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Change from pre-settlement to present-day forest composition reconstructed from early land survey records in eastern Québec, Canada

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Acer spp.; Eastern white cedar; Historical forest ecology; Land survey archives; Landscape change; Line descriptions; *Populus* spp.; Taxa dominance; Taxa prevalence

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Farrar (1995)

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Abstract

Questions: What was the tree species composition of forests prior to European settlement at the northern hardwood range limit in eastern Québec, Canada? What role did human activities play in the changes in forest composition in this region?

Location: Northern range limit of northern hardwoods in the Lower St. Lawrence region of eastern Québec, Canada.

Methods: We used early land survey records (1846–1949) of public lands to reconstruct pre-settlement forest composition. The data consist of ranked tree species enumerations at points or for segments along surveyed lines, with enumerations of forest cover types and notes concerning disturbances. An original procedure was developed to weigh and combine these differing data types (line versus point observations; taxa versus cover enumerations). Change to present-day forest composition was evaluated by comparing survey records with forest decadal surveys conducted by the government of Québec over the last 30 years (1980–2009).

Results: Pre-settlement dominance of conifers was strong and uniform across the study area, whereas dominance of maple and birches was patchy. Cedar and spruce were less likely to dominate with increasing altitude, whereas maple displayed the reverse trend. Frequency of disturbances, especially logging and fire, increased greatly after 1900. Comparison of survey records and modern plots showed general increases for maple (mentioned frequency increased by 39%), poplar (36%) and paper birch (31%). Considering only taxa ranked first by surveyors, cedar displayed the largest decrease (19%), whereas poplar (15%) and maple (9%) increased significantly.

Conclusions: These changes in forest composition can be principally attributed to clear-cutting and colonization fire disturbances throughout the 20th century, and mostly reflected the propensity of taxa to expand (maples/aspen) or decline (cedar/spruce) with increased disturbance frequency. Québec's land survey archives provide an additional data source to reconstruct and validate our knowledge of North America's pre-settlement temperate and sub-boreal forests.

Introduction

Major transformations have occurred in North American forests as a result of human activities over the 19th and 20th centuries. The harvesting of wood for the forestry industry, deforestation for agricultural purposes and urbanization, fire suppression in some areas and increased fire frequencies in others have concurrently modified disturbance regimes and the forest structure and composition (Foster et al. 1998; Lorimer 2001). As a result, modern forested landscapes are younger, more fragmented and composed of an increased proportion of pioneer tree species as compared to the pre-settlement period (Mladenoff et al. 1993; Whitney 1994; Foster et al. 1998).

Knowledge of forest ecosystem compositions prior to European settlement is useful as a reference for planning ecosystem-based management. Due to the general lack of

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natural forests in heavily modified regions, several studies have relied on land survey archives for reconstructing pre-settlement tree assemblages (e.g. Whitney 1994). The surveyors mandated to divide the land prior to settlement systematically kept records of the forest composition in their logbooks. In the northern part of the temperate zone, the most conspicuous changes observed in the forest composition since the 19th century are associated with an increased component of fast-growing tree species such as sugar maple (*Acer saccharum*), red maple (*A. rubrum*), birches (*Betula* spp.), along with a reduced importance of slower-growing species such as beech (*Fagus grandifolia*) and hemlock (*Tsuga canadensis*) (Siccama 1971; Abrams 1998; Bürgi et al. 2000; Dyer 2001). Similar changes have also occurred in the southern boreal forest, with a marked increase in the abundance of trembling aspen (*Populus tremuloides*) and a decrease of shade-tolerant conifers such as balsam fir (*Abies balsamea*), spruce (*Picea* spp.) and eastern white cedar (*Thuja occidentalis*) (Jackson et al. 2000; Friedman & Reich 2005; Pinto et al. 2008).

Two main types of survey record are available to reconstruct the composition of the forests in north-eastern North America. The type most often used consists of the identification of individual witness trees that are systematically distributed over a half-mile grid. This type of data set is mainly associated with the survey approach implemented by the General Land Office (GLO) from 1812 onward, notably in the American Midwest (Whitney 1994). The second type of data set consists of descriptive accounts of forest stand composition, in the form of ranked taxa enumeration along survey lines (Jackson et al. 2000; Scull & Richardson 2007; Fritschle 2009). These line descriptions were much less often used. In eastern Canada, where original surveying was primarily done between 1790 and 1950, line descriptions are generally the only data type available. These line descriptions have been used for the reconstruction of forest composition in the provinces of Ontario (Gentilcore & Donkin 1973; Clarke & Finnegan 1984; Jackson et al. 2000; Pinto et al. 2008) and New Brunswick (Crossland 2006). However, no study has yet been done in the province of Québec, despite the availability of such archives and the high density and good quality of surveyor observations.

The Lower St Lawrence region (hereafter LSL), located in south-eastern Québec (Fig. 1), has been intensively logged by the forest industry for more than 100 years (Boucher et al. 2009a, b). A comparative analysis of 1930 and 2002 forest maps revealed that a significant proportion of the area has shifted from coniferous to mixed-deciduous forest cover types through successive logging operations (Boucher et al. 2006, 2009a, b). However, descriptions of these general cover types at the taxonomic level are lacking. Analysis of the original survey archives of LSL can advance our understanding of the nature of these changes and their causes. This study aims to analyse the LSL survey archives in order to: (1) document the tree species composition of the pre-settlement forest, and (2) compare these data with recent forest inventory data in order to assess the compositional changes that have occurred since the 19th century.

Study Area

The study area (4834 km^2) is located between 68°08′ to 69°31′W and 47°18′ to 48°24′N (Fig. 1). It is limited to the north by an area formerly occupied by 'seignories' (i.e. a land tenure mode that prevailed alongside the St Lawrence River during the French regime until 1791), and to the south by the province of New Brunswick (Canada) and the state of Maine (USA). The study area lies in the Appalachian geological formation, which is characterized by sedimentary bedrock mostly covered by surficial deposits of glacial origin (Robitaille & Saucier 1998). The topography consists of low elevation hills in the northeast, which gradually increase in height towards the southwest to reach just over 500 m. The meteorological records of Rimouski and Dégelis (Fig. 1) respectively show mean annual temperatures of 3.9 °C and 3.0 °C and mean annual total precipitations of 915 mm and 1005 mm, 30% of which falls as snow (Environment Canada 2010).

The study area lies at the transition between the temperate deciduous and the boreal coniferous forest zones, and is situated at the northern limit of the Great Lakes–St Lawrence forest region (Rowe 1972). According to the Québec Government forest site classification system (Grondin et al. 1998), mesic sites are typically characterized by mixed stands of yellow birch (*Betula alleghaniensis*), balsam fir, white spruce (*Picea glauca*) and eastern white cedar. Some companion species become significant at the local scale and may include trembling aspen, paper birch (*Betula papyrifera*), red maple and sugar maple, the latter two being at their northern range limit.

Logging, in the form of selective cutting, began around 1820 in the LSL. At that time, wood harvesting was restricted to areas near rivers to allow the floating of logs. The main species harvested were red pine (*Pinus resinosa*), white pine (*P. strobus*) and white spruce (Boucher et al. 2009a). Almost all inhabitants lived within the riverside seignories, with practically no permanent settlement existing in the back country. The end of the 19th century was marked by the start of industrial clear-cuts, prompted by the growing international market for both saw wood and pulp wood (Fortin et al. 1993). In addition to logging disturbances, outbreaks of the spruce budworm (*Choristoneura fumiferana*) have recurred every 40 years or so during the last 450 years (Boulanger & Arseneault 2004). Fires were rare before European settlement, with a rotation period of about 800 years (Lorimer 1977).

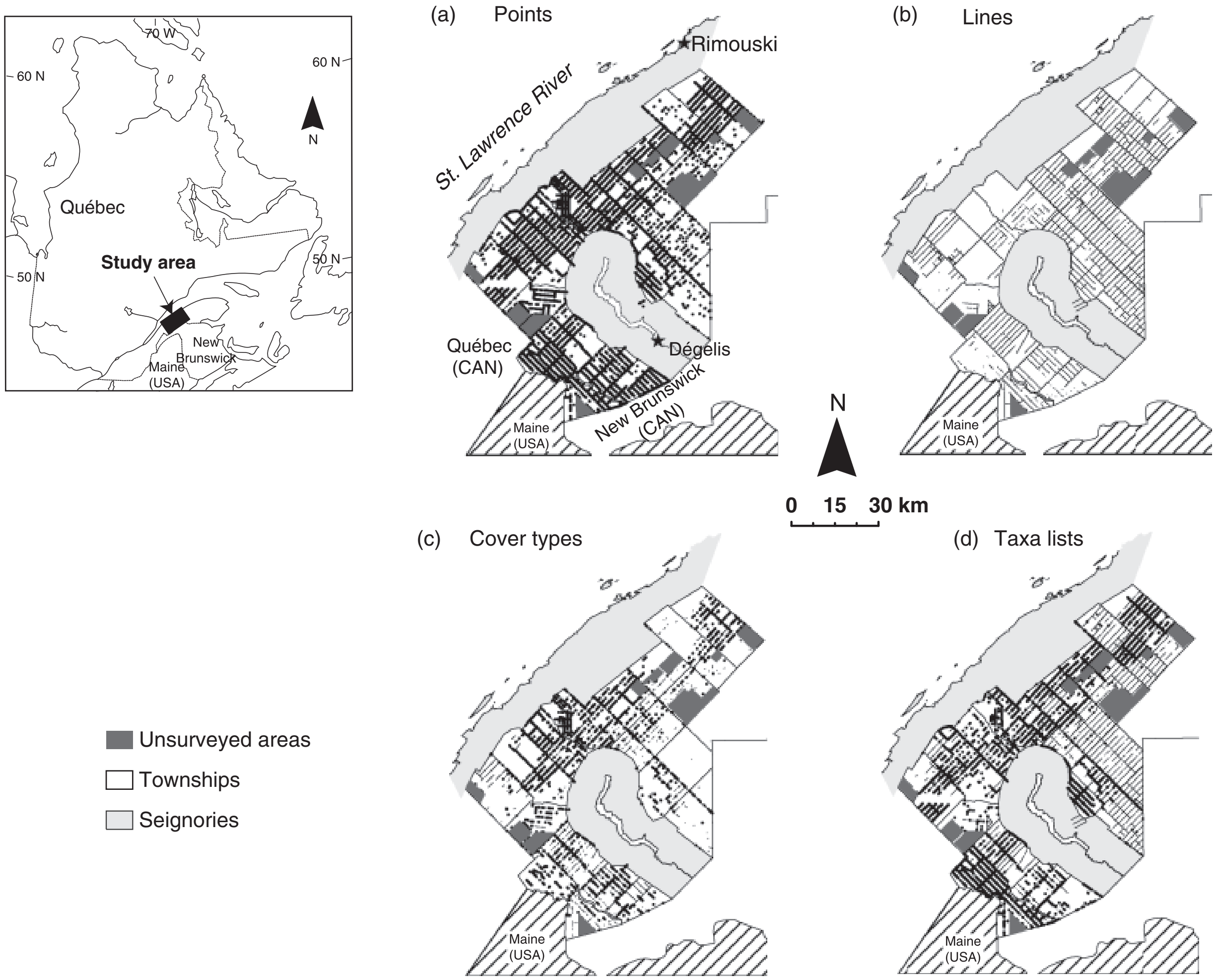

Fig. 1. Location of the study area in north-eastern North America (inset) and location of surveyor observations across the study area, according to observation geometry (points versus lines; **a**, **b**) and vegetation types (cover types versus primary taxon lists; **c**, **d**).

Methods

This study is based on 91 logbooks recording the first subdivision of 26 townships by 42 different surveyors between 1846 and 1949. In the province of Québec, public lands were subdivided into townships of approximately 16 km × 16 km (10 miles by 10 miles). Townships were further subdivided into parallel ranges 1.6-km wide. Each range was then further subdivided into lots generally measuring 100 acre (261 m × 1608 m, or 13 chains × 80 chains) by erecting posts at lot corners every 261 m (13 chains) along the range lines (1 chain = 20.1 m).

All observations (forest composition, disturbances, slope, soils, streams, etc.) along the range lines were precisely located, with surveyors reporting the distance between each observation. We classified these observations into two geometric types, line or point, according to how the surveyors recorded them. An observation was considered as a linear segment when it clearly contained both a start and an end position along the range line. A very large proportion of these linear observations were delineated by lot limits, corresponding to a length of about 13 chains (261 m; Fig. S1a, d). Conversely, an observation was considered a point when its position could be clearly located, but with no clear beginning or end along a range line. Point observations were either regularly or irregularly spaced. Regularly spaced point observations were frequently made at lot corners or at every 10 chains (201 m) (Fig. S1b, c). While logbooks generally were based on either the line or the point notation format, all logbooks contained both line and point observations.

We assumed that line and point observations could be integrated into a single database according to three shared properties. First, both the line and the point geometric types were strongly dependent on the underlying cadastral grid (Fig. S1). Second, the range of point spacings was similar to the range of line lengths, with more than 98% and more than 84% of point and line observations spaced

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at less than 35 chains (700 m), respectively. Third, the spacings of both observation types were similar to the lengths of mapped modern forest stands intersected by the same surveyed range lines (Fig. S1c, f). This suggests that both point spacing and line length are good estimators of pre-settlement forest stand extent, particularly when considering the much greater fragmentation of forest cover types in the present-day landscape as compared to the pre-settlement landscape (Boucher et al. 2006, 2009b). When combining all observations into the final database, each point observation was weighted by its mean spacing (the mean of the distances to the previous and next observations), whereas each line observation was weighted by its length. Each observation was georeferenced as a point or line using ArcGIS 9.2 (ESRI 2006) and a modern digital cadastre (scale 1:20 000) built from early land surveys.

Pre-settlement forest composition and disturbances

Disturbances recorded along the survey lines (Appendix S1) were compiled by survey date and grouped into five categories: logged, burned, windfall, settlement and paths and roads. Because the frequency of anthropogenic disturbances increased markedly during the 20th century (see results), the pre-settlement forest composition was described using only surveys made during the 19th century (1846–1900).

Surveyors described forest composition primarily in the form of ranked taxon lists, hereafter referred to as 'primary taxon lists'. Most surveyors used French names and, even if several taxa were only identified to the genus level, several of these genera correspond to only one species, given the regional species pool (Appendix S1). Although we could not find general instructions indicating the procedure for how surveyors described forest composition, three types of evidence let us assume that taxa were ranked according to their relative importance in forest stands. First, some surveyors explicitly reported that they ranked taxa according to abundance or importance. Second, almost all surveyors frequently inverted taxa pairs between consecutive observations, a practice also noticed in surveys done in other regions of Canada (Gentilcore & Donkin 1973; Jackson et al. 2000). Because of the very general use of expressions such as '*ditto*' or 'same as before' to indicate identical successive stands, inverted taxa probably reflect real changes of taxa importance. Third, the ranking of taxa was highly coherent with the surveyor's description of forest cover types, together with primary taxon lists (see below and Appendix S2).

For about 49% of all observations (4686 out of 9591) pertaining to forest composition during the 19th century, surveyors mentioned the presence of forest cover types (e.g. softwood, mixed wood, hardwood, cedar stand, etc.), instead of using primary taxon lists (Appendix S1). Excluding these cover types from our database would have biased the reconstruction of the pre-settlement forest composition because some forest stands may have been systematically described by surveyors using a cover type rather than a taxon list. We were able with some confidence to transform cover types into secondary taxon lists, because about 28% (1302 out of 4686) of all cover types mentioned also included a primary taxon list detailing the forest composition (e.g. mixed wood, fir, spruce, yellow birch, cedar). We assumed that for each cover type, the subset of observations along with the associated primary list was representative for all observations of the same cover type. Accordingly, each mention of the most important cover types could be transformed to a secondary taxon list, with the occurrence of each taxon weighted for each rank in the list (Appendix S2).

Pre-settlement versus present-day forest composition

Changes in forest composition between the pre-settlement and present-day periods were evaluated by comparing survey records with the last three decadal forest surveys (1980s, 1990s, 2000s) conducted by the Government of Québec. These surveys are intended to estimate the standing wood volume available for the forest industry (MRNF 2007) and are based on 0.04-ha sampling plots randomly stratified according to forest stand type. Unforested (agriculture, urban, etc.) and unproductive lands (marsh, peatlands, etc.) as well as inaccessible stands (slope $> 40\%$) are excluded from the survey. Within plots, individual stems are tailed according to species and 2-cm DBH classes (diameter at breast height), thus allowing computation of the basal area ($m^2\,ha^{-1}$) by species.

Several adjustments were necessary to make the two data sets comparable. First, we grouped species found in the modern plots in order to match the taxa mentioned by the surveyors (Appendix S1). Second, because of the assumption that surveyors ranked taxa according to their visual importance, taxon lists for modern plots were constructed by ranking taxa in decreasing order of basal area. Because basal area depends on both stem density and diameter, it is a good estimation of the visual importance of taxa inside forest stands. Third, only plots located within < 1.6 km (1 mile) of the nearest surveyor's point were retained based on the spacing of range lines in the pre-settlement data set.

We used three differing metrics to describe the changes in forest composition between pre-settlement and present-day conditions. First, for each period, a prevalence index was computed for each taxon and was defined as its percentage occurrence among all taxon lists (primary and secondary), whatever its rank in those lists. Second, following Scull & Richardson (2007), we computed F_{ir}, an index to determine the frequency of occurrence of each taxon at each of the first four ranking positions (i.e. $r = 1, 2, 3, 4$) out of all ranked observations:

$$F_{ir} = (N_{ir}/M_r) \times 100 \quad (1)$$

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. In this study, the dominance of a taxon refers to its frequency of occurrence at the first ranking position (i.e. for $r = 1$). When computing prevalence and F_{ir}, each taxon from a secondary list (derived from a cover type) was weighted by its frequency of occurrence at each rank in those lists. Taxa from primary lists were not weighted.

Third, for each time period we computed an index of co-occurrence (C_{ij}) for each pair of dominant and co-occurring taxa, using the following formula:

$$C_{ij} = L_i/L_j \quad (2)$$

where L_i is the number of primary taxon lists with taxon i at rank ≥ 2 when taxon j is ranked first and L_j is the number of primary lists with more than one taxon and having taxon j ranked first. Because we were particularly interested in comparing the ability of taxa to form pairs in pre-settlement versus present-day stands rather than measuring the proportion of the landscape with each pair, point and line observations were not weighted by spacing or length and secondary lists were not considered.

Comparison of forest composition between the pre-settlement and the present-day periods was put in a spatial context by dividing the whole study area into 249 adjacent cells measuring 5 km × 5 km. The dominance of each taxon was computed for each cell and each time period as the proportion of surveyors' observations (or modern sampling plots) with the given taxon in the first position in taxon lists (with the greatest basal area). Cells with insufficient numbers of surveyor observations ($n < 4$) or modern sampling plots ($n < 4$) were discarded, resulting in 180 cells (including four to 153 observations; mean = 47) and 163 cells (four to 105 plots; mean = 25) being retained for the pre-settlement and modern time period data sets, respectively. We tested several cell sizes, and found that a size of 25 km^2 permitted retention of the maximum number of cells with well-distributed observations. The grid cells were also used to compare the spatial pattern of disturbances between the 1846 to 1900 and 1901 to 1949 time periods. For each cell, we computed the prevalence of the most important disturbances observed by surveyors (fire, logging, settlement) as a percentage of all observations mentioning each disturbance type. Taxa dominance was also compared between time periods along eight altitudinal bands of 40 m situated between 140 m and 460 m above sea level. A digital elevation model built from governmental hypsometric maps (scale 1:20 000 with 10-m contour intervals; MRNQ 2000) was used to generate the altitudinal bands.

Results

The total database comprised 6598 lines and 11 423 point observations. Of those 18 021 observations, 56%, 25%, and 19% corresponded to a primary taxon list, a cover type and a disturbance type, respectively (Fig. 1).

The most frequently mentioned disturbances were fire, logging, settlement and windfall (Appendix S1). The frequency of all disturbance types increased importantly after ca. 1900, except for windfall (Fig. 2). Twentieth

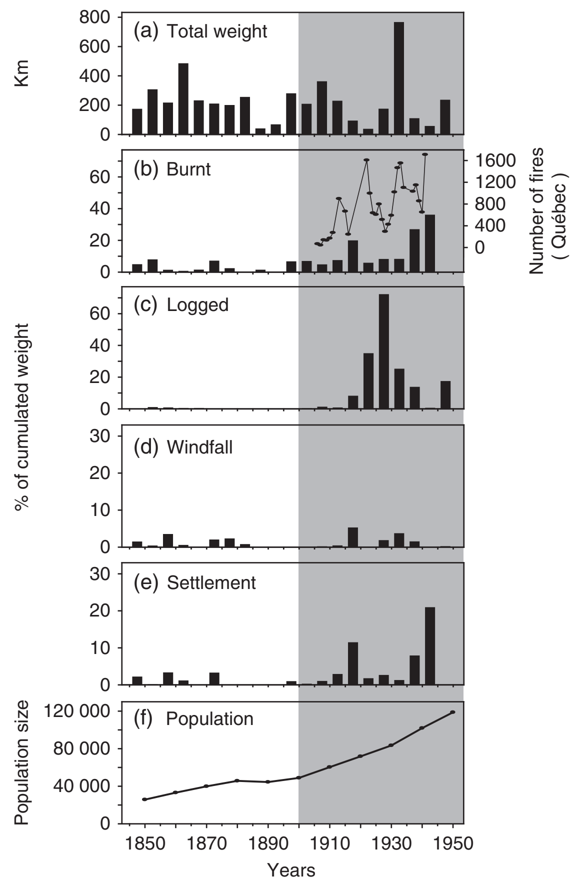

Fig. 2. Total weight of surveyor observations by 5-year time periods (**a**) and disturbance frequency according to time periods and disturbance types (**b**, **c**, **d**, **e**). For each decade, the total weight is the sum of the length of all line observations plus the mean spacing of all point observations. The trend in human population (**f**) is for the entire LSL region and was reconstructed from the government population census (Martin 1959). The number of fires reported for the entire province of Québec between 1906 and 1941 is also shown (**b**) solid line, scale at right; Québec 1906–1941). Of all these fires, 67.5% were anthropogenic, 5.5% were caused by lightning and 27% were of unknown origin.

Table 1. Taxon prevalence (percentage of taxon lists containing the given taxon) and frequency of occurrence (F_{ir}) according to the first four ranking positions in taxon lists (see equation 1). *When excluding plantations, spruce prevalence and dominance in modern forests are 65.7% and 10.0%, respectively.

Taxa	1846–1900 ($n = 8477$)					1980–2009 ($n = 4376$)				
	Prevalence (%)	F_{ir} (%)				Prevalence (%)	F_{ir} (%)			
		1	2	3	4		1	2	3	4
Cedar	52.5	32.2	7.4	11.3	10.0	34.4	13.7	5.8	6.6	6.8
Fir	67.7	21.9	26.4	18.9	26.5	81.5	19.8	25.3	22.3	17.6
Spruce	67.3	15.7	30.8	28.2	14.9	66.5*	12.1*	16.5	17.9	18.0
Maple	20.9	13.0	3.3	2.1	3.8	59.4	21.9	13.3	10.3	10.6
Yellow birch	38.8	8.5	16.6	15.1	15.1	35.6	3.7	9.5	10.7	9.4
Paper birch	31.7	4.2	6.9	16.5	22.5	63.1	8.4	13.2	18.4	21.7
Poplar	5.7	1.7	2.1	1.5	2.0	41.8	17.0	9.3	8.1	7.5
Pine	5.5	1.1	1.4	2.1	2.7	2.7	0.6	0.6	0.6	0.6
Beech	6.4	0.6	3.4	3.0	0.7	8.5	1.9	3.4	1.5	1.6
Ash	3.3	0.5	0.9	0.7	1.2	7.4	0.3	1.0	1.5	2.6
Larch	1.1	0.3	0.6	0.4	0.1	3.9	0.2	1.4	1.3	1.0
Others	1.4	0.2	0.2	0.3	0.5	8.1	0.5	0.6	0.9	2.7
Total		100	100	100	100		100	100	100	100

century disturbances were comprised primarily of logging (up to 72% of all disturbances observed during the 1925 to 1930 time period) and fire (up to 36%). The temporal coincidence of fire frequency increase and increases in human population, logging, settlement and anthropogenic fires across the entire province of Québec suggest that most fires were anthropogenic. During the 20th century, fire, logging and settlement were closely tied to each other throughout the surveyed area (Fig. S2).

During the 19th century, conifers were much more prevalent and dominant (ranked first) than broad-leaved taxa (Table 1). Fir, spruce and cedar were the most prevalent (prevalence of 52% to 67%) and dominant (15% to 32%) taxa. The most prevalent broad-leaved taxa were yellow birch (39%) and paper birch (32%), while the most dominant was maple (13%). All remaining taxa were much less prevalent and dominant. Cedar and maple occurred at greater frequencies of rank 1 than ranks 2 to 4, indicating that they tended to be dominant when present. Conversely, spruce, yellow birch and paper birch tended to occur at positions 2 to 4.

Pre-settlement dominance (percentage in the rank 1 category) of cedar, fir and spruce was strong and uniform across the study area (Fig. 3). In contrast, the dominance of maple and birches was patchy, especially for paper birch, which occurred as a dominant primarily in the northeastern part of the study area. All remaining taxa were only locally dominant. Beech did not occur at all in the northeast, beyond its modern range limit. Pre-settlement dominance was also influenced by elevation (Fig. 4). Whereas cedar and spruce were less likely to dominate with increasing altitude, maple displayed the reverse trend up to about 400 m, beyond which it was the most dominant taxon.

Comparison of survey records and modern plots showed significant changes in forest composition since the 19th century. Maple (increase of 38.5%), poplar (36.1%) and paper birch (31.4%) showed large increases in their frequencies of occurrence. Balsam fir experienced a moderate increase (13.8%), while the remaining taxa showed minor changes. Overall, conifer dominance decreased by 24.8%, from 71.2% to 46.4%, whereas broad-leaved dominance increased by 25.1% (Table 1). Cedar displayed by far the most significant dominance decrease (18.5%), whereas poplar (15.3%) and maple (8.9%) showed the most important dominance increases. Spruce prevalence remained stable between time periods, whereas its dominance decreased by 5.7% (modern spruce-dominated plantations were excluded from analysis) (Table 1). Trends of decreased cedar dominance and increased poplar and maple dominance were strong and spatially uniform across the entire study area, whereas remaining taxa showed more heterogeneous patterns of change, with patches of increased dominance intermingled with patches of diminished dominance (Fig. 3). In terms of elevation, the most important changes occurred below 360 m, where poplar dominance increased and cedar dominance decreased (Fig. 4). Maple dominance tended to show greater increase with increasing elevation.

Although forest composition has changed, the patterns of species co-occurrence remained stable since pre-settlement time periods, especially when considering conifer–conifer taxon pairs (Table 2). In both time periods,

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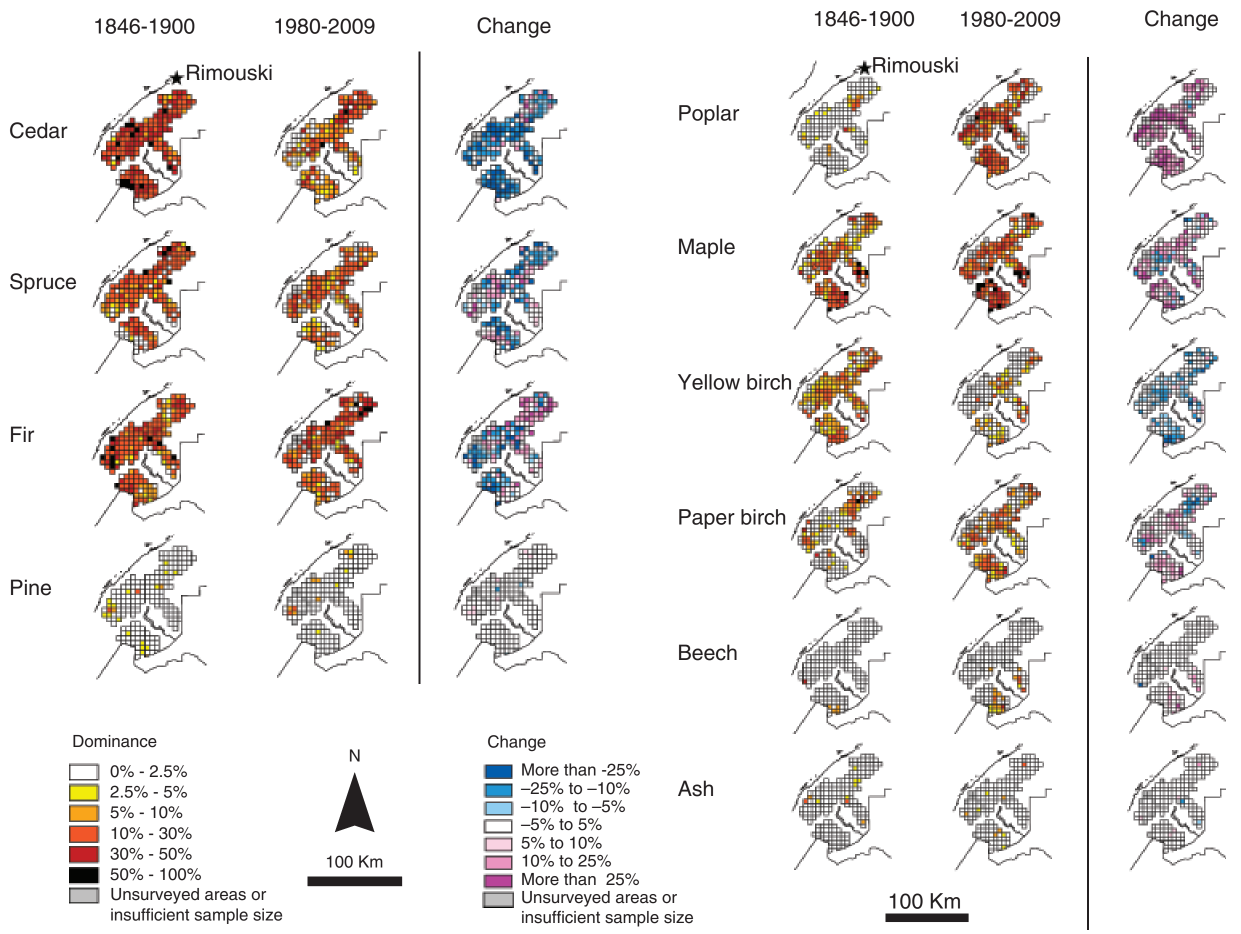

Fig. 3. Spatial patterns of taxon dominance using a grid of 25-km^2 cells across the study area. For each cell, taxon dominance corresponds to the percentage of observations with the given taxon listed first in surveyor observations (1846–1900) or the percentage of modern plots with the given taxon having the greatest basal area (1980–2009). For each cell, the change in dominance between time periods was computed by subtraction.

fir, spruce and cedar were frequently co-occurring conifers, while maple, yellow birch and beech formed the most important group of co-occurring broad-leaved taxa, followed by the poplar–paper birch pair. The most important change between time periods concerns maple. During the pre-settlement time period, only three taxa, fir, spruce and white birch, were regularly co-occurring when any other taxon was dominant. For the present-day data set, maple has become an additional frequently co-occurring taxon.

Discussion

Our study reconstructed the tree species composition of the forest prior to European settlement in the LSL region using line descriptions made by early land surveyors. Most forest reconstructions in North America have been based on witness tree data, while line descriptions have received relatively little attention (Whitney 1994). A probable reason for this is that most line descriptions involve 1.6-km (1-mile) long line segments, and consequently represent an overly generalized description of the forest, regrouping a variety of forest stands. Our study is innovative because it is based on a different type of line description, having a density of observations such that stands are identified individually. We have georeferenced all observations as a line or a point and considered ranked taxa enumerations and cover types. Even if it was not possible to verify our assumption that these different data types can be combined, given proper weighing, several weighing procedures (not shown) have produced very similar results, giving us confidence in our results. A more basic assumption is that surveyors ranked taxa according to their relative importance within the stand. This assumption is well supported by the high similarity of taxa co-occurrence between time periods, indicating at least that surveyors carefully ranked dominant taxa at first position. An additional argument is the high coherence

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between the ranking of taxa and the terms employed by surveyors to identify forest cover types.

Our reconstruction indicates that eastern white cedar, balsam fir and spruce were most prevalent, most dominant and most frequently co-occurring taxa. Paper and yellow birches were also frequent, mostly as companion species, whereas poplar and pine were infrequent and sparsely distributed over the study area. Conifer stands predominantly occupied the lowlands and lower slopes whereas deciduous, mostly maple-dominated stands, were the most frequent cover type on the highlands. Similar pre-settlement forests were documented to the south in the adjacent state of Maine (USA), where balsam fir, eastern white cedar and spruce were the most prevalent species, particularly in sectors that border the LSL region (Lorimer 1977; Cogbill et al. 2002). Our study also agrees with results obtained elsewhere in the northern temperate and southern boreal zones, reporting a greater prevalence and dominance of long-lived, late-successional species (e.g. beech, cedar, hemlock, white spruce) and lesser occurrences of fast-growing, early-successional species (e.g. birches, maples, poplars) before settlement as compared to the present-day (Siccama 1971; Abrams 1998; Bürgi et al. 2000; Dyer 2001; Friedman & Reich 2005; Pinto et al. 2008).

The onset of large-scale industrial clear-cutting for sawmills and the pulp and paper industry at the end of the 19th century appears to have been the cause behind the reduction in conifer dominance and their replacement by deciduous tree species (Boucher et al. 2006; Etheridge et al. 2006). By clearing large expanses of the landscape, clearcuts are known to encourage invasion by fast-growing species such as aspen, paper birch, maple, wild cherry, hazelnut, willow and alder (Harvey & Bergeron 1989; Archambault et al. 1998; Aubin et al. 2005; Prévost 2008). In our study, eastern white cedar was the taxon that had decreased the most in dominance since pre-settlement times. Two main factors might be associated with this trend.

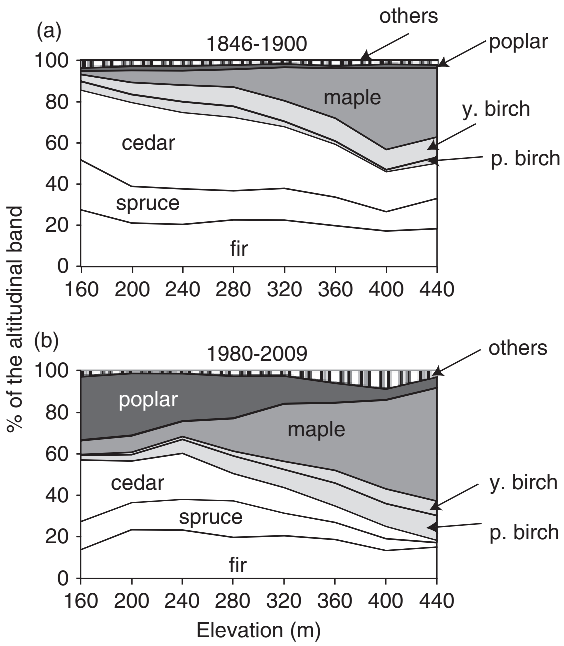

Fig. 4. Taxon dominance according to altitudinal bands. Areas below 160 m and above 440 m have been excluded due to the low numbers of observations. For each altitudinal band, dominance corresponds to the percentage of observations with the given taxon listed first in surveyor observations (**a**); (1846–1900) or the percentage of modern plots with the given taxon having the greatest basal area (**b**); (1980–2009).

Table 2. Co-occurrence between dominant (row) and co-occurring taxa (column) for the pre-settlement and present-day time periods. The classes 0, 1, 2, 3, 4 and 5 indicate 0%, 1 to 20%, 21 to 40%, 41 to 60%, 61 to 80% and 81 to 100% of co-occurrence, respectively. Dark grey: conifer–conifer taxon pairs; light grey: conifer–broad-leaved and broad-leaved–conifer taxon pairs; white: broad-leaved–broad-leaved taxon pairs. *difference of more than one class of co-occurrence between the two time periods.

	Co-occurring taxa																			
	Pre-settlement										Present-day									
	Sp	Pi	Fi	Ce	Pb	Yb	Ma	Be	As	Po	Sp	Pi	Fi	Ce	Pb	Yb	Ma	Be	As	Po
Dominant taxon																				
Spruce (Sp)		1	4	3	2	2	1	0	1	1		1	4	2	3	1	2	1	1	2
Pine (Pi)	5		4	1	2	2	1*	0	0	1*	5		3	1	3	0	3*	0	0	3*
Fir (Fi)	5	1		3	3	3	1*	1	1	1	4	1		2	4	2	3*	1	1	2
Cedar (Ce)	4	1	4		2	2	1	0	1	1	5	1	5		3	1	1	1	1	2
P birch (Pb)	4	1	4	1		1*	1*	0	1	2	3	1	5	2		3*	4*	1	1	3
Y birch (Yb)	5	1	5	3*	2		2*	1	1	1	4	0	5	1*	3		4*	1	1	1
Maple (Ma)	3	1	3	1	1*	5		2	1	1	2	1	4	1	3*	4		2	1	2
Beech (Be)	5*	0	5*	1	1	5	3*		0	0	1*	0	2*	0	1	4	5*		0	1
Ash (As)	4	0	3	3	2*	1	1	0		2	3	0	3	2	4*	2	2	0		2
Poplar (Po)	4	1	4	1	4	1	0*	0	0		4	1	5	2	4	1	4*	1	1	

First, beginning at the end 19th century, cedar was intensively harvested for the manufacture of shingles, railroad ties, telephone posts, house logs, etc. (Langelier 1906; Fortin et al. 1993). Second, this species regenerates with difficulty following both clear-cuts (Heitzman et al. 1997; Heitzman et al. 1999) and fires (Bergeron & Charron 1994) and is generally outcompeted by fast-growing species such as sugar maple, trembling aspen and balsam fir (Abrams & Scott 1989; Bergeron & Charron 1994). Since the tallest individuals selected for harvest were found on slopes with moderate inclination in pre-settlement forests (Langelier 1906; Curtis 1946), it is not surprising that this species is now restricted to moist lowlands and steep cliffs (Robitaille & Saucier 1998). Given its relatively slow growth rate and restriction to extreme sites, a reduction in the number of mature seed bearers and browsing by deer (*Odocoileus virginianus*), a successful restitution of the eastern white cedar component in the LSL forests will only be feasible through substantial restoration efforts.

In contrast to eastern white cedar, balsam fir and spruce were probably not severely affected by settlement. Balsam fir dominance was only slightly reduced as compared to its status in the pre-settlement forests, while its prevalence increased. This could be attributed to the pronounced shade tolerance of balsam fir and to the large quantity of seedlings that it usually establishes as advanced regeneration, which allows this species to rapidly resume dominance following either clear-cuts (Archambault et al. 2006; Prévost 2008) or spruce budworm outbreaks (Baskerville 1975; Blais 1983). Similarly, spruce prevalence remained stable whereas its dominance decreased moderately (when ignoring modern plantations). Since white spruce is also known to quickly recover following canopy openings (Ruel & Pineau 2002), and that these two species generally co-occur in the modern stands, maintenance or increase of their dominance is likely to occur in the near future, given the increasing use of variable retention logging practices.

Sugar maple and red maple are currently the most dominant tree taxa for the entire study area, which is surprising given that both species attain their northern range limit in the LSL region. An increase in prevalence and dominance since pre-settlement time was reported for these two species over the entire northeast North America region (Siccama 1971; Whitney 1994; Abrams 1998; Bürgi et al. 2000; Friedman & Reich 2005). Among the likely factors explaining this expansion, some studies emphasize the capacity of these species to thrive over a wide range of soil and light conditions. In addition, their high germination capacity and ability to stock advanced regeneration with seedlings make them able to quickly expand in cutover sites, old fields and burned sites and maintain themselves through a wide array of seral stages (Abrams 1998; Lin & Augspurger 2008; Fei & Steiner 2009). These characteristics have likely increased the dominance of maples on several cutover sites in the 19th and 20th century, especially on the upper or mid-slopes where maple species were already present (Boucher et al. 2006). It is also interesting to note that the very large increase in maple prevalence, from 21% to 60%, was paralleled with an increase of maple co-occurrence when several other taxa are dominant, suggesting that maples have increased their importance in several forest types and invaded new sites. Maple species are thus very likely to continue their expansion in the foreseeable future, given the continuation of anthropogenic disturbances, along with the anticipated acceleration of climate warming in the coming decades (IPCC 2007).

Although we grouped together all poplar species, most poplar observations corresponded to trembling aspen (Appendix S1). The post-settlement expansion of aspen throughout the LSL region appears to be largely associated with the increased fire frequency, as this species is known for its propensity to quickly invade burned sites, both through sexual and vegetative regeneration (Bergeron & Charron 1994; Fortin 2008). Around 35% of the pre-settlement aspen observations were associated in survey records with burns, either recent or old (data not shown). Aspen can also quickly colonize cutover sites, especially if logging operations comprise some form of soil treatment, such as scarification (Carleton & MacLellan 1994). Because aspen can maintain itself through sprouting (Cumming et al. 2000) and can colonize disturbed sites by seed, its prevalence and dominance are likely to continue to increase in the future (Fortin 2008).

The increased fire frequency that favoured aspen in the 20th century appears to be related to human activities. Despite the enactment of a fire exclusion policy enforced by law in 1870 (Blanchet 2003), subsequent governmental fire reports (Québec 1906–1941) indicate that between 1906 and 1941 more than 67% of the forest fires were anthropogenic. The fires were primarily caused by slash burning escapes, locomotive fire sparks and logging operations, with only at most 6% originating from lightning events. Similar results were estimated to occur in the adjacent provinces of New Brunswick and Nova Scotia (Wein & Moore 1977). Furthermore, during a forest inventory made at the end of the 1930s, Guay (1942) estimated that approximately 5% of Rimouski County (in the northeast of the study area) burned each year. While the author did not specify causes of such high fire rates, he strongly noted the careless attitude of the settlers in their slash burning practices.

Our findings that the pre-settlement landscapes were largely dominated by fire intolerant and late-successional species such as balsam fir, white spruce, eastern white

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cedar and sugar maple, along with the low occurrence of fire-adapted species such as aspen and pine are additional indications that fires were infrequent over the area (Boucher et al. 2009a, b). A similarly low fire frequency was proposed for the natural forests adjacent to the study area in northeast Maine (Lorimer 1977; Fraver et al. 2009) and New Brunswick (Wein & Moore 1977). However, the patchy dominance of paper birch and aspen before settlement in the northeast of the study area suggest that some fires may have naturally occurred locally in the region.

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Supporting Information

Additional supporting information may be found in the online version of this article:

Fig. S1. Frequency of surveyors' observations according to observation length (line observations) or mean spacing (point observations). Primary taxon lists (a, b) and cover types (d, e) have been considered separately. The corresponding frequency distributions for the length of modern stands intersected by the same surveyed range lines (c, f) suggest that line length and point spacing reflect the extent of pre-settlement forest stands. Note that 1 chain = 20.1 m.

Fig. S2. Spatial patterns of disturbance frequency using a grid of 25-km^2 cells across the study area. For each cell, disturbance frequency corresponds to the percentage of all surveyors' observations mentioning the given disturbance.

Appendix S1. Terms and expressions found in surveyors' logbook and corresponding categories used in this study.

Appendix S2. Deriving secondary taxon lists from cover types.