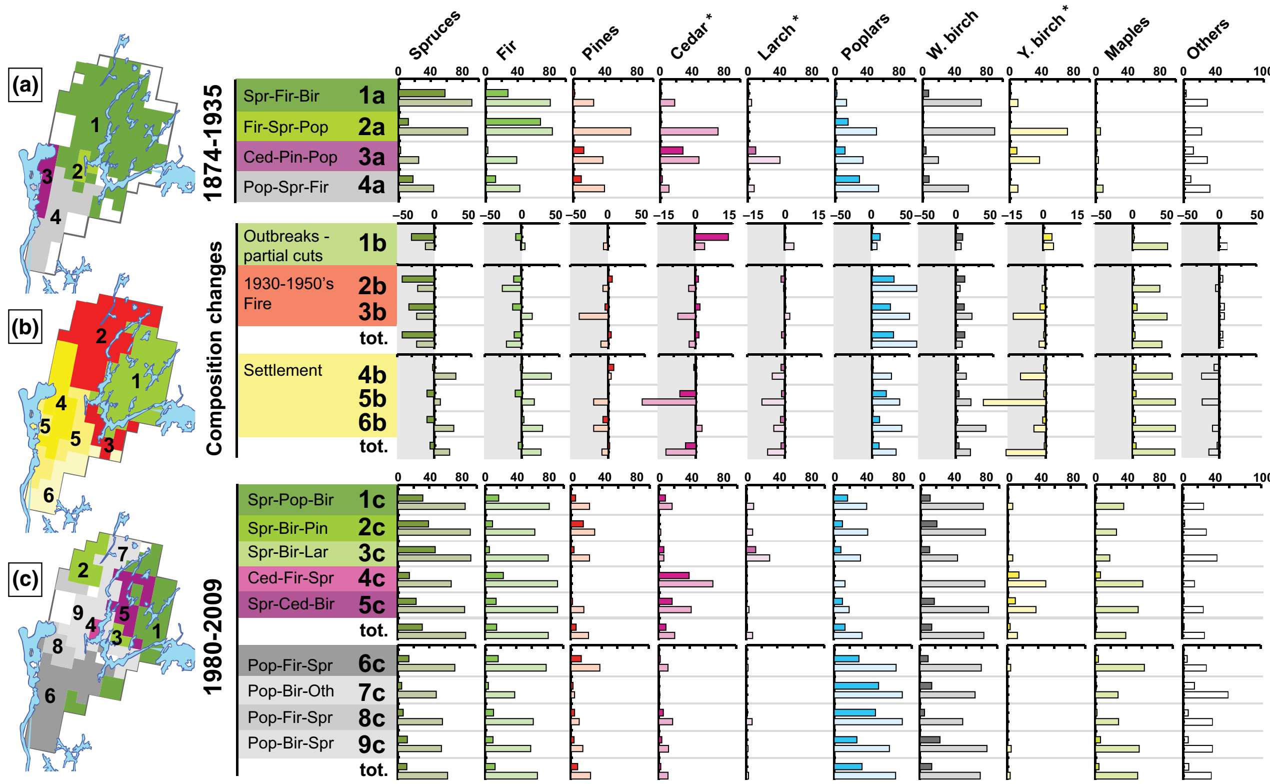

Fig. 2. Spatially constrained clustering groups with pre-industrial (**a**) and modern (**c**) compositions. Spatially constrained clustering groups with environmental and historical variables (**b**). For each taxon, histograms represent dominance index (header in full colour bar) and frequency index (bottom light colour bar) in percentage for composition groups (**a** and **c**) and differences between modern and pre-industrial composition for environment–historical groups (**b**). Composition groups are captioned by their first three dominant taxa (*Spr*: spruce, *Fir*: balsam fir, *Bir*: paper birch, *Pop*: poplars, *Ced*: white cedar, *Pin*: pines, *Lar*: larch, *Oth*: other). Note that histograms (**b**) of the taxa captioned by a * are represented on a smaller scale (−15%, +15%).

Table 1. Total prevalence index and ranked frequency index (F_{ir}) of major taxa throughout the study area for pre-industrial (1874–1935) and modern (1980–2009) periods. The dominance index corresponds to F_{ir} = 1.

Taxa	1874–1935 (n = 5207)					1980–2009 (n = 4749)				
	Prevalence (%)	F_{ir} (%) 1	2	3	4	Prevalence (%)	F_{ir} (%) 1	2	3	4
Spruces	78.1	46.5	22.9	11.0	8.6	71.7	18.9	16.2	17.1	17.1
Balsam Fir	70.4	20.8	44.9	11.6	9.4	70.7	13.0	16.9	20.3	17.4
Pines	31.5	5.2	4.0	5.2	15.3	24.2	8.0	5.2	4.6	4.8
White Cedar	19.8	3.1	2.3	5.1	16.3	15.2	5.2	2.7	2.3	3.1
Larch	8.0	1.9	3.3	2.4	2.2	4.7	0.7	1.3	1.2	1.5
Poplars	24.8	8.7	4.0	5.0	17.3	63.4	28.6	15.3	10.5	7.3
Paper Birch	65.7	7.3	15.0	55.4	17.3	78.8	15.4	23.0	20.9	17.7
Yellow Birch	14.2	1.7	3.5	4.2	13.5	6.9	1.6	1.5	1.2	1.5
Maples	1.1	0.1	0.1	0.1	0.1	48.1	3.1	8.3	12.3	16.4
Others	4.6	4.7	0.0	0.0	0.0	46.2	5.5	9.5	9.6	13.2
Total		100.0	100.0	100.0	100.0		100.0	100.0	100.0	100.0

and fir, but also including two groups where white cedar is among the three dominant taxa (Groups 4c and 5c). The remaining four modern groups cover the rest of the study area, and are dominated by poplars, spruces, paper birch and fir.

Spatially constrained clustering based on environmental and historical variables retained six groups (Fig. 2b). Group 1b correspond to mixed drainage-deposit hills not settled or burned during the 20th century. Groups 2b and 3b represent areas of mixed drainage-deposit hills which

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have largely burned over the period 1930–1950. Finally, groups 4b, 5b and 6b were mostly settled during the 20th century (cropland and urbanization) in lowlands dominated by lacustrine clay deposits.

These environmental–historical groups highlight strong patterns of compositional changes across the landscape. Groups 2b and 3b, which were burned between 1930 and 1950, experienced a sharp decrease in prevalence and dominance of spruces and fir, and concomitant strong increases of poplars. Conifer dominance generally decreased slightly in settlement groups (4b, 5b and 6b), while the prevalence and dominance of poplars and paper birch increased. Group 1b, which was not burned or settled during the 20th century, exhibited a slight decrease in spruces and fir and also experienced an increase in dominance of white cedar. Finally, maples experienced a sharp increase in prevalence over time in all groups.

Discussion

Pre-industrial composition and vegetation changes at the regional scale

Our results show a regional strong increase in early successional (poplars, paper birch) and mid-successional (maples) deciduous taxa at the expense of pre-industrial dominant conifers (mainly spruces and fir). Regional pre-industrial forest composition and post-industrial changes similar to our study area have been widely documented across eastern temperate and boreal North America (Siccama 1971; Lorimer 1977; Abrams 1998; Bürgi et al. 2000; Jackson et al. 2000; Dyer 2001; Cogbill et al. 2002; Friedman & Reich 2005; Pinto et al. 2008; Dupuis et al. 2011; Thompson et al. 2013). Studies in northern Europe have reported a post-industrial rejuvenation of forest landscapes, although modern forest management and intentional suppression of deciduous trees have shifted composition from mixed to coniferous forest (Östlund et al. 1997; Axelsson et al. 2002; Lilja & Kuuluvainen 2005).

The land survey records used in this study were conducted from the end of the Little Ice Age (Mann & Jones 2003; Moberg et al. 2005; Gennaretti et al. 2014). Regional annual mean temperatures have since increased by approximately 1 °C (http://berkeleyearth.lbl.gov/locations/47.42N-79.34W, accessed 23 Jul 2015). Eastern Canadian climate has also become moister (Tardif & Bergeron 1997; Zhang et al. 2000; Girardin et al. 2004) and, combined with fire suppression policies, has led to a sharp decrease in fire frequency (Bergeron & Archambault 1993; Bergeron et al. 2006). Such changes could have shifted regional composition from cold-adapted to warm-adapted taxa and from fire-adapted to fire-sensitive taxa (Nowacki & Abrams 2008; Hanberry et al. 2012). However, these climate-related changes do not seem to have significantly influenced our results since the taxa having experienced the greatest increase (poplars and paper birch) are boreal fire-adapted species (Perala 1991; Safford et al. 1991). Increase in prevalence of maples (mostly red maple, *Acer rubrum*; according to modern inventories) could be due to rising temperatures (Tremblay et al. 2002; Fisichelli et al. 2014; Zhang et al. 2015) and have also been associated with the decrease in fire activity (Nowacki & Abrams 2008). On the other hand, red maple is a 'super generalist' species that is largely favoured by disturbance (Walter & Yawney 1991; Abrams 1998; Fei & Steiner 2009), even including fire at its northern range limit in the study area (Zhang et al. 2015).

Pre-industrial composition at the landscape scale

Spatially constrained clustering analysis highlights spatial structure in pre-industrial composition at the landscape scale (Fig. 2a). Most of the study area was dominated by spruces (Group 1a). Currently, black spruce (*Picea mariana*) is the main species in the study area, so it is very likely that it also dominated the pre-industrial landscape. Abundant glacial and rocky deposits in this hilly region and frequent fires in the pre-industrial period (Grenier et al. 2005) promoted black spruce due to its semi-serotinous cones that allow it to establish after fires (Viereck 1983; Viereck & Johnston 1990) and to maintain strong dominance in the landscape (De Grandpré et al. 2000; Pham et al. 2004; Bouchard et al. 2008; Cyr et al. 2012).

The area that was dominated by trembling aspen (currently the main species present in the area, Group 4a) in the pre-industrial landscape corresponded to an early successional stage and, in fact, was described as an area of '*old burnt*' by surveyors in the 1880s (data not shown), which probably corresponded to a 1870s fire. Trembling aspen is a fire-adapted species and is favoured by lacustrine clay deposits (Bergeron & Charron 1994; Bergeron 2000) that are abundant in these lowland area.

Finally, the area co-dominated by white cedar and pines in the pre-industrial period represents a contradictory association (Group 3a). White cedar is a fire-sensitive and shade-tolerant late successional species (Johnston 1990; Hofmeyer et al. 2009), while white pine (*Pinus strobus*) and red pine (*Pinus resinosa*), which are currently the main pine species in this area, are fire-adapted species (Wendel & Smith 1990; Flannigan 1993; Abrams 2001). Small-scale surface fires could maintain uneven-aged stands of white pine (Quinby 1991; Abrams 2001), and could also allow the maintenance of white cedar in the landscape. Landscapes surrounding large lakes such as Lake Témiscamingue may show strong spatial variation in terms of fire frequency and intensity compared to adjacent mainland landscapes (Bergeron 1991; Drobyshev et al. 2010) and could therefore explain the occurrence of small surface fires in this area.

Native Americans and naturalness of the pre-industrial landscape

Land-use practices of Algonquin-Anishinaabe population inhabiting the study area during pre-industrial times are not documented. However, use of fire has been reported as a common practice for Algonquin tribes (Clark & Royall 1996; Williams 2003; Munoz & Gajewski 2010). Hunter-gatherer populations usually burned small patches for habitation, to improve travelling and to manage wild animal or plant populations (Lewis & Ferguson 1988; Gottesfeld 1994). Although large crown fires which have widely favoured black spruce or poplars seem mainly linked to fire-favourable climatic conditions at the end of the Little Ice Age (Bergeron et al. 2006; Clifford & Booth 2015), the Lake Témiscamingue area was an important transit path and summer occupation spot during pre-industrial times (Riopel 2002), and white cedar and pines which co-dominated in the area were important keystone species for Algonquin communities (Danielsen 2002; Uprety et al. 2013a,b). Consequently, it seems likely that the Algonquin population used to manage this area and that they promoted dominance of white cedar and pines through small-scale surface burning or other management practices. Localized modification by the native community within the forest landscape have been widely documented across northeastern America (Delcourt & Delcourt 2004; Black et al. 2006; Munoz et al. 2014) and northern Europe (Josefsson et al. 2009, 2010; Rautio et al. 2016).

Post-industrial changes at landscape scales

Areas that were widely burned during the period 1930–1950 (mostly in the 1930s) recorded a shift from dominance of fire-adapted black spruce to early successional deciduous trembling aspen. The likely explanation for this shift is the high logging activity that prevailed during the 1920s and 1930s in the study area (Lienert 1966). These cuts may have removed much of the black spruce aerial seed bank, which allowed trembling aspen to become dominant after the 1930s large fires. Settled territories also showed a shift from dominance of main pre-industrial conifers to trembling aspen and paper birch (Groups 4b, 5b and 6b), which could clearly be explained by disturbances related to settlement (land clearing, logging, settlement fires, etc.).

The northeastern part of the study area, which neither burned nor was settled during the 20th century, shows a smaller decrease in black spruce pre-industrial dominance compared to burned areas, and an increased dominance of white cedar. Increased dominance of white cedar can be attributed to spruce budworm outbreaks (Frelich & Reich 1995; Bergeron 2000; Bouchard et al. 2006b), whose main hosts are balsam fir and spruces, as well as former partial cuts of large pine and spruce trees (Heitzman et al. 1997; Larouche et al. 2011).

Implication for forest restoration and management

In this regional context, composition restoration through forest management should aim to promote conifer dominance. This could be achieved through partial cutting in mixed stands dominated by trembling aspen to accelerate succession towards coniferous stands (Man et al. 2008; Bose et al. 2014). However, considering the potential impacts of climate change, it would be important to develop an adaptive restoration plan (Harris et al. 2006; Millar et al. 2007; Choi et al. 2008). The pre-industrial dominance of some conifers (black spruce, pine) was largely the result of higher fire frequency compared to those anticipated for the future (Bergeron et al. 2006). Moreover, the increase in deciduous species abundance throughout the 20th century probably accentuated this phenomenon by decreasing forest fire susceptibility (Nowacki & Abrams 2008; Terrier et al. 2013). Restoration measures could seek to promote dominance of late successional conifers and deciduous species, which are not dependent on fire (balsam fir, white spruce, white cedar, yellow birch).

Conclusion

Combinations of environmental gradients, recurrence of natural disturbance and perhaps Native Americans' land use have structured distinct pre-industrial landscapes. Frequency and intensity of fires were the main drivers of forest dynamics and composition across the landscape. Fire remained an important driver of post-industrial compositional changes, but the appearance of Euro-American disturbances, including logging and settlement fires, disrupted historical forest dynamics. Consequently, Euro-American settlement has led to a major shift in forest composition at the regional scale, promoting a strong dominance of early successional deciduous species. Climate change did not seem to have an important influence on the compositional changes that are documented in this study.

These results document the forest naturalness within the region, and then provide results for forest management and restoration. These results also help to create a baseline for future climate-driven changes, which are predicted to be quite dramatic in biogeographic transition zones (Parmesan et al. 2005). Many forest landscapes such as our study area are recovering from major land-use changes

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(Foley 2005; Rudel et al. 2005), which can control forest dynamics much more than climate changes (Bodin et al. 2013; Abrams & Nowacki 2015; Nowacki & Abrams 2015). Thus, land-use legacies could be considerable drivers of future landscape changes and should be seriously considered when modelling and predicting future climate-driven ecological changes.

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