

Long-term compositional changes following partial disturbance revealed by the resurvey of logging concession limits in the northern temperate forest of eastern Canada

Victor Danneyrolles, Dominique Arseneault, and Yves Bergeron

Abstract: Land use changes that are linked to European settlement of North America have transformed northeastern temperate forest landscapes. Many studies report a regional increase of young early-successional forests due to high disturbance rates since the preindustrial era (fire, land clearing, and clear-cuts). In this study, we document specific compositional changes to present-day mature forest landscapes, which have only been managed with partial cutting (high-grading and diameter-limit cuts) since the preindustrial era in southwestern Quebec. We resurveyed 108 forest observations that were extracted from logbooks of former logging concession limits (surveyed between 1870 and 1890). Results highlight an increase in mid- to late-successional shade-tolerant taxa (*Betula alleghaniensis* Britton, *Thuja occidentalis* L., *Acer saccharum* Marsh.) at the expense of preindustrial dominant conifers (*Abies balsamea* (L.) Mill., *Pinus strobus* L.). Former logging activities and spruce budworm (*Choristoneura fumiferana* Clemens) outbreaks appear to be the main drivers of these changes, which were also strongly structured across the topographic gradient. To some extent, these results highlight the relevance of partial cutting management, as it has allowed long-term maintenance of a mid- to late-successional forest composition, while also pointing the need for *P. strobus* restoration. We conclude that by allowing site-specific comparisons, the resurvey of historical observations greatly improve the analytical strengths of historical reconstruction.

Key words: forest succession, historical ecology, ecosystem-based management, preindustrial forests, presettlement forests.

Résumé : La colonisation européenne de l'est de l'Amérique du Nord a engendré une profonde transformation des paysages forestiers. De nombreuses études ont décrit une augmentation des jeunes forêts de début de succession comme conséquence des forts taux de perturbation liés à la colonisation (feux, défrichement, coupes à blanc). Dans cette étude, nous documentons les changements de composition spécifiques à des paysages forestiers aujourd'hui matures, qui n'ont été exploités que par des coupes partielles (coupes d'écrémage et coupes à diamètre limite) depuis l'époque préindustrielle. Nous avons réarpenté 108 observations de composition issues de rapports d'arpentage d'anciennes limites de concessions forestières (arpentées entre 1870 et 1890). Les résultats indiquent une augmentation de taxons de milieux à fin de succession (*Betula alleghaniensis* Britton, *Thuja occidentalis* L., *Acer saccharum* Marsh.) au détriment des conifères dominant à l'époque préindustrielle (*Abies balsamea* (L.) Mill., *Pinus strobus* L.). Ces changements de composition sont principalement la conséquence des coupes et des épidémies de tordeuse des bourgeons de l'épinette, et se sont aussi largement structurés le long du gradient topographique. Ceci témoigne de la pertinence de l'aménagement par coupes partielles, puisqu'il a permis le maintien d'une composition de milieux à fin de succession. Cependant, la restauration des populations de *P. strobus* paraît aussi nécessaire. Nous concluons qu'en permettant la comparaison de sites appariés, le réarpentage d'observations historiques améliore remarquablement la compréhension des changements de composition survenus depuis l'époque préindustrielle.

Mots-clés : succession forestière, écologie historique, aménagement écosystémique, forêts préindustrielles, forêts précoloniales.

Introduction

Global change is responsible for major shifts in forest ecosystems characteristics. In northeastern North America, land use changes that are linked to European settlement have transformed forest landscapes (Whitney 1994). Modern landscapes are generally considered to be younger and composed of an increased proportion of early-successional species compared with preindustrial landscapes (Mladenoff et al. 1993; Foster et al. 1998; Dupuis et al. 2011; Thompson et al. 2013). Knowledge of forest composition prior to Euro-American settlement is therefore used as a reference for restoration and forest management (Egan and Howell 2001; Foster et al. 2003).

In northern temperate forests, several studies have reported that preindustrial landscapes were dominated by old uneven-aged forests (Lorimer and White 2003; Boucher et al. 2009), the dynamics of which were mainly controlled by natural partial disturbances (gaps, insect outbreaks). To maintain forest landscapes within their range of natural variability, ecosystem-based management of these forests should be based mainly upon different types of partial cutting (Seymour et al. 2002; Raymond et al. 2009). In southwestern Quebec, a substantial proportion of the landscape has only been managed through partial cutting (high-grading and diameter-limit cuts) since the preindustrial era. These

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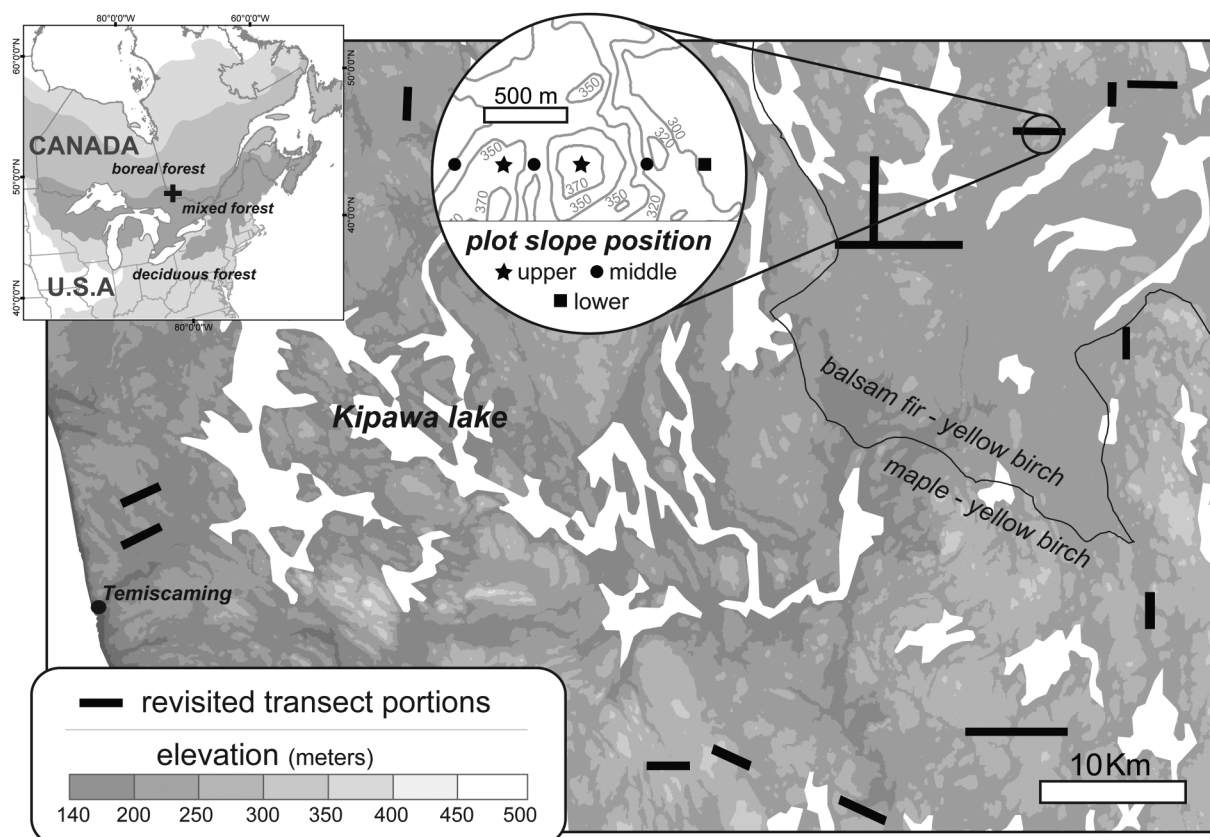
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Fig. 1. Study area, localization of resurveyed transect portions, and illustration of the three topographic positions.



present-day mature forest landscapes appear to have followed distinct postindustrial compositional trajectories, compared with those of highly disturbed landscapes, which were converted into younger early-successional forests (Dannehyrolles et al. 2016). The knowledge of long-term compositional changes after these types of partial cutting management could help in assessing the relevance of such practices and in developing management tools adapted to these mature forest landscapes.

Reconstructions of postindustrial compositional changes that are methodologically based on regional-scale comparisons between historical datasets (i.e., historical land survey data), and modern forest inventories commonly reveal general trends (e.g. Friedman and Reich 2005; Thompson et al. 2013). However, these reconstructions are not sufficiently reliable to properly characterize more precise compositional changes that concern only specific landscapes. As the main objective of this study was to document specific compositional changes that occurred in landscapes that were only managed by partial cutting, our reconstruction is based on the resurvey of historical observations (i.e., historical and modern observations that were paired at the same location). Yet, few studies have used this original methodological approach (Siccama 1971; Fahey and Lorimer 2014), even though it may allow a deeper understanding of long-term compositional changes. More particularly, we addressed two main questions: (i) what were the main drivers of these compositional changes? (ii) How have environmental gradients, particularly the topographic gradient, structured these compositional changes?

Study area

The study covers an area of about 4000 km² along the south-west boundary of the Canadian province of Quebec (Fig. 1). The forests in the study area form the northern end of the Great Lakes St. Lawrence mixed forest region (Rowe 1972), which also corresponds to the limits

between the maple – yellow birch and balsam fir – yellow birch bioclimatic domains of the provincial classification (Robitaille and Saucier 1998). The principal surface deposits are either undifferentiated or rocky glacial till. The closest weather station (Barrage Témiscamingue, 46°42'N, 76°06'W; 181 m above sea level (a.s.l.)) has recorded a mean annual temperature of 4.9 °C and annual total precipitation of 937 mm for the period 1981–2010.

Elevation varies from 290 m to 415 m (a.s.l.). Several factors that are related to topography influence forest composition (drainage, nutrient availability, soil depth, and microclimate; MacHattie and McCormack 1961). Natural stand-replacing fire rotation has been estimated to be about 200 years in duration within the balsam fir – yellow birch domain (Grenier et al. 2005) and 500 years within the maple – yellow birch domain (Drever et al. 2006). Outbreaks of spruce budworm (*Choristoneura fumiferana* Clemens) also have been identified as a major source of disturbance of forest dynamics over the last century (Bouchard et al. 2006a, 2006b).

First Nations have inhabited the study area for at least 5000 years (Riopel 2002). However, patterns of land use and management by Algonquin tribes during preindustrial times remain unknown. Logging did not begin until 1840 and was mainly focused on high-grading tall pine trees (*Pinus* spp.) until 1917 (Riopel 2002). Following the construction of a paper mill in the city of Témiscaming in 1917, diameter-limit cuts of smaller diameter spruces (*Picea* spp.) and balsam fir (*Abies balsamea* (L.) Mill.) for wood pulp became the main logging activity until the end of the 20th century (Lienert 1966), although high-grading tall trees for lumber remained frequent.

Material and methods

Site selection and field measurements

This study is based on the resurvey of 108 historical observations of forest composition that were extracted from 10 logbooks reporting

the first survey of logging concession boundaries, which were realized by four different surveyors between 1870 and 1890. These logbooks contain point observations mentioning taxa lists (e.g., "Pine, spruce, birch, cedar and a few maples"), which were usually 10 chains (about 200 m) apart along the survey lines. Point observations have been georeferenced using historical maps with a resolution of about 20 m. These 10 logbooks were selected for their consistent methodology.

A total of 108 observations that were to be resurveyed had been selected according to four criteria. (i) Observations had to be spaced at least 200 m apart to minimize spatial autocorrelation. (ii) To restrict sampling to the most ecologically accurate observations, only taxa lists mentioning at least two taxa were retained (90% of selected observations mentioned three to five taxa). (iii) To document dynamic trajectories of forests that had not experienced stand-replacing disturbance since preindustrial times, observations that were retained had to be located in present-day mature forests. These forests corresponded to a dominant age class of 90 years, 120 years, or as uneven aged in the modern forest maps (Berger 2008). Their old ages had to be confirmed in the field through the presence of old trees and irregular structure. (iv) Only observations that were located within 4 km of the road network were finally retained.

In the field, each observation point was registered using a GPS with a 10 m precision. These locations determined the centres of 11.28 m diameter circular plots of (400 m²). Within each plot, all stems greater than 10 cm in diameter at breast height (DBH, 1.3 m) were inventoried at the species level and their DBH measured. Evidence of former cuts (stumps) or spruce budworm outbreaks (numerous standing or lying dead stems) were recorded if they were recognizable either inside of or in proximity to the plots.

Database construction and analysis

For all historical and modern observations, taxa were classified according to five abundance ranks (*r*). Despite the possible existence of bias in these types of ranked list, e.g., giving more prominence to highly visible or commercially valuable taxa, a recent study demonstrated that taxa positions within lists are well correlated with their relative basal area (Terrail et al. 2014). Thus, for historical observations, taxa were ranked according to their position in the taxa list. The dominant taxon (first position in the list) was ranked as 4; the following two taxa in the list were ranked as 3 and 2, and rank 1 was assigned to the remaining taxa in the list. For example, the observation "Pine, spruce, yellow birch, cedar and a few maples" would have been transcribed as pines (*r* = 4), spruces (*r* = 3), yellow birch (*r* = 2), cedar (*r* = 1), maples (*r* = 1), and noncited taxa (*r* = 0). The same process was used to assign ranks to taxa that were inventoried in the resurveyed plots, according to their relative basal area. Some species from the modern plots were grouped at the genus level to match the taxa that were mentioned by surveyors, whereas rarely mentioned taxa (<5%) within historical and modern observations were grouped together as "others". Taxa that represented < 5% of the total basal area of a plot were removed from the list to obtain an equivalent number of taxa for historical and modern observations.

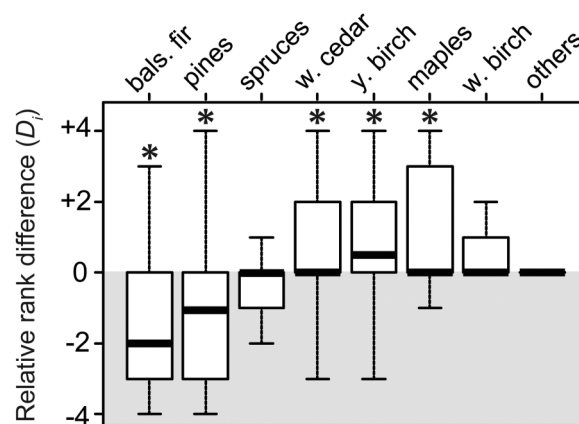
Several simple metrics were used to document changes in forest composition. First, frequency and dominance indices were computed (Scully and Richardson 2007; Dupuis et al. 2011). The frequency index represents the proportion of taxon occurrences regardless of rank (i.e., *r* ≠ 0), and the dominance index represents the proportion of taxon dominance (i.e., *r* = 4). These indices were computed for each taxon and for each period within the whole dataset and for three topographic positions (lower, middle, and upper slopes; Fig. 1). Second, a simple relative rank difference (*D_i*) was computed according to the formula:

$$D_i = R_{1880_{ip}} - R_{2014_{ip}}$$

Table 1. Dominance and frequency indices of each taxon in the 1870–1890 preindustrial period and in 2014 for the whole dataset (*n* = 108).

Taxa	1870–1890		2014	
	Dominance	Frequency	Dominance	Frequency
Balsam fir	45.9	87.2	7.3	51.4
Pines	16.5	56.9	2.8	7.3
Spruces	7.3	37.6	2.8	32.1
White cedar	8.3	41.3	27.5	59.6
Yellow birch	17.4	62.4	36.7	82.6
Maples	1.8	7.3	19.3	51.4
Paper birch	2.8	25.5	1.8	29.4
Other	0.0	6.4	1.8	12.8

Fig. 2. Relative rank difference (*D_i*) of each taxon for the whole dataset (*n* = 108). The asterisks indicate significant (*P* < 0.001) rank differences (Wilcoxon signed-rank test).



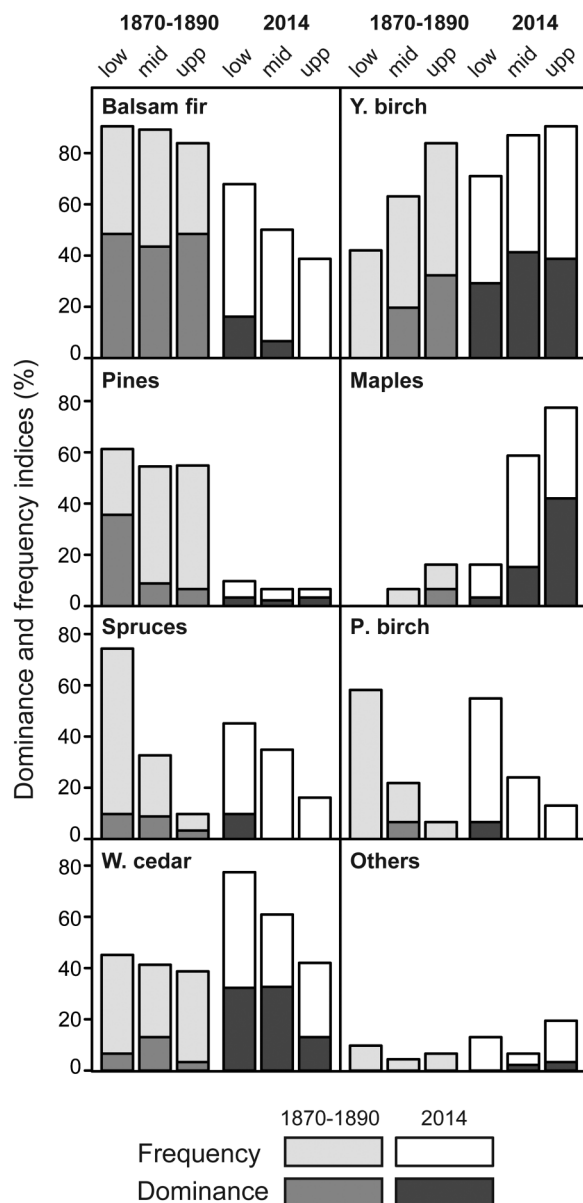
where $R_{1880_{ip}}$ corresponds to the rank of taxon *i* within plot *p* during the period 1870–1890, and $R_{2014_{ip}}$ is the rank of taxon *i* within plot *p* in 2014. Paired sample tests (Wilcoxon signed-rank tests) were used to assess the significance of rank differences ($R_{1880_{ip}}$ vs. $R_{2014_{ip}}$) for the entire dataset and by topographic position.

Results

During the preindustrial period (1870–1890), the 108 stands were dominated by balsam fir (*A. balsamea*), pines (*Pinus* spp.), and yellow birch (*Betula alleghaniensis* Britton), with dominance indices of 46%, 17%, and 17%, respectively (Table 1). Although less dominant, eastern white cedar (*Thuja occidentalis* L.), spruces (*Picea* spp.), and paper birch (*Betula papyrifera* Marshall) were frequent (41%, 37%, and 28%, respectively; Table 1). Evidence of former partial cuts (stumps) and spruce budworm outbreaks (numerous standing and lying dead stems) were found in all stands. Unfortunately, an obvious distinction between these two kinds of disturbance was not always possible, and most stands had likely been subjected to both kinds of disturbance during the 20th century.

These stands have experienced major composition changes since the end of the 19th century. Overall, balsam fir dominance decreased from 46% to 7% (Table 1), and its ranking within plots significantly decreased by an average of 1.6 ranks (Fig. 2). Balsam fir preindustrial dominance was high at the three topographic positions (Fig. 3), but its ranks mostly decreased at middle and upper slope positions (Fig. 4). Consequently, balsam fir has maintained a greater dominance on lower slopes (Fig. 3), with a high density of small stems (Fig. 5). Despite these changes, balsam fir is still one of the most frequent taxa in the study region, with an overall frequency of occurrence > 50% (Table 1).

Fig. 3. Dominance (dark grey) and frequency (light grey) of each taxon during the 1870–1890 period and in 2014 for the lower slope (low; $n = 31$), middle slope (mid; $n = 46$), and upper slope (upp; $n = 31$) positions.

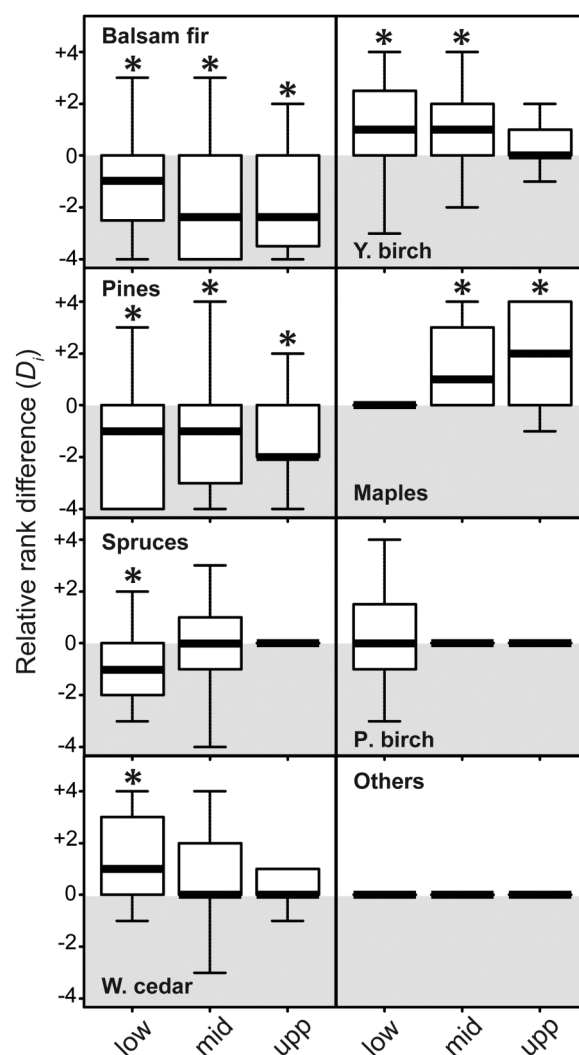


The taxon "pines" corresponds mainly to white pine (*Pinus strobus* L.; Table 2). This taxon experienced a sharp decrease in dominance (from 17% to 3%) and frequency (from 57% to 7%; Table 1) since preindustrial times. Pine rankings within plots significantly decreased for the entire dataset (Fig. 2) at all topographic positions (Fig. 4), especially on lower slopes where pine was very dominant during preindustrial times.

Overall, yellow birch dominance increased from 17% to 37%, and its frequency also increased from 62% to 83% (Table 1). Its rank within plots significantly increased for the whole dataset (Fig. 2), particularly on lower and middle slopes where it was less abundant during preindustrial times (Figs. 3 and 4). Yellow birch is currently characterized by low densities of large stems (Fig. 5). Its dominance and frequency are constant along the topographic gradient (Fig. 3).

Dominance and frequency of white cedar have increased from 8% to 28% and from 41% to 60%, respectively (Table 1). White cedar

Fig. 4. Relative rank difference (D_i) of each taxa for the lower slope (low; $n = 31$), middle slope (mid; $n = 46$), and upper slope (upp; $n = 31$) positions. The asterisks indicate significant ($P < 0.01$) rank differences (Wilcoxon signed-rank tests).



ranking within plots has significantly increased for the entire dataset (Fig. 3), especially on lower and middle slope positions (Fig. 4), where cedar is currently the most abundant taxon.

The taxon "maples" corresponds mainly to sugar maple (*Acer saccharum* Marsh.; Table 2). This taxon experienced the strongest increase in dominance (from 2% to 19%) and frequency (from 7% to 76%; Table 1). Maple ranking within plots significantly increased for the whole dataset (Fig. 2), especially on middle and upper slopes (Fig. 4) where maples currently are remarkably abundant.

Spruces and paper birch have not experienced significant changes in their abundance in the whole dataset (Fig. 2) and at all topographic positions, except for spruces, which decreased significantly on lower slopes (Fig. 3).

Discussion

Our results attest to major compositional shifts in mature stands over the last 130 years. Industrial logging started towards the end of the 19th century with the high-grading of tall pines and then intensified from 1917 (Témiscaming paper mill construction) onward with diameter-limit cutting of smaller spruces and balsam fir (Lienert 1966; Riopel 2002). These former management practices were mainly focused on harvest and did not aim to favour

Fig. 5. Overall structural characteristics of the present-day forests (total) and of the four currently most abundant taxa by topographic position (low, lower slope; mid, middle slope; upp, upper slope). DBH, diameter at breast height (1.3 m).

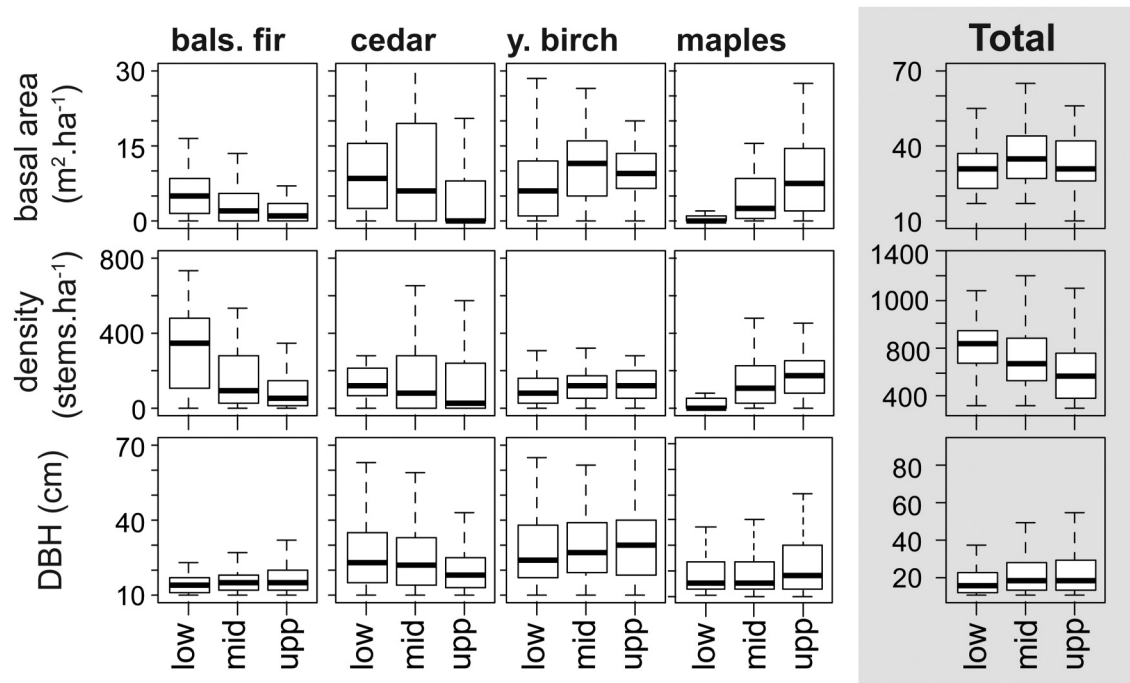


Table 2. Dominance and frequency indices of pines, maples, and spruces that were cited by surveyors (1870–1890) and identified in the field (2014). In many cases, surveyors cited these taxa at the genus level, so the data have been regrouped by genus level for the remaining analyses.

Taxa	1870–1890		2014	
	Dominance	Frequency	Dominance	Frequency
White pine	16.5	27.5	2.8	7.3
Red pine	—	—	—	0.9
Pines	—	29.4	—	—
All pines	16.5	56.9	2.8	7.3
Sugar maple	—	—	19.3	40.7
Red maple	—	—	—	30.6
Maples	1.8	7.3	—	—
All maples	1.8	7.3	19.3	51.3
White spruce	—	—	0.9	28.7
Black spruce	—	—	1.9	8.3
Spruces	7.3	37.6	—	—
All spruces	7.3	37.6	2.8	32.1

Note: “Pines” represents the frequency at which surveyors referred just to “pines” in their lists, whereas “All pines” represents the frequency regrouping all references to pines (i.e., white pine, red pine, and pines). “Maples” and “Spruces” are defined similarly.

particular stand characteristics. Intensive exploitation of pines was undoubtedly the main factor explaining their disappearance from these stands. Diameter-limit cuts at the beginning of the 20th century may also explain, in part, the decline in balsam fir abundances. The widespread mortality in balsam fir populations caused by the two major spruce budworm outbreaks of the 20th century (1910–1930 and 1970–1990; Bouchard et al. 2006a, 2006b) has been superimposed on the impacts of logging activities. Surprisingly, the abundance of spruces has not significantly decreased in these stands (except on lower slopes), although they represented the main target species for the paper industry. This likely reflected the fact that spruces were not particularly domi-

nant in these stands in preindustrial times, and thus, their diminution is not as marked as for balsam fir or pines.

Parallel with the decrease in abundance of balsam fir and pines, our results highlight a strong increase in mid- to late-successional, shade-tolerant taxa (yellow birch, white cedar, sugar maple). As such, our results contrast with the increase in early-successional, shade-intolerant taxa (e.g., poplars, paper birch) that has been documented in highly disturbed area within the region (Pinto et al. 2008; Danneylrolles et al. 2016) and more generally in northeastern North America (e.g., Friedman and Reich 2005; Boucher et al. 2006; Bouchard et al. 2006a; Dupuis et al. 2011; Thompson et al. 2013). Canopy openings created by partial cuts and spruce budworm outbreaks are clearly the main driver that favoured the recruitment of shade-tolerant taxa (Heitzman et al. 1997; Gasser et al. 2010; Duchesne and Prévost 2013; Larouche and Ruel 2015). Moreover, the large amount of stumps and rotten wood generated by these disturbances may have favoured the regeneration of yellow birch (Lambert et al. 2016) and sugar maple (Caspersen and Saprundoff 2005).

The compositional changes were also significantly structured across the topographic gradient. Lower slopes remained dominated by conifers (white cedar, balsam fir, spruces), whereas upper slopes became dominated by hardwood species (sugar maple and yellow birch). These divergent trajectories could be explained by distinct site characteristics. First, the colder and moister microclimate of poorly drained lower slopes may have favoured the increase in white cedar, where it can multiply by layering (Hofmeyer et al. 2009), while also allowing balsam fir and spruce to maintain an important abundance. Conversely, well-drained upper slopes, which lie outside of cold air drainage areas, were particularly favourable to the development of sugar maple (Barras and Kellman 1998). A second possible explanation for these divergent trajectories is that lower slopes were dominated by conifers in preindustrial times, whereas the upper slopes were largely dominated by yellow birch. Thus, the greater abundance of deciduous litter could have promoted the establishment of sugar maples at middle and upper slope positions (Barras

and Kellman 1998; Caspersen and Saprunoff 2005), whereas conifer-dominated lower slopes have been more resistant to the development of hardwoods.

Conclusions

Our study documents the long-term cumulative effects of partial cutting management and spruce budworm outbreak on northeastern temperate forest composition. Although these former management practices (high-grading, diameter-limit cuts) focused on harvest and did not aim to favour particular stand characteristics, they allowed mid- to late-successional forest composition to persist. Thus, to some extent, our results highlight the relevance of partial cutting management in northeastern temperate forests.

Nevertheless, these former management practices have led to significant compositional changes, which bring out an important avenue for restoration and management of these mature forest landscapes. Particularly, white pine populations that had been present in the area for thousands of years (Liu 1990) and were largely removed by the early 20th century logging activities should be restored. Stands and seed-trees preservation could ensure the establishment of white pine trees in adjacent cuts areas (Upstey et al. 2013). However, the strong expansion of sugar maple has led to stable deciduous stands, given that maple litter tends to inhibit regeneration of conifers (Barras and Kellman 1998). Thus, these stands should be carefully managed to maintain or reintroduce white pine. Irregular shelterwood systems can allow the maintenance of mid shade-tolerant species such as white pine or yellow birch in uneven-aged stands dominated by shade-tolerant species (Raymond et al. 2009; Suffice et al. 2015). Moreover, enrichment planting within patch cuts (Fahey and Lorimer 2013; Hébert et al. 2013) could be used to reintroduce white pine in stands from which it was completely removed.

More broadly, our study also demonstrates the analytical strength of site-specific comparisons through the resurvey of historical observations (Fahey and Lorimer 2014). This methodological approach was highly relevant to characterize compositional changes with precise spatial resolution and allowed us to distinguish different dynamics trajectories across the topographic gradient. Such an approach can be used to complement regional-scale comparisons between historical land survey data and modern forest inventories (e.g. Friedman and Reich 2005; Thompson et al. 2013) to refine our knowledge of postindustrial dynamics trajectories across disturbance or environmental gradients.

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