



The Changing Disturbance Regime in Eastern Canadian Mixed Forests During the 20th Century

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How strong was the anthropogenic imprint in the disturbance regime of eastern Canadian mixed forests during the 20th century? And how did it alter the tree species composition? To answer these questions, we reconstructed the 20th century anthropogenic disturbance regime and analyzed its impact on modern forest composition using historical and modern forest inventory and map data. Between 1895 and 2005, an equivalent of 144% of the study area has been logged and 19% burned. The logging rotation period has shortened from 152 years in 1895–1935 to 47 years in 1965–2005, due to increased industrial capacity. The fire rotation period decreased from 1668 years in 1895–1925 to 200 years during the peak of human settlement (1925–1955), and then increased to 2925 years in 1955–2005. The geographical progression of anthropogenic disturbances in the landscape has reflected the socio-economic context. During the 20th century, logging moved inland from the margins of the main water courses, reflecting the shift in wood transport from log driving on rivers to the densification of the road network in the second half of the 20th century. Most fires were located at low altitude, close to private lands suggesting ignitions from anthropogenic origins. Fire prone species (poplars) are mostly found within burned areas. Despite these disturbances, forest composition remained relatively stable, suggesting resilience of regional forest ecosystems.

Keywords: anthropogenic, disturbances, mixed forests, composition, disturbance characteristics

INTRODUCTION

Land use practices have become an important driver of forest ecosystem dynamics at several spatial scales since the onset of the industrial revolution. Present-day forests worldwide must cope with human related increase of disturbance frequency, intensity, and extent (Foster et al., 1998; Steffen et al., 2004; Foley et al., 2005; Ellis et al., 2010; Danneyrolles et al., 2019). These anthropogenic disturbances trigger shifts in disturbance regimes (Frelich, 2002), which in turn alter the composition and structure of forest communities and landscapes (Houghton, 1994; White and Jentsch, 2001; Foster et al., 2003; Nowacki and Abrams, 2015; Trumbore et al., 2015; Danneyrolles et al., 2019). Anthropogenic fires and logging represent increased large scale mortality compared to preindustrial background levels (Trumbore et al., 2015). Thus, it is important to document how human activities have modified the disturbance regime in forest ecosystems and their consequent impact on forest composition and structure.

At the interface of boreal and deciduous biomes in eastern North America, forest landscapes have been subject to intensive industrial logging and settlement fires for more than a century (Foster et al., 1998; Lorimer, 2001; Blanchet, 2003; Friedman and Reich, 2005; Boucher et al., 2009b, 2014). While, the pre-industrial disturbance regime in this region was dominated by windthrows, insect outbreaks, rare natural fires, and anthropogenic fires of debated frequency and intensity (Fahey and Reiners, 1981; Frelich and Lorimer, 1991; Williams, 2000; Lorimer and White, 2003; Simard et al., 2006; Blarquez et al., 2018), logging has become one of the main causes of tree mortality in the post-industrial landscape (Canham et al., 2013). Logging creates large open sites suitable for early successional tree species colonists. As a result, it has shifted overstory tree composition from uneven aged, old growth and shade-tolerant stands to even aged, young, shade-intolerant stands (Keenan and Kimmins, 1993; Foster et al., 1998; Fuller et al., 1998; Abrams, 2003; Boucher et al., 2009c; Danneyrolles et al., 2019). Relative to pre-industrial conditions, post-industrial forests often show an increase in sugar maple (*Acer saccharum*) (Brisson and Bouchard, 2003; Dupuis et al., 2011; Terrail et al., 2019), red maple (*Acer rubrum*) (Whitney, 1994; Whitney and DeCant, 2003), poplars (*Populus* spp.) (White and Mladenoff, 1994; Foster et al., 1998; Fuller et al., 1998; Leahy and Pregitzer, 2003), and white birch (*Betula papyrifera*) (Siccama, 1971; Whitney, 1994; Abrams, 1998; Bürgi et al., 2000; Hall et al., 2002; Leahy and Pregitzer, 2003; Dupuis et al., 2011), while shade tolerant species like white spruce (*Picea glauca*) and northern white cedar (*Thuja occidentalis*) have generally decreased (Jackson et al., 2000; Friedman and Reich, 2005; Boucher et al., 2006; Dupuis et al., 2011).

Although anthropogenic disturbances in the 19th and 20th centuries have combined with pre-industrial disturbances, their characteristics (rotation period, size, frequency, disturbance interval, and spatial pattern) are often poorly documented compared to the pre-industrial disturbance regime. Similarly, the link between anthropogenic disturbances and long term forest compositional changes has often been suggested, rather than demonstrated, because of the lack of data allowing spatially explicit reconstructions of disturbance regime and landscape composition. In this study we used archival (~1920) and modern forest maps and forest inventory plots to reconstruct the spatially explicit history of the post-industrial anthropogenic disturbance regime and parallel forest composition changes of the 20th century in a large area (3217 km²) of the eastern Canadian mixed forest. More specifically, our main objective is to quantify the main parameters (spatial pattern, rotation period, and extent) of the anthropogenic disturbance regime of the 20th century and evaluate what was the relative influence of these anthropogenic disturbances on the development of present-day vegetation?

MATERIALS AND METHODS

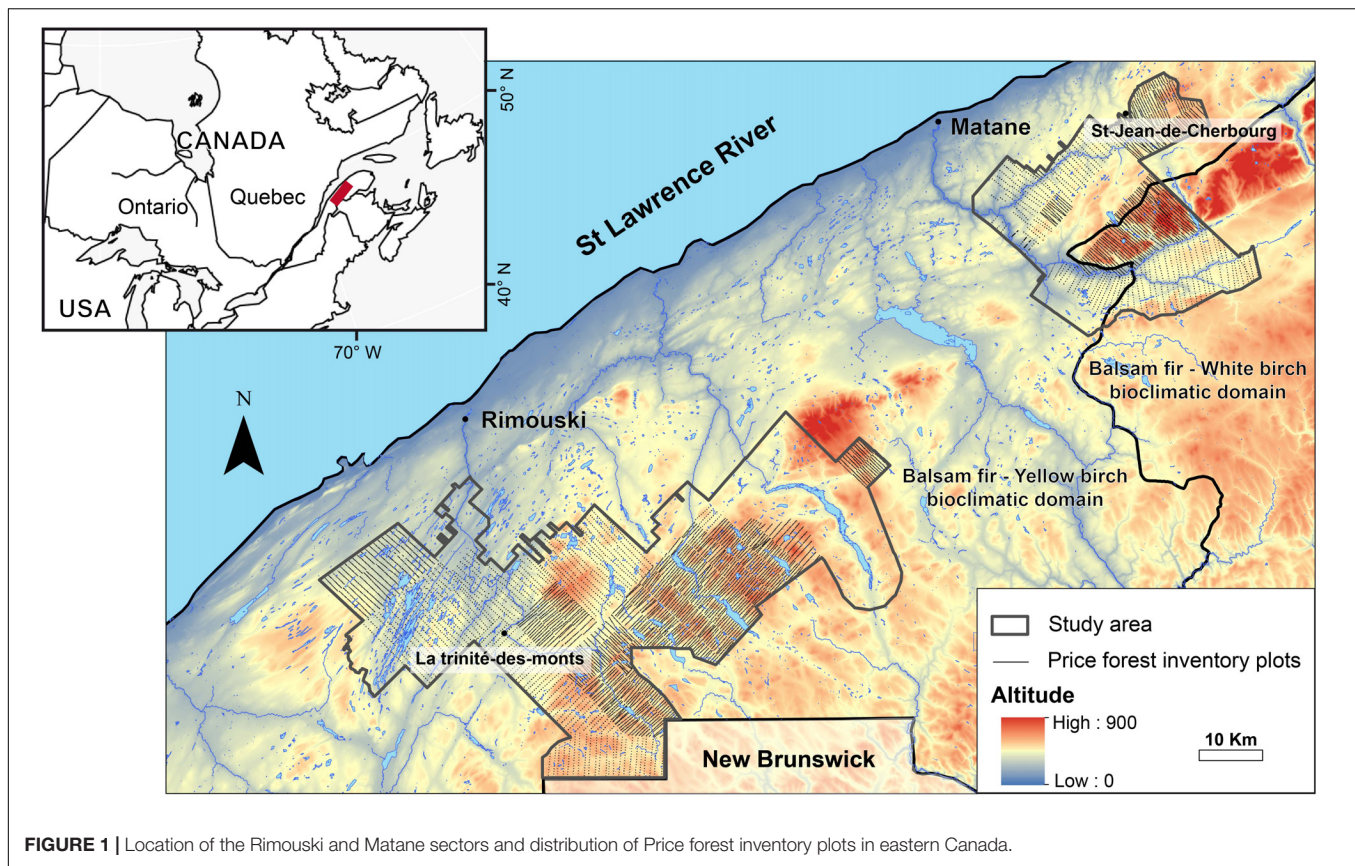
Study Area

The study area is located in the Lower Saint Lawrence Region (LSL) in the south-east of the province of Quebec, Canada (47° 92' N to 48° 91' N and 66° 84' W to 68° 86' W).

It is delineated to the north by the St. Lawrence River and to the south by the province of New Brunswick and lies within the Appalachian geological formation, characterized by sedimentary bedrock. The topography generally consists of low elevation hills with moderate slopes with mean and maximum elevations of 350 m and 910 m, respectively. Surface deposits are mainly from glacial and *in situ* weathering origins. The meteorological data (1981–2010) of Rimouski (20 m a.s.l.), Trinité-des-Monts (260 m a.s.l.), and Saint-Jean-de-Cherbourg (320 m a.s.l.) (Figure 1) show mean annual temperatures of 4.4°C, 2.5°C, and 1.9°C and annual total precipitations of 959 mm, 1100 mm, and 1138 mm, respectively, 30% of which falls as snow (Environment Canada, 2019).

This area is situated at the northern limit of the Great Lakes-St. Lawrence mixed forests at the transition between the temperate deciduous and the boreal coniferous forests (Rowe, 1972). Up to 75% of the study area corresponds to public forest, mostly in the backcountry, whereas 25% is private land, mostly along the St. Lawrence River. The study area is composed of two former forest concessions of the Price Brothers & Company: the Rimouski (2279 km²) and Matane (938 km²) sectors. Price Brothers & Company operated in the LSL region since the 19th century until the first half of the 20th century. The two sectors belong to the balsam fir-yellow birch bioclimatic domain (temperate mixedwoods), although the south-eastern part of the Matane sector, which is higher in elevation with steeper slopes, is located in the balsam fir-white birch domain (southern boreal forest) (Robitaille and Saucier, 1998; Grondin et al., 1999). Balsam fir (*Abies balsamea*), white spruce, and yellow birch (*Betula alleghaniensis*) are abundant in mesic sites in the balsam fir-yellow birch bioclimatic domain, while balsam fir, white spruce and white birch are abundant in mesic sites in the balsam fir-white birch domain. In both domains, trembling aspen (*Populus tremuloides*) and balsam poplar (*Populus balsamifera*) are also present. Sugar maple and red maple generally occupy hill tops and reach their northern range limit in the study area. Black spruce (*Picea mariana*) and northern white cedar generally occur on organic deposits along water courses (Robitaille and Saucier, 1998).

The study area has been subject to extensive anthropogenic fires, logging practices of increasing severity and spruce plantations during the 19th and 20th centuries. Fires were frequent at the margins of inhabited areas during the early 20th century due to slash burning for land clearing and agriculture (Fortin et al., 1993; Terrail et al., 2019). In the second half of the 20th century, population stabilization and effective fire suppression (Blanchet, 2003) decreased the frequency of fires to very low values. Logging practices during the 19th century and until the 1930s were mainly selective winter harvesting of large pine and spruce trees (Fortin et al., 1993; Boucher et al., 2009a). Logs were then transported to saw mills using water courses (Proulx, 1985). Forest operations slowed down during the great economic depression of 1929–1939 and vigorously recovered following the Second World War due to the increasing demand for residential construction material. In the 1940s, the rarefaction of large diameter trees prompted a progressive transition to the pulp and paper industry exploiting smaller diameters of spruce



and balsam fir (>3 inches DBH). This phase was also marked by the progressive introduction of chainsaws and log transport by trucks (Fortin et al., 1993). In the 1970s, dramatic changes occurred over the landscape, due to mechanization and the increased cutting rate in the snow-free season (Boucher et al., 2009a). Meanwhile, a severe spruce budworm outbreak (SBW) (*Choristoneura fumiferana*) between 1975 and 1992 (Boulanger and Arseneault, 2004) triggered extensive salvage logging and consecutive large scale spruce plantations (Fortin et al., 1993). To our knowledge, there is no documentation of pre-European anthropogenic disturbances in the LSL region. Nevertheless, Aboriginal influence in modifying the natural fire regime has been documented elsewhere in eastern North America (Williams, 2000; Blarquez et al., 2018), and could have participated in influencing pre-industrial forest composition.

Sources and Types of Maps Data

We digitized and georeferenced maps from several sources (Table 1). In their study, Boucher et al. (2009b) digitized and analyzed maps produced during an exhaustive 1930 forest inventory by the Price Brother's & Company. Along with these data, in the present study we discovered maps of a significant extension of the 1930 inventory and digitized stand age as well as all disturbance polygons. We also georeferenced and digitized 61 maps of the Price archive fund showing logged areas, logging provisions and fire polygons for different sections of the Rimouski and Matane sectors. These historical maps were georeferenced

using lakes and confined rivers from Quebec ministry of natural resources' modern maps (MFWP). In addition, we used a map of the LSL region made from a 1938 aerial survey showing fires of the ~1900–1938 period (Hébert, 1938). This map was previously analyzed by Terrail (2013). Our database also included more recent fire polygons obtained as shapefiles from the fire protection agency in Quebec (SOPFEU). Finally, we used the four decadal forest inventory maps produced by the Quebec's ministry of Forests, Wildlife and Parks (MFWP) from ground surveys and aerial photographs taken in 1973–1974, 1985–1986, 1993, and 2004, respectively. We digitized disturbance polygons for the first and second decadal inventory maps, while the third and fourth decadal maps were directly obtained as digitized polygons by the MFWP.

Creating a homogenous database of all disturbance polygons was somewhat challenging, mostly due to the variable resolution of maps and the occasional repetition of some polygons in different data sources, sometimes with different dates. When a same polygon was repeated on two maps with a spatial mismatch, both polygons were merged. When dates were inconsistent for a same polygon on two different maps, the oldest date was kept, as it indicates the first mention of the occurrence of the disturbance polygon. On the maps, logging polygons between 1895 and 1965 were identified as Cut Over zones, without a precise logging type. However, these cut over zones were most likely diameter limit selective logging operations, based on written accounts of logging practices at that time

(Price Brothers and Company Limited, 1944; Fortin et al., 1993) as well as an analysis of forest diameter structure in survey plots in 1930–1931 of logged areas against unlogged forest (see **Appendix 1** and **2**). Logging polygons for the period 1965–2005 were classified as partial cuts (25–75% basal area removal) or total cuts (more than 75% basal area removal) based on Quebec's department of forests decadal inventories. The 1970s SBW severity was equally categorized by Quebec's department of forests into moderate outbreaks (between 25 and 75% defoliation) and severe outbreaks (more than 75% defoliation).

The four main disturbance categories that have been considered in our analyses are (1) fire (1895–2005), (2) logging (1895–2005), (3) plantations (1955–2005), and (4) SBW (1975–2005). Although the natural or anthropogenic origin of fires is not directly known, their spatial pattern indicates a predominant anthropogenic origin (Terrail, 2013). In addition, even if a plantation is not a disturbance *per se*, plantations were included in our analysis as a human-imposed forest recovery pattern that caused important compositional difference compared to naturally regenerated stands.

The SBW of 1975–1992 and windthrows are considered natural disturbances in our database for which we have spatial information. Two additional outbreaks occurred in the region during the 20th century in 1947–1958 and 1914–1923 (Boulanger and Arseneault, 2004) for which we have no spatial information. Hence, the impact of SBWs during the 20th century might be under-estimated in our database. It is also important to note that SBWs might be indirectly influenced by human activity through climate change (Gray, 2008). Yet, we included the spatial data we have of the 1970s SBW to compare its extent and rotation period and to examine its interactions with previous and subsequent anthropogenic disturbances. Areas impacted by windthrows are negligible in extent compared to other disturbances and are only included for descriptive purposes of the disturbance regime. For each disturbance type, we estimated affected area (km² and % of the study area), rate (% of the study area /year) and rotation period (i.e., the time necessary for a disturbance to cover an area equivalent to the study area; Frelich, 2002). We also calculated the affected area disturbed per decade and the cumulative area disturbed for the four main disturbance types.

Sources and Types of Sampling Plots Data

We assessed tree composition in 1930–1931 and in 1985–2005. For the 1930–1931 period, we used a detailed forest inventory conducted by the Price Brothers & Company in a total of 16 345 rectangular plots (10 × 100 m) of 0.1 ha each, systematically distributed across the Rimouski and Matane sectors (**Figure 1**). Tree taxa (>3 inches; ~ 7.6 cm) were then tallied by 2 inches DBH classes. We georeferenced plots from their location on a 1930 map at the scale of 1: ~ 16000. Some taxa in the historical forest inventory were grouped at the genus level: Maples (*Acer* spp.), Spruces (*Picea* spp.), Pines (*Pinus* spp.), and Poplars. Other taxa were identified at the species level: balsam fir, yellow birch, white birch, northern white cedar, black ash (*Fraxinus nigra*), American larch (*Larix laricina*), and American elm (*Ulmus*

Americana). Similarly, present-day forest composition (1985–2005) was described from the sampling plots of the second, third and fourth decadal forest inventories (1985–1986, 1993, and 2004) conducted by the MFWP. The first inventory was excluded because plot location is not georeferenced. During these inventories, circular sampling plots of 0.04 ha were randomly stratified according to forest stand type, excluding non-forested, unproductive and inaccessible (slope > 40%) stands. Within plots, tree taxa were tallied by 2 cm DBH classes, although DBH classes <8 cm were excluded to match the 1930 plot database. We grouped the diametral structure (Density of stems / 10 cm diameter class) for each time period. Plots of the 1985–2005 time period were separated into two categories: naturally regenerated stands and plantations. We divided the study area into 333 grid cells of 3 km by 3 km. The cells contained at least four (4) inventory plots per period. We calculated the mean basal area per taxa for redundancy analysis (RDA). The study area division in 3 km by 3 km grid cells should attenuate the bias associated with the uncertainty of historical inventory sampling plots position and the variable resolution of maps used to reconstruct disturbance history. The historical inventory sampling plots position uncertainty range from 0 to 340 m and the resolution of maps used range from 1: 16 000 to 1: 190 000 (**Table 1**).

Redundancy Analysis

Two redundancy analyses (RDA) were performed. First, we used RDA in order to examine the effect of environment and vegetation composition in 1930–1931 on subsequent occurrence of disturbances. Second, we performed a partial RDA after controlling for environment and pre-industrial vegetation in order to examine the influence of disturbances on present-day forest composition. A grid of 333 cells of 3 km by 3 km covering the study area was generated to calculate, within each cell, disturbance cover percentage, environmental variables and basal area of tree taxa in 1930–1931 and 1985–2005. We calculated the cover percentage of Fire (1895–2005), Cut Over (1895–1935), Cut Over (1935–1965), Partial Cut (1965–2005), Total Cut (1965–2005), Plantations (1955–2005), and SBW (1975–2005). For environmental variables (**Table 2**), we used the mean value of 10 random points per grid cell to calculate altitude (m), slope (°), aspect (°), closest distance from main rivers (m), closest distance from secondary rivers and lakes (m), and closest distance from private lands (m). Cells located inside private lands have a distance of 0 m. We also calculated soil deposit types and drainage classes cover per cell. For the two RDAs, we selected only significant variables using forward selection with the package *vegan* in R (**Tables 4, 5**). Disturbances, taxa basal area of 1930–1931 and 1985–2005 variables were Hellinger transformed while environmental variables were standardized to zero mean and unit variance. The variation explained was reported using the adjusted *R*², which takes the number of predictor variables and sample size into account to prevent the inflation of *R*² values. A permutation test was applied to test for the significance of the models and axes. Partial RDAs were also performed to calculate the individual adjusted *R*² for each variable in environmental and forest composition of 1930–1931 and 1985–2005 datasets.

TABLE 1 | Historical maps of disturbance polygons in the study area.

Period	Number of maps	Map scale	Category mapped	Region covered	Source
1895–1931	1	1 : ~16 000	Logging, fire, windthrow, former agricultural land	Entire Rimouski and Matane sectors	Price Fund. Québec National Archives, Chicoutimi
1940–1952	2	1 : ~16 000	Logging, fire	Portions of Rimouski and Matane sectors	Price Fund. Québec National Archives, Chicoutimi
1945–1957	9	1 : ~32 000	Logging, fire	Portions of Rimouski and Matane sectors	Price Fund. Québec National Archives, Chicoutimi
1934–1945	8	1 : ~63 000	Logging	Portions of Rimouski and Matane sectors	Price Fund. Québec National Archives, Chicoutimi
1923–1955	24	not shown	Logging, fire	Portions of Rimouski and Matane sectors	Price Fund. Québec National Archives, Chicoutimi
1923–1938	1	1 : ~190 000	Fire	Entire Rimouski and Matane sector	Inventaire des ressources naturelles du Bas saint Laurent 1938. Quebec National Archive (ANQ-E16-P5_1938), Québec
1973–2005	4	1 : 20 000	Logging, fire, spruce budworm outbreaks, plantations	Entire Rimouski and Matane sector	Forest maps of the four decadal forest inventories. Ministry of Natural Resources of Quebec (MRN)
1932–1987	–	Polygon shapefiles	Fire	Entire Rimouski and Matane sector	SOPFEU database

TABLE 2 | Environmental variables used in the RDA analysis.

Variables	Description
Altitude (m)	Obtained from hypsometric curves (1: 20 000 maps) of Quebec's department of forests then transformed into a 400 m ² cell raster in ArcGIS 10.0.
Slope (°)	Calculated from the altitude raster using spatial analyst tools in ArcGIS 10.0.
Aspect (°)	Calculated from the altitude raster using spatial analyst tools in ArcGIS 10.0.
Distance from main rivers (m)	The closest distance to the four main rivers in the study area: Rimouski, petite Rimouski, Matane and petite Matane rivers. This variable was considered in the analysis due to the historical context of log transport method along the main watercourses.
Distance from secondary rivers and lakes (m)	The closest distance to secondary rivers and lakes in the study area.
Distance from private lands (m)	The closest distance from a private land. This variable was considered to test the hypothesis of the anthropogenic origin of fire polygons which are expected to be situated closer to private lands.
Superficial deposit	Cover percentage of the 7 deposit types: Alteration, fluvial, glacial, fluvio-glacial, lacustrine, marine, and organic
Drainage class	7 classes ranging from excessive to very bad according to Quebec's department of forests classification

TABLE 3 | Parameters of the 20th century disturbance regime in the study area.

Category	Time span	Number of years	Covered area (km ²)	Percent total landscape (%)	Rate (percent per year)	Rotation period (years)
Fire	1895–2005	110	596	19	0.2	594
	1895–1925	30	58	2	0.06	1668
	1925–1955	30	483	15	0.50	200
	1955–2005	50	55	2	0.04	2925
Logging	1895–2005	110	4633	144	1.3	76
	1895–1935	40	844	26	0.7	152
	1935–1965	30	1219	38	1.3	79
	1965–2005	40	2750	80	2	47
Plantations	1955–2005	50	571	18	0.4	282
Spruce budworm	1975–2005	30	1019	32	1.1	95
Windthrows	1895–2005	110	11	0.35	0.003	3000
All disturbances (Excluding plantations)	1895–2005	110	6259	195	1.7	56

TABLE 4 | Environmental and 1930–1931 basal area variables retained by forward selection in the RDA model to explain the 20th century disturbances.

Variable	Acronym	Individual adjusted R^2	Cumulated adjusted R^2	p -value	Within group selection order
Environmental variables					
Distance from main rivers	Main Rivers	0.084	0.088	≤ 0.001	1
Distance from private lands	PR	0.067	0.164	≤ 0.001	2
Weathering deposit	Wthr	0.013	0.204	≤ 0.001	3
Distance from closest water course	Water	0.007	0.220	≤ 0.001	4
Glacial deposit	Glac	0.012	0.233	≤ 0.001	5
Fluvial deposit	Fluv	0.004	0.240	< 0.01	6
Slope	Slope	0.009	0.246	< 0.01	7
Altitude	Alt	0.007	0.253	< 0.01	8
Aspect	–	–	–	> 0.05	–
Drainage	–	–	–	> 0.05	–
Fluvio-glacier deposit	–	–	–	> 0.05	–
Lacustrine deposit	–	–	–	> 0.05	–
Marine deposit	–	–	–	> 0.05	–
Organic deposit	–	–	–	> 0.05	–
Taxa basal area 1930					
<i>Picea</i> spp.	Pic30	0.076	0.079	≤ 0.001	1
<i>Thuja occidentalis</i>	Tho30	0.001	0.101	≤ 0.001	2
<i>Betula alleghaniensis</i>	Bea30	0.030	0.117	≤ 0.001	3
<i>Pinus</i> spp.	Pin30	0.017	0.128	< 0.01	4
<i>Abies balsamea</i>	Abb30	0.018	0.139	< 0.01	5
<i>Betula papyrifera</i>	Bep30	0.014	0.146	< 0.01	6
<i>Fraxinus</i> spp.	Fr30	0.006	0.151	< 0.05	7
<i>Ulmus</i> spp.	Ulm30	0.009	0.156	< 0.05	8
<i>Acer</i> spp.	Ace30	0.005	0.161	< 0.05	9
<i>Larix laricina</i>	–	–	–	> 0.05	–
<i>Populus</i> spp.	–	–	–	> 0.05	–

Gray colored variables are not significant.

TABLE 5 | Disturbance variables retained by forward selection in the RDA model to explain taxa basal area in 1985–2005.

Disturbance variables	Acronym	Individual adjusted R^2	Cumulated adjusted R^2	p -value	Within group selection order
Partial cut (1965–2005)	CP05	0.021	0.021	≤ 0.001	1
Fire (1895–2005)	FIRE	0.014	0.035	≤ 0.001	2
Plantations (1955–2005)	PL	0.011	0.046	≤ 0.001	3
Spruce Budworm outbreak (1975–2005)	SBW	0.008	0.051	≤ 0.001	4
Partial cut (1935–1965)	CO65	0.005	0.055	≤ 0.001	5
Clear cut (1965–2005)	CT05	0.005	0.059	≤ 0.001	6
Partial cut (1895–1935)	CO35	–	–	> 0.05	–

Gray colored variables are not significant.

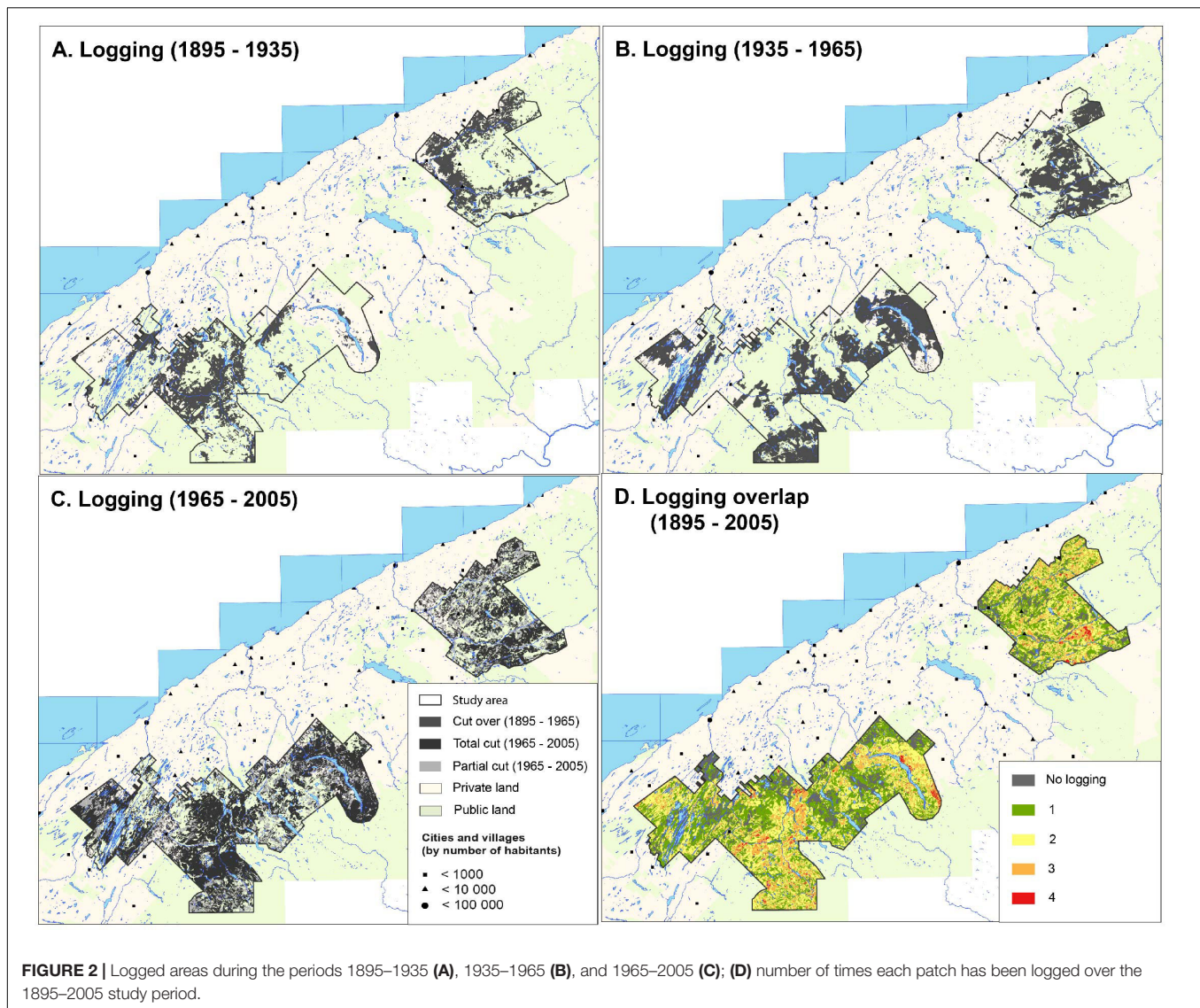
These analyses were performed using the R 3.0.3. software (R Development Core Team, 2016).

RESULTS

Description of the 20th Century Disturbance Regime

During the 20th century, logging was the most widespread disturbance type, followed by fire, the 1970s SBW and plantations. Windthrows were negligible compared to other considered disturbances, with a rotation period of 3000 years

(Table 3 and Figures 2, 3). The cumulative area logged between 1895 and 2005 attained 144% of the study area (Figure 4B). This indicates the some zones were logged more than once over the last 110 years. In total, 84% of the study area has been subjected to partial and/or total cut: 39% has been logged once, 34% twice, 10% thrice, and 1% logged four times. 16% of the study area has not been logged in our database. Approximately a third of the non-logged area has burned during the last century (Figure 2D). The unlogged, unburned area might have been subjected to non-documented anthropogenic disturbances absent from our data base, is located in inaccessible areas for logging, or reflects the bias associated to maps variable scales in our database.

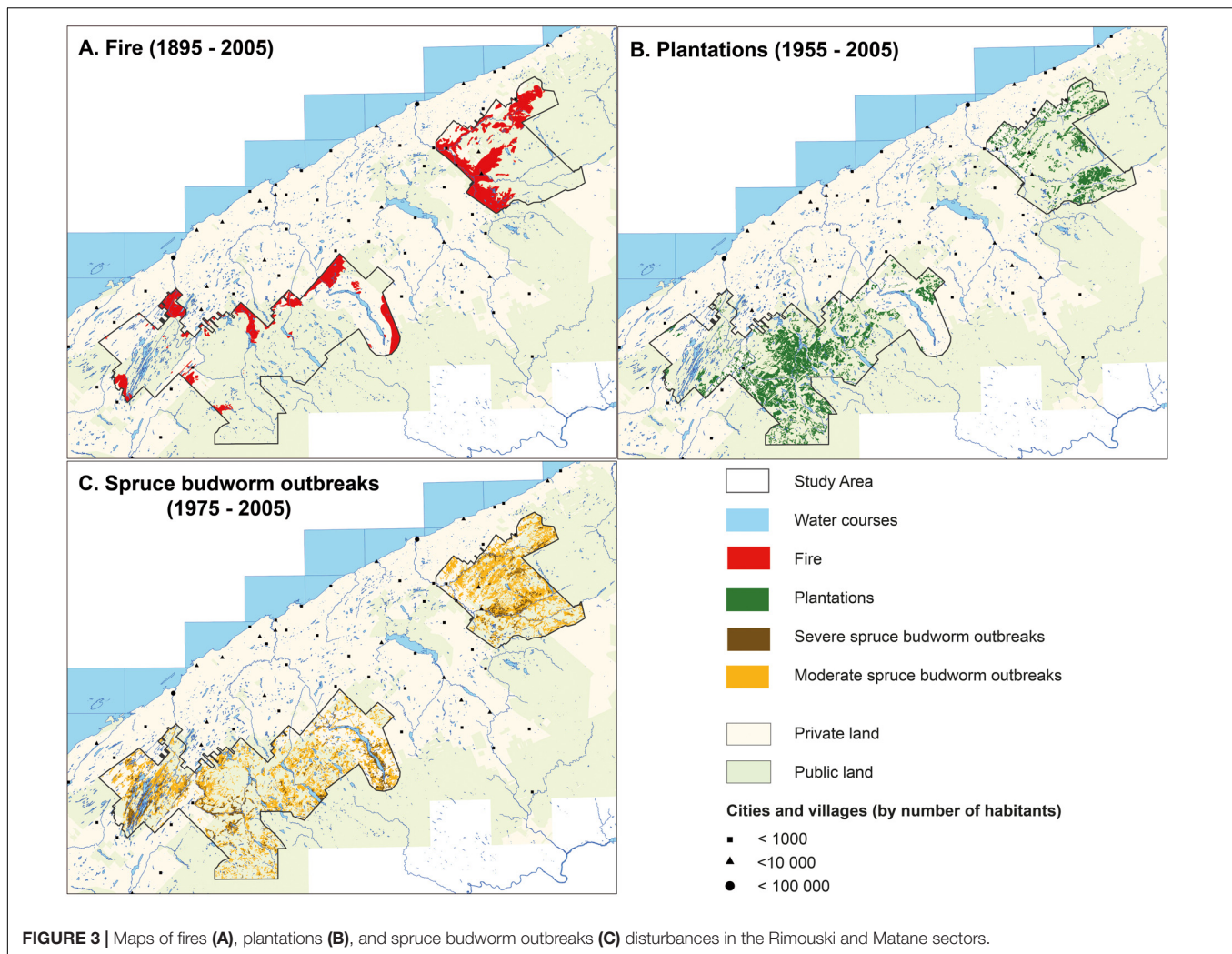


Logging rotation period in the study area between 1895 and 2005 corresponds to 76 years. However, logging rotation period has continuously shortened throughout the 20th century, due to increasing industrial capacity, from 152 years in 1895–1935, to 79 years in 1935–1965, and 47 years in 1965–2005 (Table 3). Fire events were clustered around 1925–1955 (Figure 4A), in conjunction with the population increased in the study region (Figure 4E). Between 1895 and 2005, fires burned 19% of the study area (Figure 4A), corresponding to a rotation period of 594 years. The fire rotation period decreased from 1668 years in 1895–1925 to 200 years in 1925–1955. Following the peak of settlement in the late 1950s, the fire rotation period increased to 2925 years (Table 3). Large scale plantations are relatively recent in the region and have covered 17.8% of the study area between 1955 and 2005 with a peak of 362 km² between 1985 and 1995 (Figure 4C). SBW data are available only for the recent time (1965–2005) and show a peak of 486 km² area affected between 1974 and 1986. The total area affected by the outbreak

is 31.7% (Figure 4D) corresponding to a rotation period of 95 years (Table 3).

Spatial Structure of Anthropogenic Disturbances

The RDA model indicates that the anthropogenic disturbances regime of the 20th century has been spatially structured by environmental variables and by the 1930–1931 tree composition (Adjusted $R^2 = 32\%$; Figure 5). This structure reflects human settlement and land-use history during the 20th century. The first RDA axis (20% of constrained variance) mostly expresses increasing distance from main rivers to the left (Individual $R^2_{adj} = 0.084$; Table 4) as well as the basal area of spruces in 1930 (Pic30; Individual $R^2_{adj} = 0.076$). The second axis (6% of constrained variance) shows a gradient from high Pines basal area in 1930 (Pin30, Individual $R^2_{adj} = 0.017$), steep slope (Individual $R^2_{adj} = 0.009$) and weathering deposit (Individual $R^2_{adj} = 0.013$) up to Glacial deposit (Individual



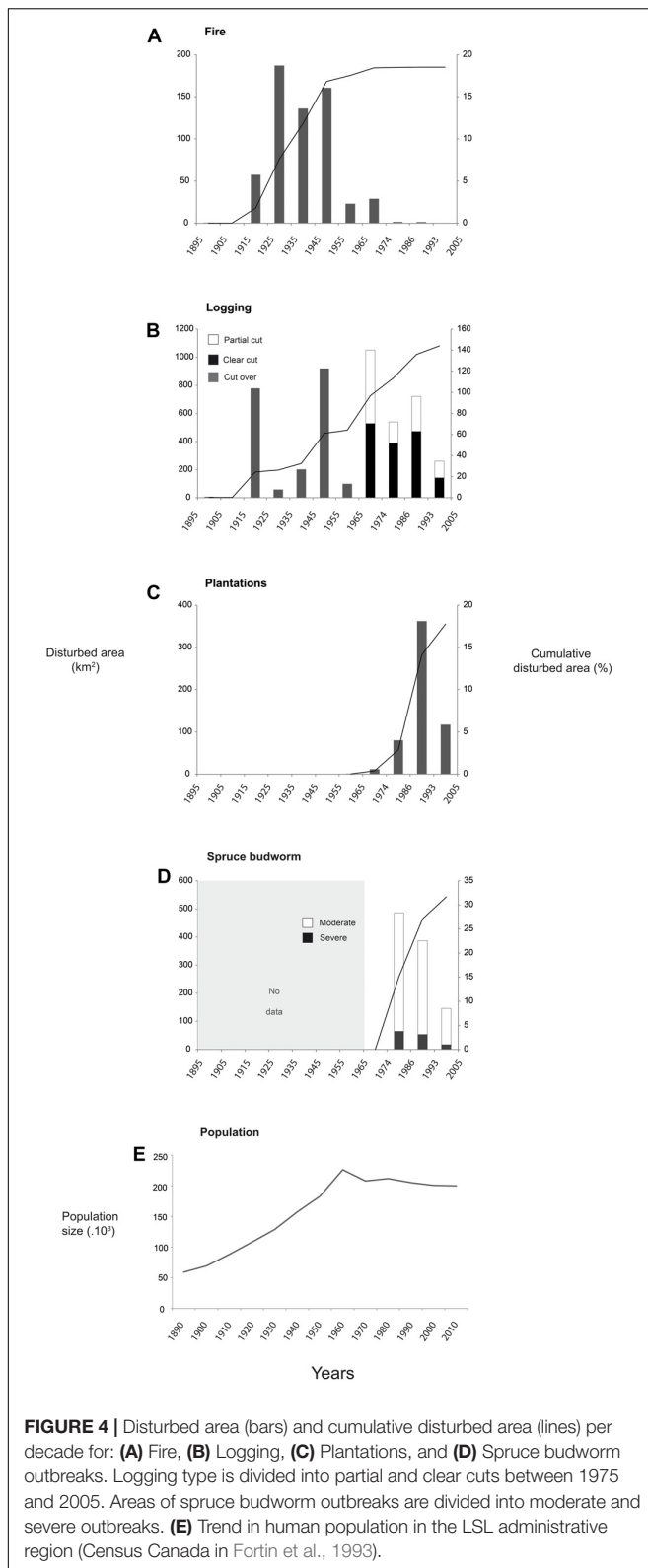
$R^2_{adj} = 0.012$) and high birch basal area in 1930 (Bea30 and Bep30, respectively, with Individual $R^2_{adj} = 0.030$ and 0.014). Distance from private lands (PR; Individual $R^2_{adj} = 0.067$) and altitude (alt, Individual $R^2_{adj} = 0.007$) are explained by both the first and second axis of the RDA. Cut over zones between 1895 and 1935 (CO35) are situated next to main rivers. Between 1935 and 1965, logging activities (CO65) moved away from main rivers (situated in the opposite direction of CO35 in the multivariate space) toward areas where spruces were still abundant. Between 1965 and 2005 logged areas (CP05 and CT05) became diffuse across the study region and showed no specific spatial location in the multivariate space. Plantations (1955–2005; PL) occurred in flat zones, while SBW is observed in steep zones. Finally, fires (1895–2005) occurred in low altitude areas close to private lands.

Modern Taxa Composition and Diameter Structure

According to the partial RDA, the 20th century disturbance regime explained 6% of the modern basal area (1985–2005) in the

landscape (**Figure 6**). The first RDA axis mostly express a gradient of partial cut (1965–2005) (CP05; Individual $R^2_{adj} = 0.021$; **Table 5**) while the second axis shows a gradient from fire (FIRE; Individual $R^2_{adj} = 0.014$) to spruce budworm outbreak (SBW; Individual $R^2_{adj} = 0.008$). The third axis shows a gradient of plantation (PL; Individual $R^2_{adj} = 0.011$). Partial cuts between 1965 and 2005, fires and plantations explain 4.6% out of the 6% of the variance among disturbance variables. Trembling aspen (Pot) is correlated to burned areas. Sugar maple (Acs) and yellow birch (Bea) are correlated to partial cuts between 1965 and 2005. Black spruce (Pim) is associated with plantations. Northern white cedar (Tho) is not explained by any studied disturbance type as it is perpendicular to all disturbances in the multivariate space.

Between historical (1930–1931) and present-day (1985–2005) periods, we observed a change in basal area and diameter structure of tree taxa. Total basal area increased noticeably by $5.1 \text{ m}^2/\text{ha}$ in naturally regenerating stands, while it decreased by $2.8 \text{ m}^2/\text{ha}$ in plantations (**Table 6**). Most plantations were likely thinned at the time of sampling. The increase in basal area in naturally regenerating stands is largely due to a threefold increase



of northern white cedar by 2.7 m²/ha and a nine fold increase in maples by 1.5 m²/ha. This increase was accompanied by an increase in the density of northern white cedar in all diameter

classes and an increase in maples density for small diameter classes (Figures 7, 8). A slight increase in basal area for spruces, balsam fir and poplars and a decrease in yellow birch and white birch also occurred (Figure 8), although an increased density of stems in small diameter classes occurred for these species in naturally regenerated stands (Figure 7). In plantations, 41% (7.1 m²/ha) of the mean basal area is represented by Spruces (Table 6) with a significant increase in stem density in the smallest diameter class for this taxa compared to historical and modern naturally regenerated stands values (Figure 7). The mean basal area of secondary natural regeneration of balsam fir (fir has not been planted) in plantations represent 44% (7.6 m²/ha). Balsam fir density has slightly increased in the smallest diameter class compared to historical and modern naturally regenerated stands values (Figure 7).

DISCUSSION

Anthropogenic Disturbance Regime of the 20th Century

During the 20th century, anthropogenic disturbances were omnipresent in the landscape, as for other regions of the eastern North American mixed forests (Foster, 1992; Whitney, 1994; Friedman and Reich, 2005). Fire activity was concentrated at low elevation during the settlement period, close to private lands suggesting ignitions from anthropogenic origins (Figures 3A, 5). Logging activities expanded from around main rivers during the first half of the 20th century toward inland areas and higher altitude by the second half of the century (Figures 2, 5), marking the transition from log transport by watercourses to the use of forest roads and trucks. Moreover, 18% of these logged zones have been subsequently transformed into plantations, mostly between 1985 and 1995, during the last SBW (1975–1990). Planted zones were chosen in backcountry accessible sectors and mostly planted with insect resistant black spruce (Pim), while the less accessible sectors on steeper slopes were disturbed by the SBW outbreak (Figures 5, 6).

Before European settlement, the pre-industrial disturbance regime of south-eastern Quebec and northern New England was dominated by secondary disturbances like windthrows and insect outbreaks (Blais, 1961; Lorimer, 1977; Bormann and Likens, 1979; Payette et al., 1990; Frelich, 2002; Lorimer and White, 2003). For the LSL region, this can be inferred from the old-growth, uneven aged forest structure of the pre-settlement forest, which was also dominated by fire-sensitive species (balsam fir, white spruce, eastern white cedar) (Etheridge et al., 2005; Boucher et al., 2009b; Dupuis et al., 2011). The very long rotation period we estimated for windthrows in the study area over the 20th century (about 3000 years; less than 1% of the landscape affected; Table 3) is considerably longer than the value of 1150 years estimated by Lorimer (1977) for Northern Maine between 1793 and 1827. This discrepancy may emphasize a relatively low occurrence of large windthrows in the study area. Indeed, wind storms that create large canopy openings are known to be infrequent in this type of mixed forests (Frelich and Lorimer, 1991; Lorimer and White, 2003). Nevertheless, windthrows could

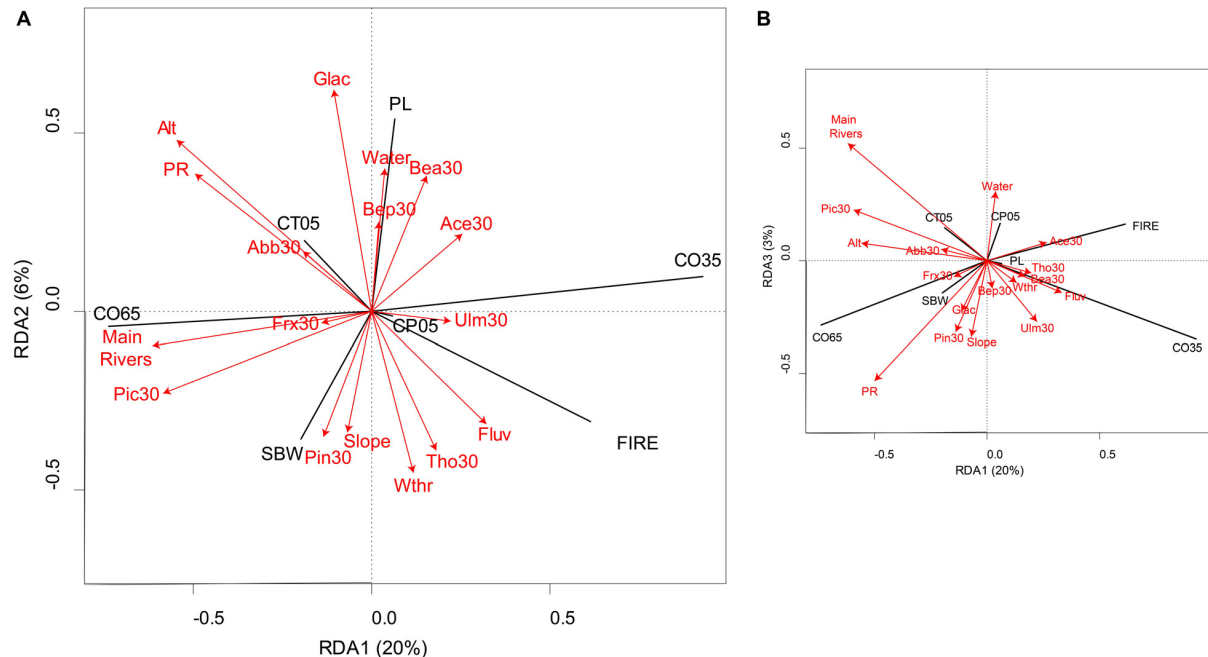


FIGURE 5 | Redundancy analysis (model adjusted $R^2 = 32\%$) of the 20th century disturbances (black lines) correlated to 17 explanatory variables (red vectors) in two driver sets (environmental variables and taxa basal area in 1930). Projections showed using (A) first and second ordination axes, and (B) first and third ordination axes. $N = 333$ cells of 3×3 km. FIRE: Fire (1895–2005), PL: Plantations (1955–2005), SBW: Spruce Budworm outbreaks (1975–2005), CO35: Cut over (1895–1935), CO65: Cut over (1935–1965), CP05: Partial cut (1965–2005), CT05: Clear cut (1965–2005). Acronyms of explanatory variables are indicated in the Table 4.

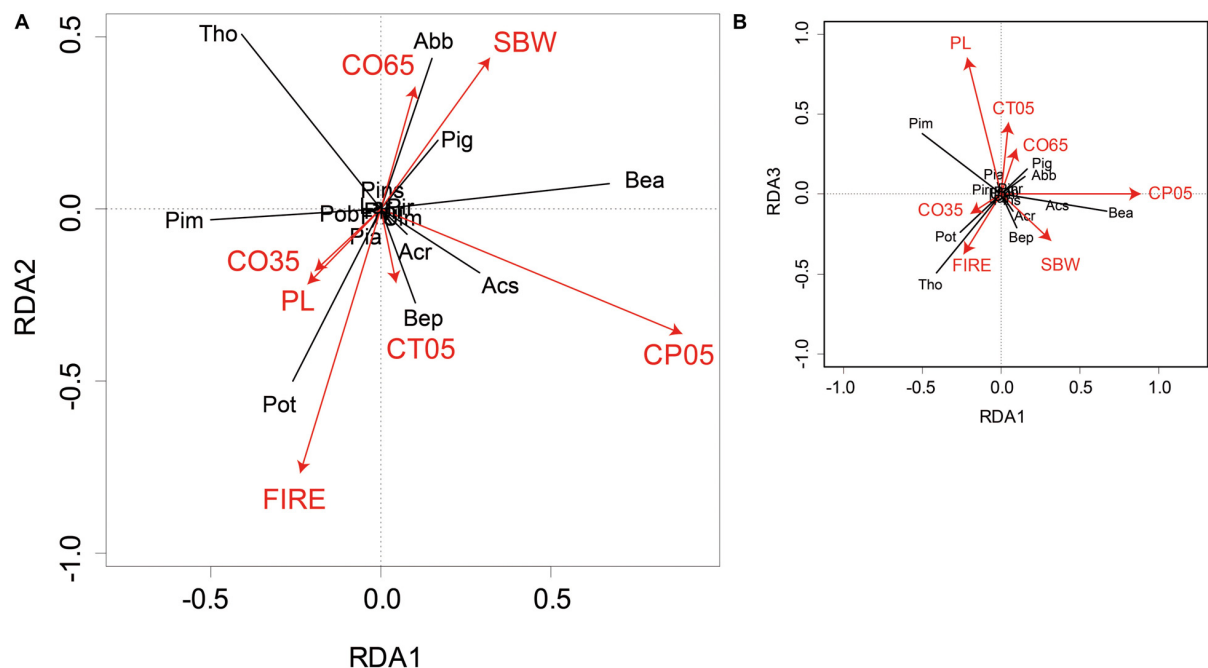


FIGURE 6 | Redundancy analysis (model Adjusted $R^2 = 6\%$) of taxa basal area in 2005 (black lines) correlated to 7 disturbance explanatory variables (red vectors). Projections showed using (A) first and second ordination axes and (B) first and third ordination axes. $N = 4573$ temporary plots of the 2nd, 3rd, and 4th government decennial inventories. Frx, Ash; Abb, Balsam fir; Tho, Northern white cedar; Ulm, American elm; Lar, American larch; Acr, Red maple; Acs, Sugar maple; Pobl, Balsam poplar; Pot, Trembling aspen; Pins, White pine; Pinr, Red pine; Pim, Black spruce; Pla, Norway spruce; Pir, Red spruce; Pig, White spruce; Bea, Yellow birch; Bep, White birch. Acronyms of explanatory variables are indicated in the Table 5.

TABLE 6 | Taxa basal area (m²/ha \pm sd) in 1930–1931 (*N* = 16804) and 1985–2005 for the whole study area.

Species	Latin name	Acronym	1930–1931	1985–2005	
				Natural regeneration	Plantations
Common name					
Balsam fir	<i>Abies balsamea</i>	Abb	9.2 (\pm 6.3)	9.8 (\pm 9.2)	7.6 (\pm 8.7)
American larch	<i>Larix laricina</i>	Lar	0.01 (\pm 0.3)	0.06 (\pm 0.62)	0.00 (\pm 0.07)
Spruces	<i>Picea</i> spp.	Pic	3.6 (\pm 3.8)	4.7 (\pm 5.5)	7.1 (\pm 7.6)
Norway spruce	<i>Picea abies</i>	Pia	–	0.04 (\pm 1.07)	0.7 (\pm 4.3)
White spruce	<i>Picea glauca</i>	Pig	–	3.3 (\pm 4.3)	3.2 (\pm 5.2)
Black spruce	<i>Picea mariana</i>	Pim	–	1.2 (\pm 3.9)	3.0 (\pm 5.9)
Red spruce	<i>Picea rubens</i>	Pir	–	0.1 (\pm 0.9)	0.2 (\pm 1.5)
Pines	<i>Pinus</i> spp.	Pin	0.03 (\pm 0.38)	0.07 (\pm 0.74)	0.00 (\pm 0.03)
Red pine	<i>Pinus resinosa</i>	Pinr	–	0.02 (\pm 0.40)	0.00 (\pm 0.03)
White pine	<i>Pinus strobus</i>	Pins	–	0.05 (\pm 0.61)	0.00 (\pm 0.00)
Northern white cedar	<i>Thuja occidentalis</i>	Tho	1.6 (\pm 4.5)	4.3 (\pm 10.6)	0.3 (\pm 2.4)
Conifer basal area		–	14.5 (\pm 8.5)	18.9 (\pm 14.0)	14.9 (\pm 2.5)
Maples	<i>Acer</i> spp.	Ace	0.18 (\pm 1.1)	1.7 (\pm 4.5)	0.3 (\pm 1.4)
Red maple	<i>Acer rubrum</i>	Acr	–	0.7 (\pm 2.0)	0.1 (\pm 0.8)
Sugar maple	<i>Acer saccharum</i>	Acs	–	1.0 (\pm 4.0)	0.2 (\pm 1.1)
Yellow birch	<i>Betula alleghaniensis</i>	Bea	1.8 (\pm 3.2)	1.7 (\pm 3.3)	0.7 (\pm 2.0)
White birch	<i>Betula papyrifera</i>	Bep	3.6 (\pm 3.5)	2.3 (\pm 0.2)	1.0 (\pm 1.9)
Black ash	<i>Fraxinus nigra</i>	Frx	0.02 (\pm 0.3)	0.04 (\pm 0.43)	0.00 (\pm 0.01)
Poplars	<i>Populus</i> spp.	Pop	0.05 (\pm 0.58)	0.8 (\pm 3.6)	0.4 (\pm 2.4)
Balsam poplar	<i>Populus balsamifera</i>	Pob	–	0.3 (\pm 2.4)	0.1 (\pm 1.3)
Trembling aspen	<i>Populus tremuloides</i>	Pot	–	0.5 (\pm 2.6)	0.3 (\pm 2.0)
American elm	<i>Ulmus americana</i>	Ulm	0.01 (\pm 0.22)	0	0
Deciduous basal area		–	5.7 (\pm 5.0)	6.4 (\pm 7.2)	2.5 (\pm 4.3)
Total		–	20.2 (\pm 9.3)	25.3 (\pm 12.4)	17.4 (\pm 10.7)

Basal area for the 1985–2005 period is divided into two groups according to origin: natural regeneration (*N* = 3797) or plantation (*N* = 385).

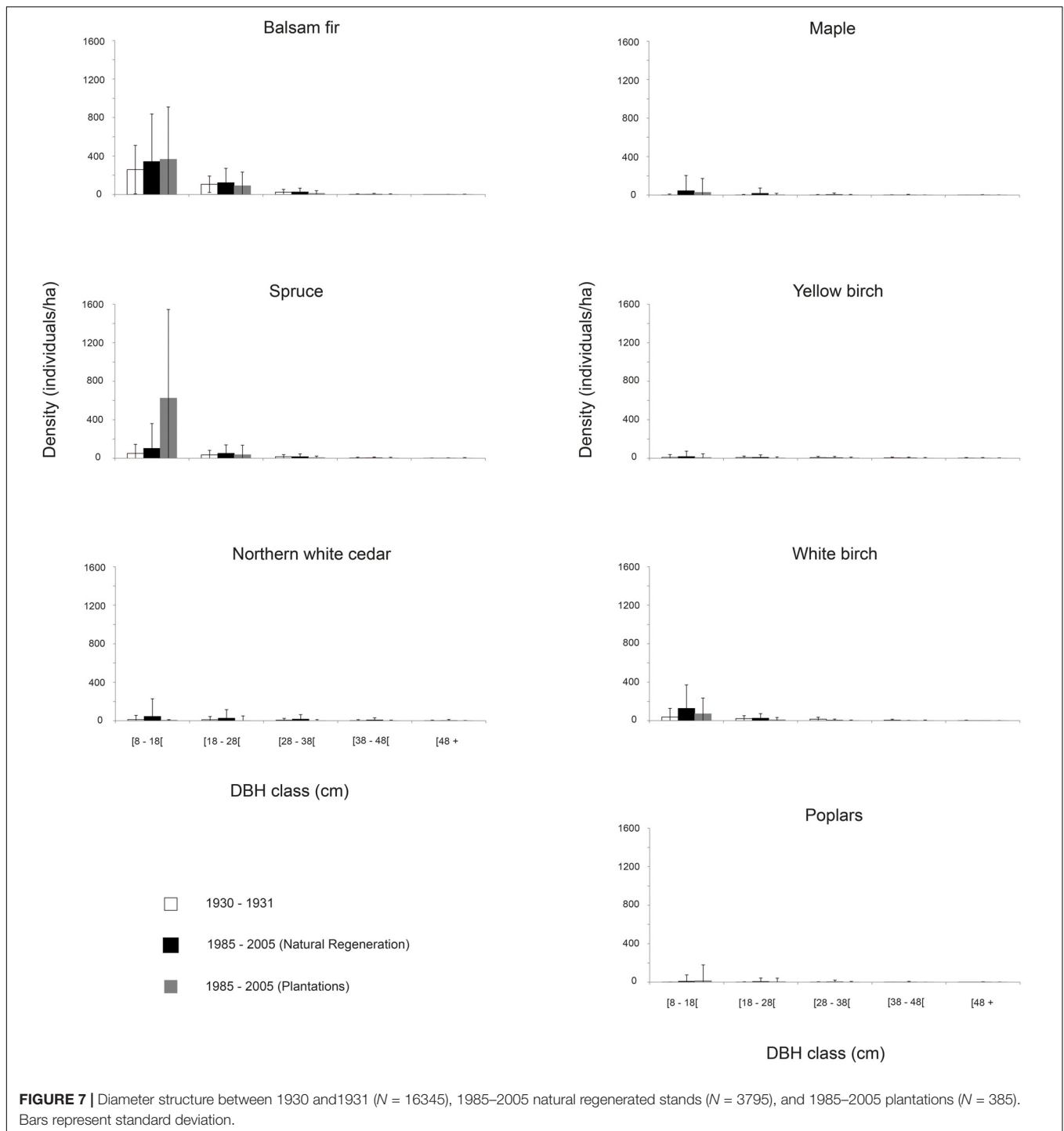
be more frequent with high harvesting intensity in partial cut stands (Montoro Girona et al., 2019). Although tree ring evidence indicate a time interval of 40 years between successive SBWs in the LSL region over the past 450 years (Boulanger and Arseneault, 2004), the rotation period for presettlement SBW s is hard to calculate due to the lack of spatial data.

Escaped-settlement fires and extensive logging during the 20th century have strongly altered the type, rotation period, severity and extent of disturbance events (Table 3). Compared to a fire rotation period of 200 years at the peak of human settlement in the region (1925–1955), the value of 1668 years calculated for the 1895–1925 interval is closer to values suggested elsewhere for pre-industrial landscapes of the temperate zone. Natural fires were documented to be rare in the presettlement land surveys in the temperate forests of eastern North America (Siccama, 1971; Lorimer, 1977; Foster et al., 1998). For example, recently burned areas covered 10% of the landscape in Northern Maine shortly before settlement, with a rotation period estimated to be 800 years (Lorimer, 1977). An even longer fire rotation period of 1240 was reported for spruce-fir forests in Maine (Fahey and Reiners, 1981). At the same time logging evolved from partial cutting diameter-limit management, associated to the saw mill industry, at the beginning of the century to total cutting, associated to the pulp and paper industry, by the end of the century (Fortin et al., 1993; Boucher et al., 2009a,c). In the past decades, efforts for forest sustainable management suggested more partial cutting

as an alternative to clearcutting in the province of Quebec and elsewhere in eastern North America (Landres et al., 1999; Harvey et al., 2002; Lindenmayer and Franklin, 2002). Overall, logging covered 144% of the study area between 1895 and 2005, with 45% of the study area logged more than once.

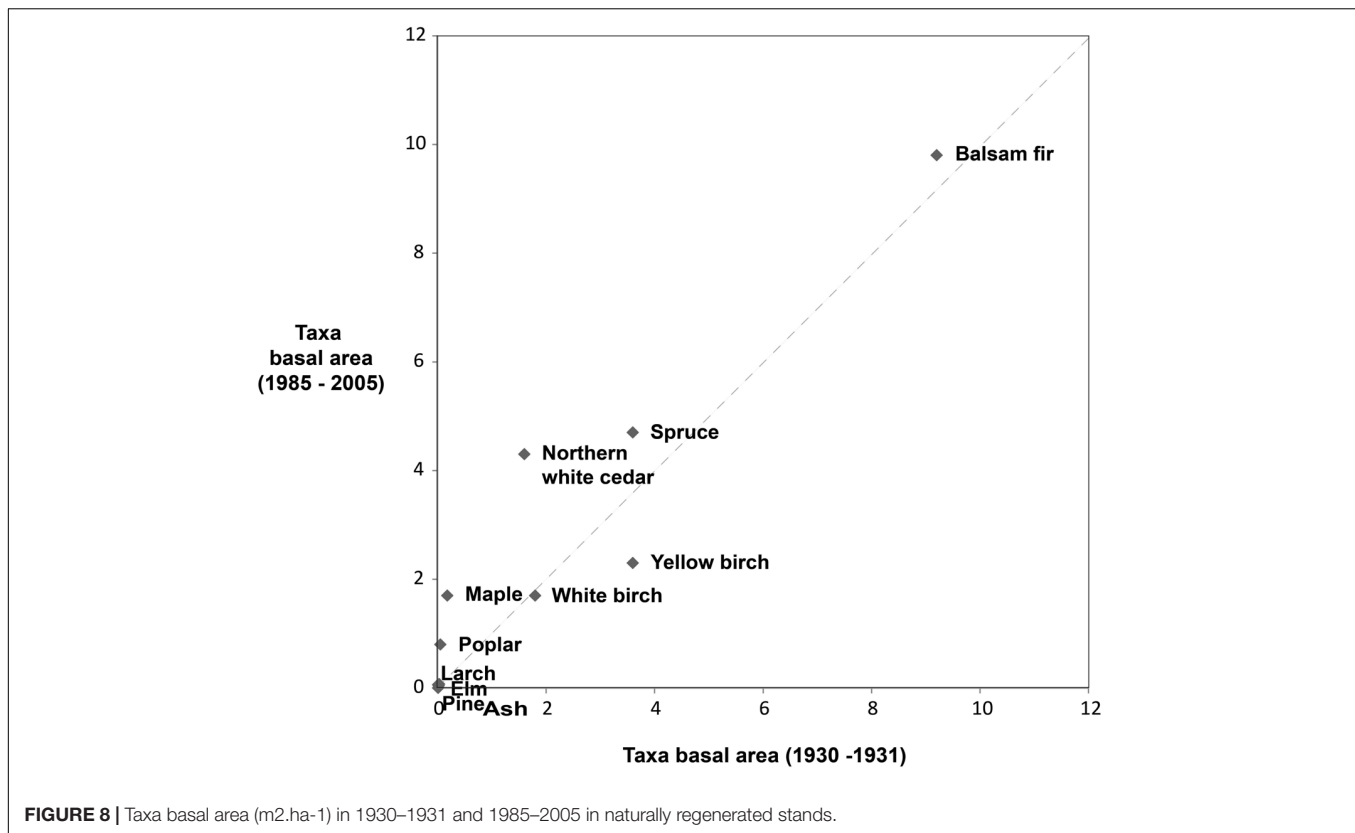
20th Century Anthropogenic Disturbances Impact on Present Day Forest Composition

Mixed forests in our study area showed resilience in terms of composition, despite the omnipresence of anthropogenic disturbances during the 20th century. There is a correlation between tree taxa basal area in 1930–1931 and present-day taxa basal area (Figure 8). At the beginning of the century, diameter limit selective logging was conducted in winter and with minimal machinery (Fortin et al., 1993). This might have protected coniferous regeneration and limited the expansion of early successional deciduous tree species, contributing to the overall observed resilience of forests to logging operations at the beginning of the 20th century (Table 5). A study of Boucher et al. (2017) have used a similar database and disturbance data, as in this study, in the southern boreal forest of central Quebec, and have concluded that logging have a minor impact on compositional change.



Disturbances of the 20th century explain only 6% of present-day tree composition (**Figure 6**), suggesting that they have not been an important agent of forest reorganization in our study area. This contrasts with more salient views in the literature which emphasize the impact of anthropogenic disturbances on forest composition (Whitney, 1994; Foster et al., 1998; Fuller et al., 1998; Friedman and Reich, 2005; Dupuis et al., 2011; Boucher et al., 2014; Fortin, 2018; Danneyrolles et al., 2019).

Many of these studies use vegetation data from historical land surveys (frequency of occurrence and dominance). The difference between our study area and other studies using historical land surveys might be that our study area is mostly located in public territory, while these studies were mostly located in private lands. More severe and frequent anthropogenic disturbances are likely to occur in private lands, as in the case of anthropogenic fires in our results (**Figure 5**). Moreover, the response of vegetation



to disturbances might be site specific and could have been attenuated by the use of a 9 km² grid cells. The influence of total cuts on vegetation composition might not be fully ceased by our analysis (CT05 adj $R^2 = 0.005$; **Table 5**). Although naturally regenerated stands originating after total cuts between 1965 and 2005 cover 25% of the study area, many of the trees in these stands are 40 years old or younger and have smaller DBH than the 7 cm minimum DBH for trees measured in our database. Finally, the relatively short period of disturbance data availability (110 years) in this study and lacking data for some disturbance episodes (SBW) might have contributed in diminishing the effect of disturbances in present-day forest composition. Disturbances that have occurred long before our study might as well have a non-measured influence.

Despite the relatively low importance of disturbances to explain the present-day forest composition, some taxa responded to disturbances in an individualistic manner, reflecting their functional traits. The increase of early successional trembling aspen in naturally regenerated stands compared to the 1930–1931 time period (**Figures 6–8** and **Table 6**) is correlated to the important increase in fire events. Several previous studies have linked the increase of trembling aspen with anthropogenic fires in eastern North America (Bergeron, 2000; Cleland et al., 2001; Friedman and Reich, 2005; Boucher et al., 2014, 2017; Terrail et al., 2019). We also found that the fire sensitive balsam-fir (Rowe, 1972) is mostly abundant away from fire polygons (**Figure 6**). Species usually associated with gap dynamics, such as yellow birch and sugar maple, are correlated to partial cuts (1965–2005). These species might have benefited from the

elimination of shade tolerant competitors in partial cuts as well as in areas impacted by SBW (**Figure 6**; Palik and Pregitzer, 1992; Abrams, 1998; Nie et al., 2018). Moreover, red and sugar maples produce a large quantity of seeds and can grow rapidly when exposed to light (Fei and Steiner, 2008; Nolet et al., 2008). In addition, management practices which aim at preserving yellow birch seed trees in logging operations might have favored the abundance of this species.

Planted areas have also participated to the observed present-day forest composition at the landscape level. They are human made ecosystems which are less diverse than naturally regenerated stands (**Table 6**), as 41% of plantations basal area is composed of spruces against 19% in natural regenerated stands (**Table 6** and **Figure 7**). Other tree species found in planted stands consist in naturally regenerated balsam fir and early successional white birch.

Surprisingly northern white cedar, a late successional shade tolerant species increased in basal area and was not correlated to disturbances (**Table 6** and **Figure 6**). This result is somewhat contrary to the general tendency of the decreased cedar abundance in eastern Canadian mixed forests, even though variable between regions (Danneyrolles et al., 2017). Its present-day increase and distribution in the landscape is probably better explained when environmental factors are considered. Northern white cedar is usually found in zones with poor drainage, organic deposit and in low altitude (Robitaille and Saucier, 1998). The study area's position in public territory might have also made northern white cedar exploitation less frequent. Yet, the interaction with partial natural and human disturbances (insect

outbreaks and partial cuts) combined with an abundant advanced regeneration of northern white cedar was suggested to explain the dominance of this species (Heitzman et al., 1997; Ruel et al., 2014; Danneyrolles et al., 2017).

Determining the contribution of anthropogenic disturbances on forest composition should be studied along with other agents and their interactions at various spatial and temporal scales (Krankina et al., 2005; Gimmi et al., 2010; Landhäusser et al., 2010; Fisichelli et al., 2014; Nowacki and Abrams, 2015; Plieninger et al., 2016; Vayreda et al., 2016; Danneyrolles et al., 2019). For example, Boisvert-Marsh et al. (2019) have suggested that disturbance of the last 40 years have been less important than climate change to explain present-day forest composition, whereas Danneyrolles et al. (2019) concluded the contrary at the scale of the last century. Moreover, the characteristics of disturbances themselves (extent, frequency, intensity, type, return interval) and their combination might also have different influences on vegetation composition (Turner, 2010). In the present study, the conjugated analysis of disturbance history and associated compositional change over the transition period encompassing the early settlement of the population and the deployment of industrial forestry suggest moderate change in forest cover composition despite extensive anthropogenic disturbances in this representative eastern Canadian mixed forest.

Our study supports the recommendations of forest ecosystem management practices to use partial cutting to maintain the forest in its natural range of variability (Landres et al., 1999; Harvey et al., 2002; Lindenmayer and Franklin, 2002). On the other hand, further investigation is needed to study the impact of clear cutting as the length and data of our study don't permit the estimation of the impact of this stand replacing disturbance. Paleocological

studies which could encompass longer time-frames could present precious complementary information on forest composition and natural disturbance history at the millennial scale.

DATA AVAILABILITY STATEMENT

The datasets generated for this study are available on request to the corresponding author.

AUTHOR CONTRIBUTIONS

TE has conducted the research, data analysis and manuscript writing of this paper. DA and LS have participated significantly in the development of the methods and the revision of the manuscript. YB has participated by rendering the historical inventory data available and has participated with DA and LS in obtaining funding for the research project.

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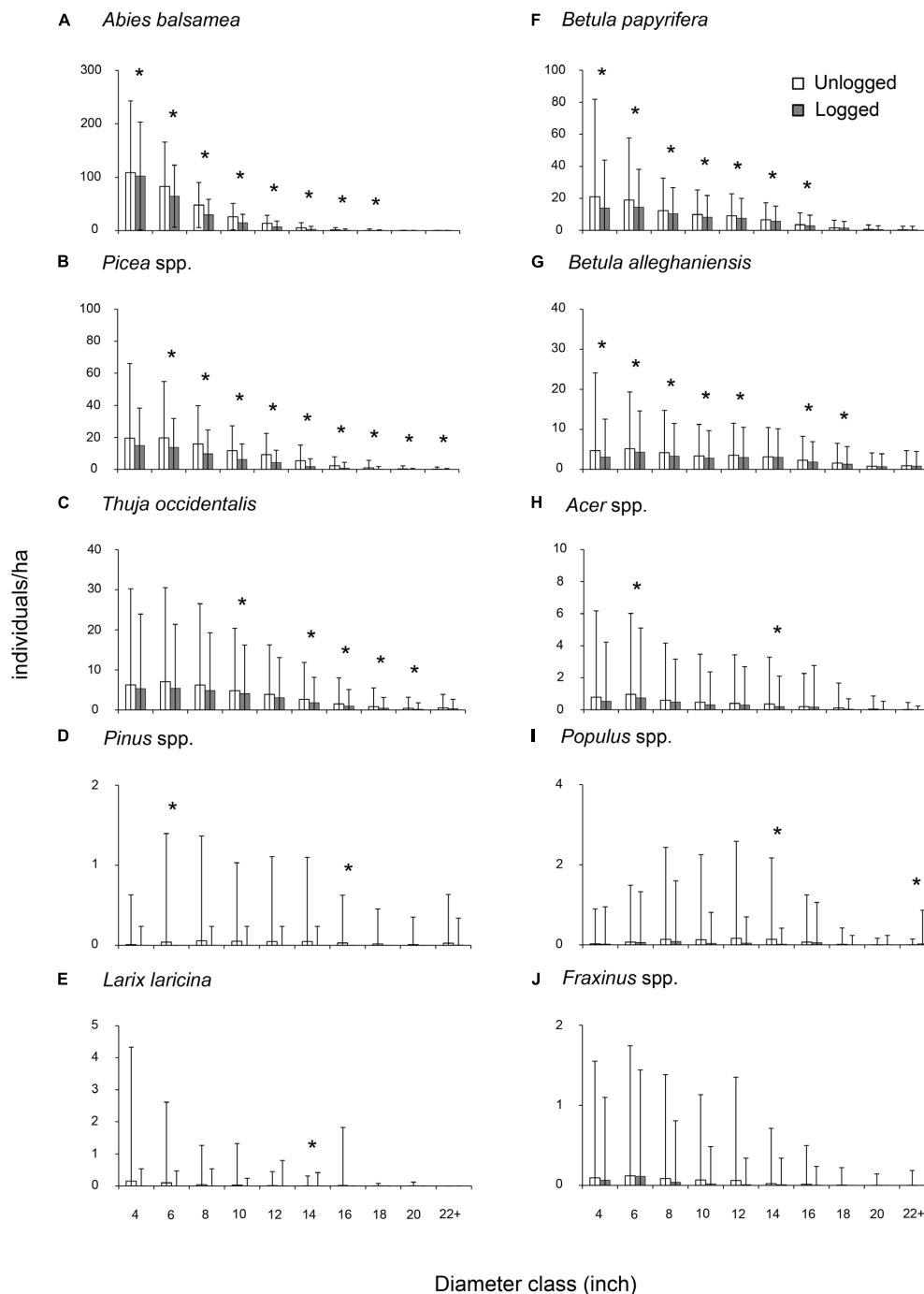
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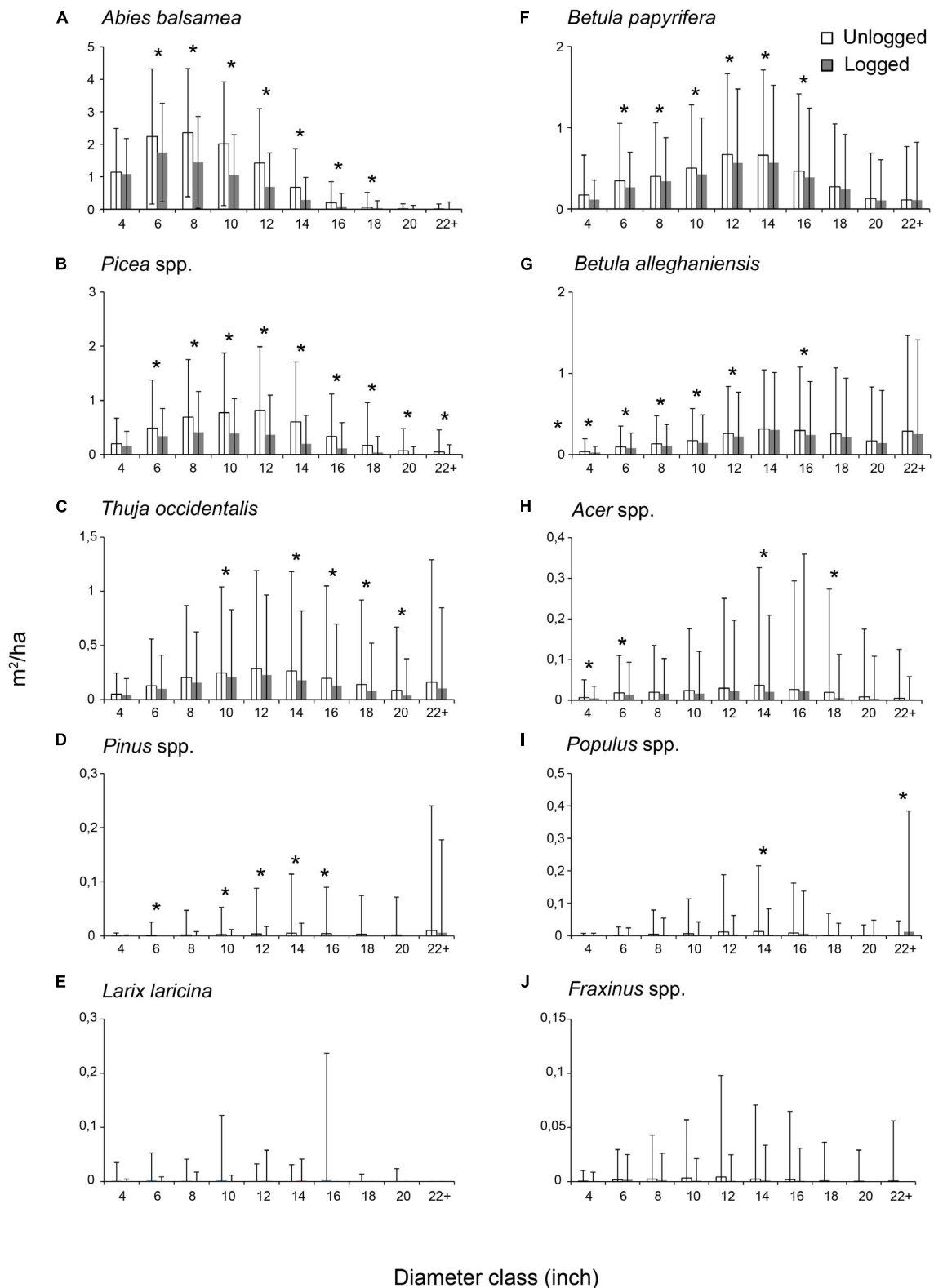
Conflict of Interest: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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APPENDIX



APPENDIX 1 | Stem density per diameter class per species in previously unlogged ($N = 14\,634$) versus logged plots ($N = 1\,822$) in 1930–1931. Bars represent standard deviation, Asterisks (*) indicate a statistically significant difference in stem density between unlogged and logged plots for a given diameter class (Wilcoxon test; $p < 0.05$).



APPENDIX 2 | Basal area per diameter class per species in previously unlogged ($N = 14\,634$) versus logged plots ($N = 1\,822$) in 1930–1931. Bars represent standard deviation, Asterisks (*) indicate a statistically significant difference in basal area (m²/ha) between unlogged and logged plots in a given diameter class (Wilcoxon test; $p < 0.05$).