



## Eastern white cedar long-term dynamics in eastern Canada: Implications for restoration in the context of ecosystem-based management



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### ABSTRACT

Eastern white cedar (*Thuja occidentalis* L.) has been identified as a target tree species for ecological restoration in northeastern North America. Insight into long-term population dynamics since preindustrial times is key to guiding restoration efforts. In this study, we used a large set of early land survey data to assess the status of eastern white cedar in preindustrial forests across a large area (78,000 km<sup>2</sup>) of eastern Canada, and to evaluate subsequent population changes. In addition, we used early forest inventory data, which were available for a restricted portion of our study area, to assess the role of white cedar early dynamics in the success of its subsequent development. Our results show that the species was frequent (29.1%) and dominant (13%) in preindustrial forest landscapes. However, preindustrial frequency and dominance of white cedar displayed broad spatial variability, which suggests that several factors controlled its abundance. Following European settlement and logging, white cedar dominance and frequency decreased respectively by –6.2% and –12.1%, and these changes were also variable across the study area. Southern populations experienced the less pronounced decrease, and even a substantial increase in frequency in many areas that were affected by agricultural land abandonment. Northern populations experienced the largest decrease, especially on private lands. However, some northern areas locally experienced an increase in white cedar frequency and dominance due to partial natural and human disturbances (insect outbreaks, partial cutting). The presence of advanced regeneration at the time of partial disturbance is a key factor that allows white cedar to become dominant. These results help to identify areas with important needs and potential for restoration and support partial cutting systems with protection of advanced regeneration as a promising management practice for promoting white cedar.

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### 1. Introduction

A long-term ecological perspective is essential for planning ecosystem conservation and restoration (Higgs et al., 2014; Jackson and Hobbs, 2009; Willis et al., 2007). Forest historical baselines help identify target species and set quantitative objectives for restoration (Egan and Howell, 2001; Lindbladh et al., 2007). In northeastern North America, early land survey records have been widely used to reconstruct long-term changes in forest characteristics (Cogbill et al., 2002; Lorimer, 1977; Rhemtulla et al., 2009a;

Tulowiecki and Larsen, 2015) and, thus, may provide key knowledge for the successful restoration of the target species.

Eastern white cedar (*Thuja occidentalis* L.) is a long-lived tree species that is native to the northeastern mixed and boreal forests of North America (Fig. 1). It is considered to be a fire-sensitive and very shade-tolerant, late-successional species (Hofmeyer et al., 2009; Johnston, 1990). This tree species exhibits strong plasticity regarding habitat characteristics, with an optimal growth on mesic uplands, but can also develop well in both poorly drained lowlands, limestone cliffs or acidic outcrops (Hofmeyer et al., 2009; Johnston, 1990). A decrease in white cedar populations since preindustrial times has been reported by several studies throughout its natural range, a trend that has been associated with past logging, as well as the sensitivity of the species to stand-replacing disturbance (fire, clear-cut; Aubé, 2008; Dupuis et al., 2011; Jackson

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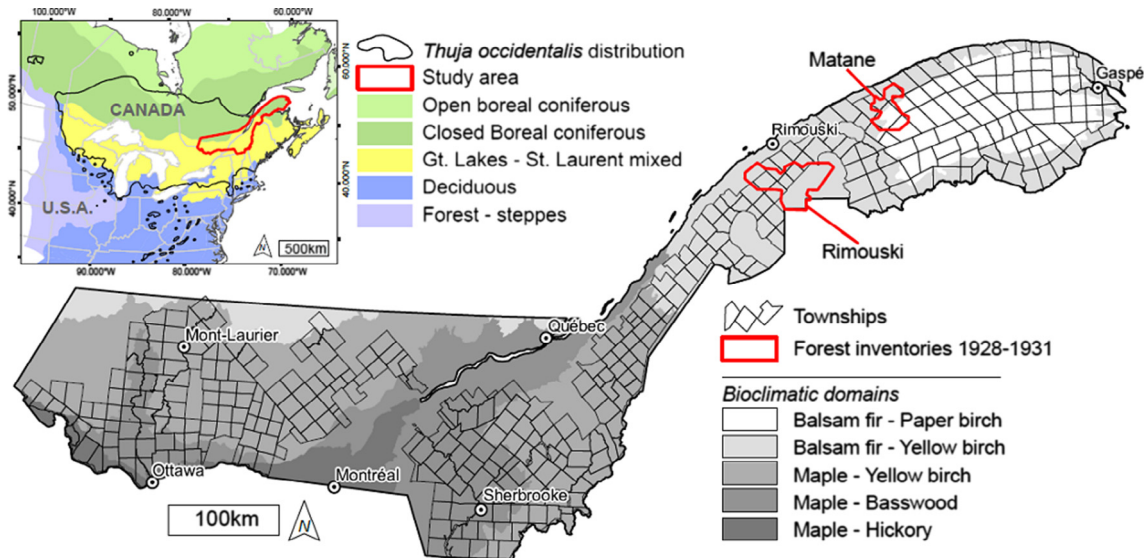


Fig. 1. Study area, location of historical land survey records and early forest inventories.

et al., 2000; Pinto et al., 2008) and to white-tailed deer (*Odocoileus virginianus*) browsing (Cornett et al., 2000; Heitzman et al., 1997; Rhemtulla et al., 2009b). White cedar is valued ecologically (e.g., old growth characteristics, wildlife habitat; Bouffroy et al., 2012; Grondin and Cimon, 2003), economically (mostly for specialized products such as shingles; Bouffroy et al., 2012) and spiritually by several First Nations (e.g., Danielsen, 2002). While these characteristics make white cedar an appropriate target species for restoration and ecosystem-based forest management in northeastern North America (Bouffroy et al., 2012; Grondin and Cimon, 2003; Horsley et al., 2003), challenges remain about how to achieve it. First, because compositional changes since the preindustrial era have not been spatially uniform (e.g., Danneyrolles et al., 2016a; Thompson et al., 2013), it is important to identify areas at the landscape-scale with important needs and potential for restoration (Bolliger et al., 2004; Zenner and Almendinger, 2012). Second, while partial cutting management is usually recommended to enhance white cedar growth and recruitment (e.g., Larouche et al., 2011; Ruel et al., 2014), white cedar may be outperformed by its competitors in absence of regeneration in treated stands (Hofmeyer et al., 2009, 2010). Thus, an in-depth understanding of white cedar population trends across space since the preindustrial era could greatly help to identify key factors that may guaranty restoration success.

In this study, we used an extensive set of early land survey data (1795–1940) to assess the abundance of white cedar in preindustrial forest landscapes of southern Quebec, and to evaluate population changes throughout this region. In addition, we used early forest inventory data (1928–1930) which were available for a restricted portion of our study area, to assess the importance of white cedar early dynamics (i.e., release as advanced regeneration) in the success of its long-term development. We discuss three general questions: (1) which factors controlled white cedar abundances in preindustrial forests? (2) Which factors have determined changes in white cedar populations? (3) What are the implications of our results for white cedar restoration?

## 2. Material and methods

### 2.1. Study area

The study area covers 78,000 km<sup>2</sup> in the southern part of Quebec, eastern Canada, and represents an east-west climate gradient

that extends for more than 1000 km within the northern range of white cedar (Fig. 1). Forests in this region represent a transition between temperate mixedwood and boreal conifer-dominated forests (Rowe, 1972). They encompass five bioclimatic domains, according to the ecological land classification of Quebec (Robitaille and Saucier, 1998; Fig. 1). Mean annual temperature (1981–2010) ranges from 6.8 °C to –2.2 °C from south to north, while mean annual total precipitation ranges from 850 mm to 1000 mm moving from east to west. The region is characterized by sedimentary bedrock of the Appalachian Mountain Chain to the east and metamorphic bedrock of the Canadian Shield to the west, which are both covered by surface deposits of alteration and glacial origins (Robitaille and Saucier, 1998).

### 2.2. Early land-survey and forest inventories data

Early land-survey data were extracted from logbooks reporting the original survey of 366 townships between 1795 and 1940 (Fig. 1). In the Province of Quebec, public lands were divided into townships of about 16 km × 16 km, and further subdivided into parallel ranges that were 1.6-km wide. Surveys were conducted along the boundaries of the township and range lines, where surveyors also described forest composition (Dupuis et al., 2011). In this study, only observations that mentioned lists of taxa (e.g., “pine, spruce, white birch and a few maples”) were retained, and were precisely georeferenced using historical and modern digital cadastral maps. Terrail et al., (2014) have compared these taxa lists with early forest inventories (1928–1931; see description below) available for a restricted portion of our study area (Fig. 1), and have shown that the position of taxa in the taxon list reflects their relative basal area. Thus, a rank was assigned to each taxon that was listed according to its position in the taxon list. Surveyors' observations also are divided into two geometric types: line descriptions and point observations. Observations were considered as linear segments when they clearly contained both a start and an end position along the range line, which were usually delineated by lot limit (about 260 m). Conversely, observations were considered as points when their position could be clearly located, but with no clear beginning or end along a range line, and were frequently distributed at each lot corners (about 260 m) or at every 10 chains (about 200 m). In order to incorporate these two types into the same database, a weight was assigned to each observation that represented the length of line observations and the mean spacing

of point observations, respectively (Dupuis et al., 2011). In order to exclude observations of forests that had been affected by logging, only surveys conducted before 1900 were retained, except for central Gaspésie (<7% of total observations), where logging remained rare until the mid-20th century. Finally, these records permitted the construction of a database comprising 117,970 observations (taxa lists) of forest compositions.

A large dataset from an early forest inventory (1928–1930) was also available for a restricted zone covering 3127 km<sup>2</sup> (Fig. 1). This inventory was conducted between 1928 and 1930 by the Price Brothers Company to evaluate the available wood volume on its timber limits (Terrail et al., 2014). Linear plots of 1012 m<sup>2</sup> (100.6 m × 10.06 m) were inventoried every 100–300 m along transects, which in turn were spaced at distances of 120–1700 m. In each plot, stems were classified and counted by species and 2-in. (5.1 cm) diameter at breast height (DBH; 1.3 m) classes, with a minimum DBH of 3 in. (7.6 cm). The forest type, age class, and occurrence of disturbances (fire, cutting, windthrow) were also recorded for each plot. In order to describe forests that had not been affected by human activities, only plots that were uncut and 80-years or older at the time of the inventory ( $n = 8827$ ) were retained for the analysis.

Both historical datasets (early land-survey and forest inventories) were compared with the Quebec government's decadal forest inventories from the three last decades (1980–2010s) to assess changes in modern forest characteristics since the preindustrial era. These inventories are based on 0.04-ha plots, which were distributed through stratified random sampling according to the different types of productive forest stands. Within these plots, all stems >2 cm DBH of each species are measured and inventoried, and only stems >7 cm DBH were used to calculate basal area (m<sup>2</sup> ha<sup>-1</sup>) by species. Spruces, poplars and maples species found within the modern inventories were grouped at the genus-level to match the taxa that were mentioned by surveyors. Only plots that were located within a maximum distance of 1.61 km from historical observations were retained for comparison, to ensure that modern and historical data are not too far apart, while retaining a maximum number of modern plots ( $n = 79,957$ ).

### 2.3. Data analysis

Early land-survey data were used to assess preindustrial white cedar abundance with two indices: dominance and frequency (Dupuis et al., 2011; Scull and Richardson, 2007). The dominance index refers to the cumulative weight of observations for which white cedar is ranked first in taxa lists, divided by the total weight of all observations. Similarly, the frequency index refers to the cumulative weight of observations in which white cedar is mentioned in taxa lists regardless of its rank in those lists, divided by the total weight of all observations. The accuracy of these two indices has been previously validated by comparison with early forest inventories (Terrail et al., 2014). This study has shown that frequency is a more comprehensive description but may underestimate some taxa, while dominance is a more robust metric to describe the abundance when dealing with the most abundant taxa. Thus, we have chosen to use both indices in order to provide a more complete description of white cedar abundance in preindustrial landscapes. These indices were calculated for the whole study area and for each bioclimatic domain (Fig. 1). The same indices were calculated with modern inventories using taxon-relative basal area. Taxa that represented <5% of the total basal area of a modern plot were removed from the list to obtain an equivalent number of taxa for historical and modern taxa lists. To assess spatial patterns of white cedar dominance and frequency, these indices were also mapped using a grid of 5 km × 5 km cells (25 km<sup>2</sup>) including at least four observations in both datasets,

resulting in a total of 2729 cells. Frequency was mapped as relative rank of frequency, which corresponds to the rank of white cedar frequency relative to the frequencies of other taxa that were present in a given cell (Terrail et al., 2014).

Cedar frequency and dominance at the 5 km × 5 km cell level were used as the basis for several statistical analyses. First, we tested whether modern frequency and dominance were greater or lesser than in preindustrial times using one-tailed permutation tests (10,000 replications) based on paired cells, for the whole study area and by bioclimatic domain. For each subset, we tested both alternative hypothesis (greater and lesser) and retained the one with the smallest  $p$ -value. Second, for both preindustrial and modern periods, we partitioned variation in white cedar frequency into components that were explained by climatic and topographic variables through partial linear regression (Legendre and Legendre, 2012). Only white cedar frequency was retained since it represents a more comprehensive metric than dominance (Terrail et al., 2014). Seventeen mean annual climatic variables (1981–2010 period) were interpolated from a weather station network using BioSIM 10.2 (Régnière and Bolstad, 1994; Environnement Canada, 2016). Ten topographic variables were extracted from a 30-metre resolution digital elevation model (elevation, slope, aspect) and from modern forest maps (drainage, six types of surface deposits; Berger, 2008). The complete list and descriptions of predictor variables are given in the supplementary material (Table S1). In the analysis, all climatic and topographic variables were used in both raw and squared form, to model potential non-linear relationships between predictors and response variables. Forward selection with permutation tests on the increase in  $R^2$  at each step (999 permutations, 5% significance level) was then used on both climatic and topographic variables sets separately, in order to select variables best explaining variation in white cedar frequency (Blanchet et al., 2008), and which were retained in the final model. Forward selection and variance partitioning analyses were performed in R with the *ordstep* and *varpart* functions, respectively, both included in the *vegan* package (v. 2.2; Oksanen et al., 2014).

In order to assess the effects of land-use and natural disturbances on changes in white cedar abundance at the 5 km × 5 km cell level, we used a conditional inference tree analysis, which is a specific form of regression tree analysis (De'ath and Fabricius, 2000; Hothorn et al., 2006). This non-parametric method uses predictor variables to reiteratively partition a dataset into subsets that are increasingly homogeneous with regard to the response. Partitions are based on the lowest  $P$ -values (obtained by permutation tests; 9999 replications) that are computed across all levels of all predictor variables. Change in white cedar frequency was used as the response variable, since this metric is more comprehensive than dominance (Terrail et al., 2014). Seven predictor variables that were linked to natural disturbance (fire and spruce budworm outbreak; *Choristoneura fumiferana* Clemens) and land-use (agricultural abandonment, cuts, plantations, land tenure, road networks) were used in the analysis (for a detailed description of the predictor variables, see Table S1). Based on previous studies (de Blois and Bouchard, 1995; Dupuis et al., 2011), we expected potentially divergent dynamics between southern and northern populations. Therefore, we also used latitude as an eighth predictor variable. Conditional inference tree analysis was performed in R with the *ctree* function that was included in the *party* package (v. 1.0–20; Hothorn et al., 2006).

Early forest inventories by Price Brothers were used to examine the changes in abundance of white cedar at a finer scale and with more accurate metrics. Within the two landscapes covered by these data (Rimouski and Matane; Fig. 1), we calculated mean white cedar basal area using early forest inventories and modern forest plots. Mean basal area was then calculated separately for upland (>400 m a.s.l.) and lowland (>400 m a.s.l.) areas, and for

the three main surface deposits (glacial, alteration, organic; Fig. S1; supplementary materials). We tested whether modern basal area was greater or lesser than in preindustrial times using one-tailed permutation tests (10,000 replications) for the whole dataset and by elevation and surface deposit categories. For each subset, we tested both alternative hypothesis (greater and lesser) and retained the one with the smallest  $p$ -value. Mean basal area was also mapped using a grid of 3 km  $\times$  3 km cells (9 km<sup>2</sup>) consisting of at least four observations in both datasets (early forest inventories and modern plots). To assess the importance of white cedar advanced regeneration on its change in basal area, we also mapped mean density of the smallest stems class recorded in early forest inventories (large saplings and small poles; DBH comprised between 7,6 cm and 12,7 cm).

### 3. Results

In preindustrial times, white cedar was frequent in southern Quebec (overall frequency of 29.1%; Table 1), and to a lesser extent dominant (13.0%; Table 1). However, both metrics exhibited substantial variation across the study area (Fig. 2). The species was particularly frequent and dominant in the balsam fir–yellow birch bioclimatic domain (38.9% and 18.4%, respectively; Table 1). White cedar was also frequent and dominant in the maple–yellow birch domain (27.6% and 10.8%, respectively; Table 1), and in the maple–basswood domain (23.5% and 13.6%, respectively; Table 1). It was less frequent and dominant in the maple–hickory and balsam fir–paper birch domains, at the southern and northeastern sections of the study area, respectively (Table 1, Fig. 2). A moderate proportion of overall variability in white cedar preindustrial frequency was explained by the climatic variables alone (11%; Fig. 3), while the joint effect of climatic and topographic variables explained another moderate fraction of the variation in frequency (8%; Fig. 3). Nevertheless, the higher white cedar frequency and dominance sector in the northeastern half of the study area represents the most striking pattern that existed at preindustrial times (Fig. 2).

White cedar frequency and dominance have decreased significantly throughout the whole study area since the preindustrial period (–12.1% and –6.2%, respectively; Table 1). Despite this general decreasing trend, white cedar also increased in both frequency and dominance in localized areas (Fig. 2.). Regarding frequency, 45.1% of cells displayed a decrease in frequency ranks, but 14.4% exhibited an increase. Similarly, 27.6% of cells recorded a decrease of more than 10% in dominance, yet 8.9% of the cells showed an increase of more than 10%. Our conditional inference tree analysis reveals that latitude is the first variable explaining this variability in changes of white cedar frequency (Fig. 4). Cells that recorded an increase in frequency are mostly located south of 46.34°N, particularly in areas that had experienced agricultural land abandonment (>2% of cell surface; Fig. 4). Conversely, the decrease in

white cedar frequency was more pronounced north of 46.34°N. Within this northern portion of the study area, cells that were lightly affected by spruce budworm outbreaks (<17% of cell surface) and with a higher proportion of private tenure (>10.8% of cell surface) recorded the most pronounced decreases in white cedar frequency (Fig. 4). As a result of these changes, the proportion of variance in white cedar frequency that was explained by the climatic variables alone had decreased (–8%; Fig. 3), while the proportion explained the joint effect of climatic and topographic variables slightly increased (+2%, respectively; Fig. 3).

At smaller spatial extent and finer resolution, our analysis of early forest inventories allows a deeper insight into sectors where white cedar abundance has locally increased. In the 1930s, total mean white cedar basal area was 2.09 m<sup>2</sup> ha<sup>–1</sup> (Table 2) and was distributed relatively homogeneously within the landscape (Fig. 5), although basal area was greater in lowland areas and on organic deposits (Table 2). Between the 1930s and modern times, our results record a significant increase in white cedar total basal area (+2.29 m<sup>2</sup> ha<sup>–1</sup>; Table 2), which was concentrated away from upland areas and glacial deposits where changes were less or not significant (Table 2). The greatest increase occurred on organic deposits (+14.74 m<sup>2</sup> ha<sup>–1</sup>; Table 2) and on lowlands area (+3.04 m<sup>2</sup> ha<sup>–1</sup>; Table 2) with abundant lake and river shores (Fig. 5), where white cedar was already more abundant in the 1930s. Moreover, our analysis shows that the area that experienced the highest increase in white cedar basal area (more than +10 m<sup>2</sup> ha<sup>–1</sup>; Fig. 5) corresponds to areas that showed the highest density of small stems of white cedar in the 1930s (large saplings and small poles; 7.6–12.7 cm DBH; Fig. 5). In this area, white cedar dominance increased (Fig. 2) at the expense of its competitor species (*Abies balsamea* [Mill.], *Picea* spp., *Betula* spp.; Fig. S2, supplementary materials).

### 4. Discussion

#### 4.1. White cedar variability in preindustrial forests

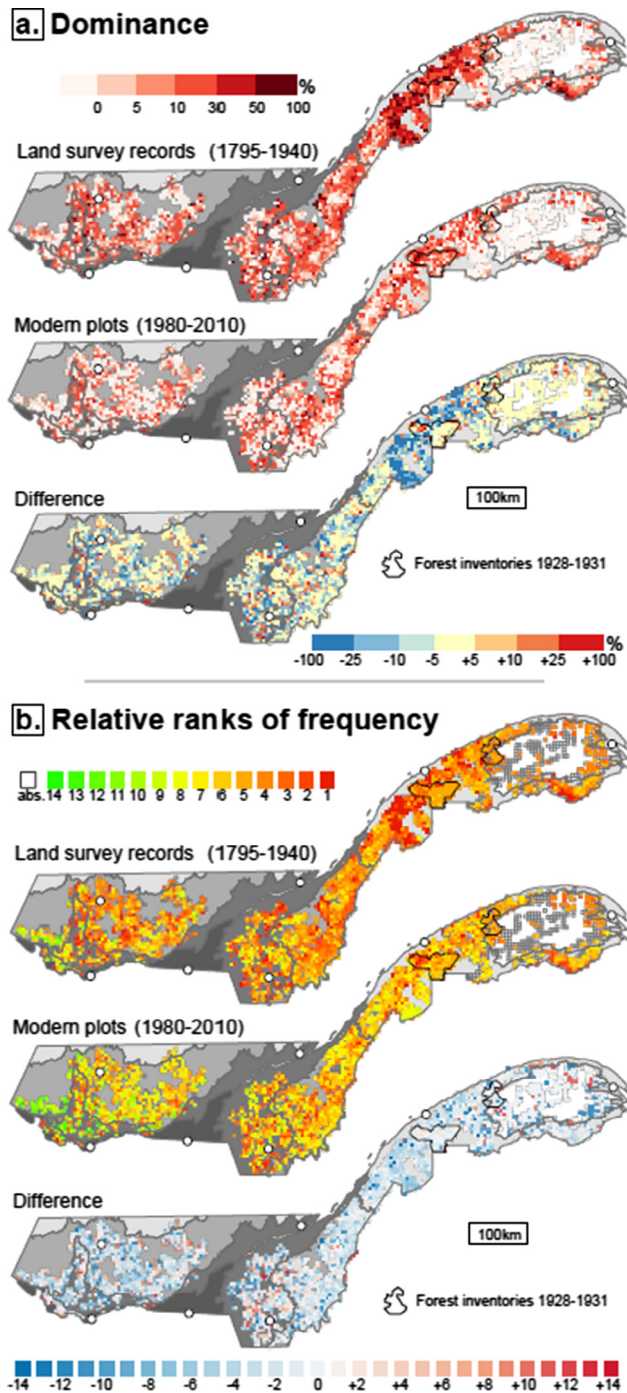
White cedar was an important tree species in southern Quebec preindustrial forest landscapes, with a frequency of nearly 30% and a dominance that was greater than 10%. However, the broad spatial variability in white cedar dominance and frequency suggests that several factors controlled its preindustrial abundance.

Our results suggest the influence of the climate gradient in structuring preindustrial white cedar abundance. The balsam fir–yellow birch bioclimatic domain, which is a transitional zone between temperate and boreal climates (Robitaille and Saucier, 1998), appears to provide optimal conditions for white cedar development. In areas further south, the warmer climate benefited more temperate tree species (e.g., *Betula alleghaniensis* Britton; *Acer* spp.) at the expense of white cedar (Barras and Kellman, 1998; Goldblum et al., 2010). Conversely, the colder boreal climate could

**Table 1**

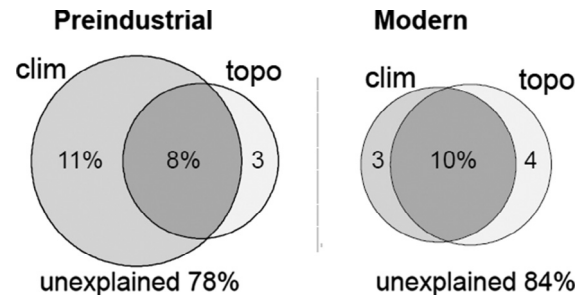
Dominance and frequency of white cedar in each time period (Pre.: preindustrial, Mod.: modern), for the whole study area and each bioclimatic domain. The  $\Delta$  indicate the results of cell-based permutation paired tests (+/– alternative hypothesis; \* $P > 0.05$ ; \*\* $P > 0.01$ ; \*\*\* $P > 0.001$ ; NS. Non-significant, all  $p$ -values are shown in Table S3; supplementary materials). Private (Private) and agricultural lands (Agri.) refer to the proportion of overall land area in the bioclimatic domain that are currently in this land use category. The total area represents the area covered by the 5 km  $\times$  5 km cells in each bioclimatic domain.  $n$  = number of observations.

Vegetation zone	n		Dominance (%)			Frequency (%)			Private %	Agri. %	Tot. area km <sup>2</sup>
	Pre.	Mod.	Pre.	Mod.	$\Delta$	Pre.	Mod.	$\Delta$			
Fir – Paper birch	5728	7203	2.8	2.9	NS	11.3	5.1	–***	7	0	7030
Fir – Yellow birch	40,957	22,397	18.4	9.0	–***	38.9	19.9	–***	51	7	17,197
Maple – Yellow birch	57,994	33,588	10.8	5.7	–***	27.6	16.6	–***	68	7	28,168
Maple – Basswood	12,307	9574	13.6	7.8	–***	23.5	19.9	–**	93	24	11,119
Maple – Hickory	984	987	6.1	9.4	+***	8.3	19.5	+***	96	36	928
Total	117,970	73,749	13.0	6.8	–***	29.1	17.0	–***	58	10	64,442



**Fig. 2.** Maps of white cedar dominance (a), and relative frequency (b) by cells of 25 km<sup>2</sup>. For each index, maps show the index that was calculated from land survey records (1795–1940) and from modern plots (1980–2010), as well as the difference between the two periods.

have limited white cedar establishment. For example, the species was completely absent above an elevation of 600 m in a mountainous sector at the northeastern extremes of our study area. However, both climatic and topographic variables explained only 22% of the preindustrial variability in white cedar frequency at the 25 km<sup>2</sup> cell scale. This may reflect the fact that white cedar abundance can be controlled by much finer-grain variation in landscape conditions (e.g., micro-climate, micro-topography, hydrography, drainage; Fahey et al., 2012), which cannot be revealed by our broad-scale analysis. Besides, the high preindustrial abundance of



**Fig. 3.** Variance partitioning of white cedar frequency in preindustrial and modern periods. Diagrams show the percent of variance in frequency that is explained by two sets of climatic (clim) and topographic (topo) variables, and their overlap. Correlation of single variables with white cedar frequency are shown in Table S2; supplementary materials.

white cedar in the northeastern sector of the study area may likely be explained by its complex topography shaping large areas of minerotrophic depressions, organics soils, lakes and river shores rather than the broad-scale climatic and topographic gradients (Lafamme et al., 2016).

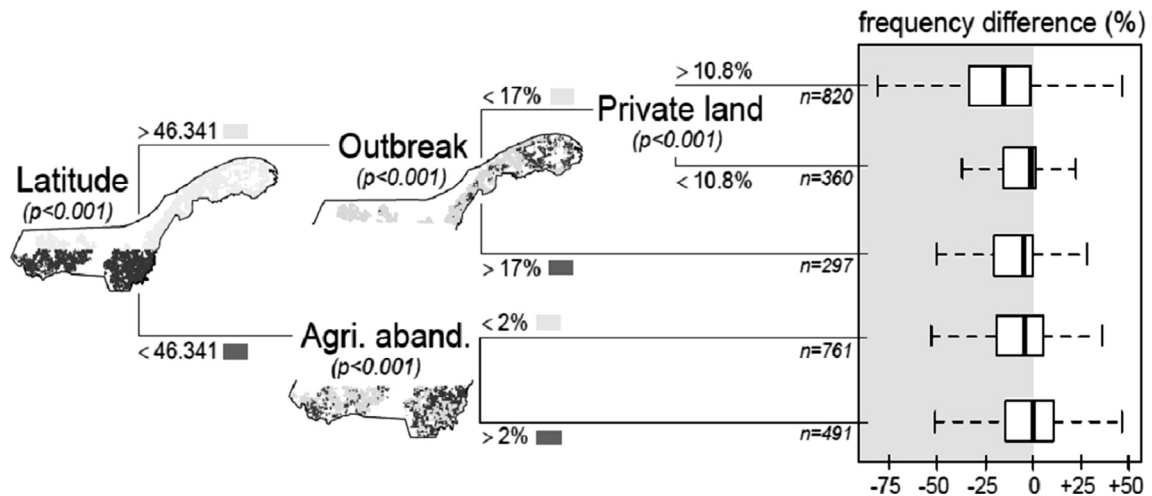
Large-scale patterns of preindustrial disturbances may also explain a part of the spatial variability in white cedar abundance. Preindustrial landscapes of southwestern Quebec were subject to relatively high fire frequency (Drever et al., 2006; Grenier et al., 2005) and tended to be dominated by fire-adapted taxa (e.g., *Picea mariana* [Mill.] BSP, *Pinus* spp.; (Danneyrolles et al., 2016a). Conversely, the moister climate of the eastern part of the province were less susceptible to fire and, thus, forest dynamics were primarily controlled by partial disturbances (e.g., insect outbreaks, windthrow; Boucher et al., 2009; Lorimer and White, 2003; Payette et al., 2017), which permitted the development of late-successional fire-sensitive taxa, such as white cedar (Bergeron, 2000; Bouchard et al., 2006; Frelich and Reich, 1995).

#### 4.2. Variability in white cedar abundance changes

While our results reveal a general trend of decreasing white cedar dominance and frequency from preindustrial times to present-day (Table 1), changes in white cedar abundance have also been variable throughout the study area (Fig. 2). More particularly, our results highlight divergent dynamics between northern and southern populations (Fig. 4).

Northern areas (>46.34°N; Fig. 4) where white cedar was most abundant during preindustrial times have experienced the largest decrease in white cedar frequency. As a shade-tolerant late-successional species, white cedar can be sensitive to stand-replacing disturbances (Heitzman et al., 1999; Hofmeyer et al., 2009; Johnston, 1990). Following European settlement, stand-replacing disturbances (land clearing, clear-cut logging, escaped-settlement fire) became more frequent and were closely linked to land allotment (Boucher et al., 2014; Whitney, 1994). We speculate that this explains why the decrease in white cedar frequency was greater in areas with the greatest proportion of privately owned lands. Moreover, white cedar has been intensively harvested for many settlement-related purposes (e.g., shingles, fences, railroad ties; Aubé, 2008; Dupuis et al., 2011; Langelier, 1906) and white cedar processing plants were mainly present in the northern part of our study area throughout the 20th C. (Gilbert and Rouleau, 2013).

Yet, northern areas that were strongly affected by spruce budworm experienced a less pronounced decrease in white cedar frequency compared to other northern areas. This is not surprising since partial disturbances, such as insect outbreaks, are known to



**Fig. 4.** Conditional inference tree showing a hierarchy of relationships between the potential predictor variables and changes in white cedar frequency between preindustrial and modern times. Predictor variables retained by the analysis are latitude, percentage of cell surface that was affected by spruce budworm outbreak, by agricultural land abandonment, and percent of private lands.  $n$  represents the number of cells in final groups that were determined by the analysis.

**Table 2**

Changes in mean basal area of white cedar between early forest inventories (1928–1931) and modern plots (1980–2010) by groups of elevation and of main surface deposits. Standard deviations in basal area are shown in parentheses,  $n$  corresponds to the number of plots by groups and  $\Delta$  indicates results of permutation tests (+/– alternative hypothesis; \* $P > 0.05$ ; \*\* $P > 0.01$ ; \*\*\* $P > 0.001$ ; NS. Non-significant; all  $p$ -values are shown in Table S4; supplementary materials).

Elevation	1928–1931		1980–2010		$\Delta$
	n	Basal area	n	Basal area	
Uplands (>400 m)	4485	1.29 (4.50)	1222	1.59 (6.77)	+*
Lowlands (<400 m)	4342	2.91 (5.75)	1888	5.95 (12.20)	+***
<i>Surface deposit</i>					
Glacial	5540	1.87 (4.82)	1750	1.91 (6.59)	NS.
Alteration	2292	1.36 (3.58)	1235	3.72 (8.93)	+***
Organic	495	7.25 (9.66)	292	21.99 (19.02)	+***
Total	8827	2.09 (5.22)	3389	4.38 (10.77)	+***

be an important factor allowing white cedar recruitment in the canopy layer (Bergeron, 2000; Bouchard et al., 2006; Frelich and Reich, 1995; Ruel et al., 2014). Prior to the second half of the 20th century, many forest landscapes were managed by partial cutting (e.g., high-grading, diameter-limit cutting), which also may have enabled better maintenance of white cedar population (Danneyrolles et al., 2016b; Heitzman et al., 1997; Larouche et al., 2011; Larouche and Ruel, 2015). Areas that were covered by our early forest inventories, where white cedar basal area has increased, are evidence of these long-term effects of partial disturbance. Since the 1930s, these landscapes have experienced two spruce budworm outbreaks (Boulanger and Arseneault, 2004) and have been essentially managed by partial cutting (mostly diameter-limit cutting; Boucher et al., 2009). These results also largely support the expectation that disturbance must be combined with an abundant white cedar pre-established regeneration to enable the species to become or remain dominant (Hofmeyer et al., 2009, 2010; Ruel et al., 2014).

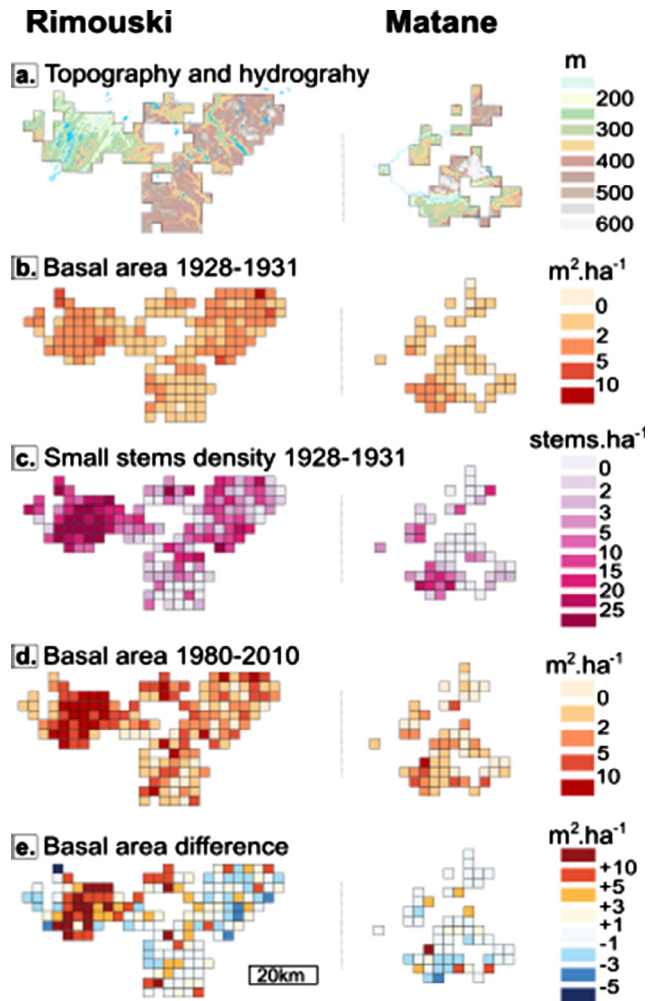
In the southern half of the study area, where white cedar was less abundant during preindustrial times, populations experienced a less pronounced decrease in frequency, and even an increase in many cells. More particularly, a substantial proportion of cells that were affected by agricultural abandonment, even in small proportion (>2% of cell area), recorded an increase in white cedar frequency. White cedar establishment on abandoned pasture lands has been documented in southern Quebec (de Blois and Bouchard, 1995). Browsing on competitors by cattle has likely promoted the establishment of these secondary white cedar stands,

which then developed into dense pure stands through vegetative proliferation (Lamy et al., 1999).

While it was not considered in our analysis, browsing by white-tailed deer may also have affected white cedar populations. As an indirect consequence of European settlement, white-tailed deer populations have increased throughout the whole range of white cedar since the preindustrial era (Côté et al., 2004). For white-tailed deer, cedar is more palatable than several of its associated species (Hofmeyer et al., 2009), and cedar stands provide good conditions for deer congregation in winter deer-yards (Morrison et al., 2003; Sabine et al., 2001). These combined factors may have led to a lack of white cedar regeneration, as has been reported in the US Great Lake States (Cornett et al., 2000; Hofmeyer et al., 2009; Rooney et al., 2002). White-tailed deer reaches its northern distribution limits in our study area and, thus, browsing should have resulted in localized impacts, depending upon deer population density (Larouche et al., 2011).

#### 4.3. Implications for white cedar restoration and management

Our study confirm the potential for white cedar restoration at its northeastern range, but also confront the commonly accepted idea that white cedar decline is a pervasive phenomenon throughout its range. White cedar populations have particularly declined in the northern area, while they experienced a less pronounced decrease, and even a substantial increase in frequency in many areas that were affected by agricultural land abandonment. This suggests better opportunities for restoration in the northern part



**Fig. 5.** Changes in eastern white cedar basal area between early (1928–1931) and present-day (1980–2010) forest inventories in Rimouski and Matane landscapes. Maps shows topography and hydrography (water body in blue; a), mean basal area per cell in 1928–1931 (b), mean density of small stems (7.6 cm to 12.7 cm in DBH) of white cedar per cell in 1928–1931 (c), mean basal area per cell in 1980–2010 (d) and changes in white cedar mean basal area per cell between early forest inventories and modern plots (e). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

of the study area. These opportunities may also be enhanced in the context of climate change with a projected increased climate suitability for white cedar at its northern range (Gagné et al., 2015; Périé et al., 2014). White cedar preindustrial abundance appears to have been mainly related to suitable landscape conditions (e.g., minerotrophic depressions, lake and river shores, organic deposits) and the species has experienced its most remarkable increase under these conditions. Due to the limited dispersal capacity of white cedar (Johnston, 1990), unaided recolonization could prove difficult on sites from which it had previously been totally removed (Asselin et al., 2001). Thus, these suitable habitat conditions should be targeted for restoration (Laflamme et al., 2016), as they may facilitate the re-installation of white cedar in the surrounding landscape matrix (Fahey et al., 2012).

Our results also highlight that the establishment and release phases caused by partial disturbance are key to maintain white cedar in stands and inform on approaches to restore the species. The combination of an abundant advance white cedar regeneration and partial disturbance is decisive to enable white cedar to become dominant (Hofmeyer et al., 2009, 2010; Ruel et al., 2014). Consequently, partial cutting (e.g., shelterwood or selection systems)

with protection of advanced regeneration appear to be an optimal silvicultural practice for promoting white cedar. Canopy openings created by partial cutting could also be used to establish new seedling cohorts (Larouche et al., 2011). Interventions that can facilitate white cedar recruitment in the sapling- or pole- size classes, including control of competitors or deer browsing, would thereafter be recommended (Hofmeyer et al., 2010). When regeneration is totally absent, enrichment planting within partial cuts openings should be considered (Larouche et al., 2011), as also proposed for the restoration of other long-lived conifers (e.g., Fahey and Lorimer, 2013; Hébert et al., 2013).

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## Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.foreco.2017.06.024>.

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