Millennial disturbance-driven forest stand dynamics in the Eastern Canadian taiga reconstructed from subfossil logs

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Summary

1. Although wildfire is the main natural disturbance factor driving changes in the North American boreal forest, understanding how the fire history of the last millennium shaped the present-day landscape diversity is a difficult task due to the lack of palaeoecological reconstructions with high spatial (few hundreds of square metres) and temporal (annual) resolutions.

2. We combined a detailed inventory of the present-day lakeshore forest of two lakes of the Eastern Canadian taiga with the dendrochronological dating of the subfossil logs that accumulated in the littoral zones facing these shores. Our objective was to compare the millennial impact of wildfires among stands of various structures and compositions. Past stem densities and fire years were reconstructed from log recruitment rates and dating of charred logs.

3. Multivariate analysis of the present-day lakeshore forest revealed three and two homogeneous shore segments per site (i.e. clusters). Cluster 1 at both sites exhibited denser forest, higher dead wood values and a higher percentage of balsam fir, a fire-sensitive species.

4. In total, 426 and 611 subfossil logs (mostly black spruce) were crossdated over the last ~1400 years. Their dendrochronological analysis confirmed that each lakeshore cluster, identified from the traits of the present-day forest, experienced a specific fire history over the last millennium (i.e. 0–5 fires of variable severity) that locally influenced forest composition, tree density and growth. Each fire triggered a specific forest structure trajectory characterized by a different stem density and rate of recovery.

5. *Synthesis.* This study provides a long-term perspective that helps explain how the present-day landscape diversity in the Eastern Canadian taiga reflects the site-specific fire history over the last millennium. Fires have caused persistent and cumulative impacts resulting in a progressive opening of the forest cover along with balsam fir exclusion. Present-day landscapes are mosaics of forest stands characterized by different times since fire and different post-fire forest structure trajectories.

Key-words: *Abies balsamea*, boreal forest, dendrochronology, determinants of plant community diversity and structure, fire ecology, paleoecology, *Picea mariana*, Quebec, successional trajectory

Introduction

Many ecosystems depend on or are well-adapted to the occurrence of disturbances (Le Goff & Sirois 2004; Brunbjerg *et al.* 2012; Newbery *et al.* 2013). However, disturbances may also produce long-term alterations of the natural landscape (He *et al.* 2002; Vanderwel, Coomes & Purves 2013), as well as a degradation in ecosystem functioning (Villnäs *et al.* 2013; Zwicke *et al.* 2013) or a creation of divergent successional pathways (Folke *et al.* 2004; Johnstone *et al.* 2010; Harvey & Holzman 2014). Spatiotemporal variation in disturbance frequency and severity is an agent of ecological diversity in several biomes (Fraterrigo & Rusak 2008).

For example, the North American boreal forest is characterized by large and frequent stand-replacing wildfires (Johnson 1992; Stocks *et al.* 2003) and is dominated by even-aged communities of fire-adapted species such as black spruce (*Picea mariana* (Mill.) B.S.P.) and jack pine (*Pinus banksiana* Lamb.) (Johnson 1992; Sirois 1995). Although spruce and pine stands recover rapidly after fire due to their serotinous

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cones (i.e. cones that remain closed and disperse seed following a fire), tree density and forest composition vary according to several factors, such as the magnitude of the pre-fire seed banks (Greene & Johnson 1999), the time since the last fire (Morneau & Payette 1989), the severity of the fire (Arseneault 2001) and the duration of the fire-free interval preceding the last fire (Lavoie & Sirois 1998). In these environments, fire frequency and severity are the dominant drivers of change in forest structure and composition at both the site and landscape levels and also determine ecosystem net primary production and the regional carbon balance (Bond-Lamberty *et al.* 2007).

In Eastern Canada, these short-term (decadal to secular) fire effects have been superimposed onto a longer-term, large-scale climate-induced decrease in conifer stem density, which was also mediated by fire disturbance (Payette & Gagnon 1985). The boreal biome of the region is subdivided into three main latitudinal bands from south to north: the closed-crown forest, the spruce-lichen woodland (hereafter referred to as the taiga) and the forest tundra (Fig. 1; Saucier *et al.* 2003). Across these bands, many black spruce stands failed to recover or shifted to more open woodlands after fire over the last 600–900 years, following the Medieval Climate Anomaly and even during the 20th century (Payette & Gagnon 1985; Sirois & Payette 1991; Payette & Morneau 1993; Lavoie & Sirois 1998; Girard, Payette & Gagnon 2008; Payette, Filion & Delwaide 2008; Boiffin & Munson 2013). In the two northern latitudinal bands, a decreasing occurrence of fire-sensitive balsam fir (*Abies balsamea* (L.) Mill.) was also observed (Arseneault & Sirois 2004; de Lafontaine & Payette 2010). Here, forest stands with abundant fir are today scattered in areas less affected by fire, frequently along streams and lakeshores (Sirois 1997; Arseneault, Boucher & Bouchon 2007). It has been hypothesized that these stands are remnants of a previously widespread closed-canopy spruce-fir vegetation zone, similar to that occurring further south, established more than 5000 years ago when fires were less frequent due to a more humid climate (Sirois 1997; Arseneault & Sirois 2004; Boucher, Arseneault & Hétu 2006; Ali *et al.* 2008; de Lafontaine & Payette 2010).

The taiga of Eastern Canada (Fig. 1), comprises a mosaic of spruce-lichen woodlands of various post-fire ages, stem densities and fir abundance, along with numerous lakes and peatlands in concave landforms (Fig. S1 in Supporting information). Deciphering how these spatially variable forest structures and compositions reflect long-term fire and climate impacts is a difficult task due to the lack of palaeoecological records available to reconstruct millennial forest dynamics with both high spatial and temporal resolutions. Dendrochronology can be used to reconstruct forest dynamics at the stand level with an annual resolution, but such reconstructions are limited to a few centuries because of fast decay of dead wood (Bond-Lamberty & Gower 2008). Conversely, pollen and charcoal and plant macroremains allow the reconstruction of long-term vegetation changes and fire histories (e.g. Carcaillet *et al.* 2010; Payette *et al.* 2012; Senici *et al.* 2013) but provide no direct information on past tree density or growth trends and the dating of disturbances relies on radiocarbon
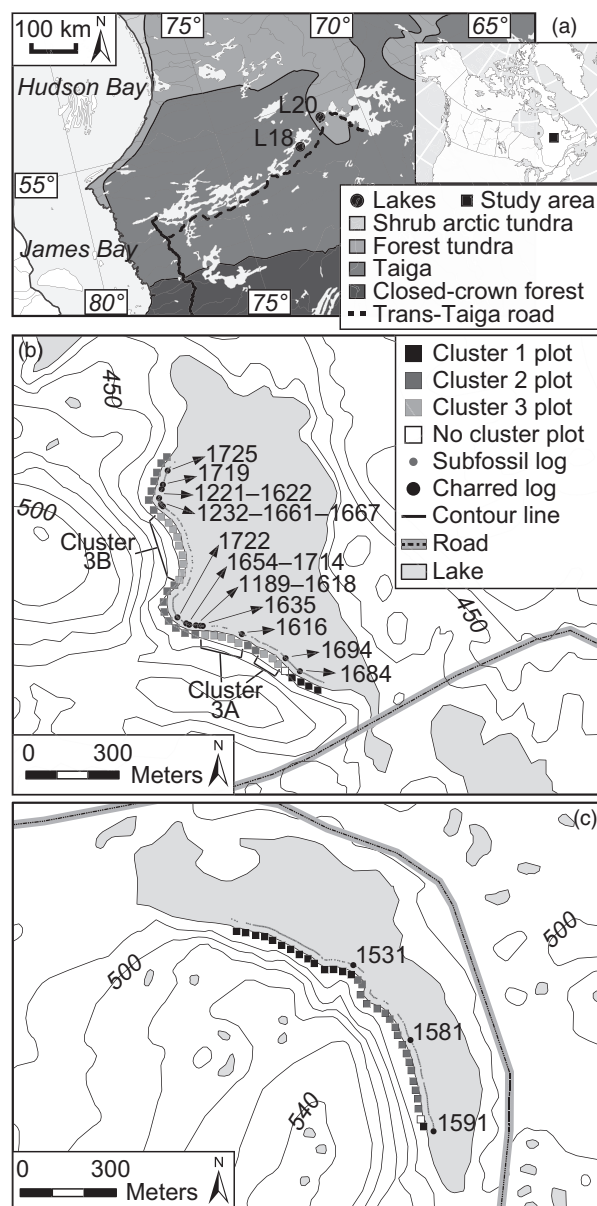

Fig. 1. Map of the study area in the northern taiga of Eastern Canada (a) and of lake L18 (b) and L20 (c) with plots assigned to the corresponding cluster. In b and c, the outermost tree-ring dates of charred subfossil logs are also shown. If two or more charred logs are facing the same plot, their outermost tree-ring dates are separated by a minus sign.

methods that are less precise than dendrochronology. Furthermore, contrary to fire impacts, pollen data are not stand-specific because of pollen mobility.

In this study, we first conducted a detailed inventory of the present-day lakeshore forest structure and composition of 2.2 kilometres of shoreline situated along two boreal lakes. Subsequently, we used dendrochronology to analyse the large stocks of submerged subfossil logs that accumulated in the littoral zones facing these same shores to reconstruct the millennial impacts of wildfires on lakeshore forest stands. Our objective was to verify whether variations in the forest structure and composition of the present-day lakeshore forest at

each site can be attributed to varying fire histories during the last millennium. Our hypotheses are that (i) there is a negative correlation between past wildfire frequency and present-day tree density and balsam fir abundance and that (ii) impacts of past fires have been spatially heterogeneous even within a given site and have persisted over several centuries.

Materials and methods

STUDY SITES AND SAMPLING

Two lakes, hereafter called L18 (54.25 N, 72.38 W) and L20 (54.56 N, 71.24 W), were the object of this study. They are located at the interface between the taiga and the forest tundra of Northern Quebec in Eastern Canada (Fig. 1). Black spruce is the prevalent tree species and a mosaic of post-fire spruce-lichen woodlands characterizes the region (Fig. S1). Other less abundant tree species include balsam fir and tamarack (*Larix laricina* (Du Roi) K. Koch). The regional burn rate is about 0.2% per year (Boulanger *et al.* 2012). The mean annual temperature is −3 °C and the average annual precipitation is 760 mm, of which 550 falls as rain (La Grande IV weather station; 22 years of observations, Environment Canada 2014). The region is located in the northern part of the balsam fir range and east of the jack pine range limit. The easternmost jack pine stands are located about 10 kilometres westward of L18.

The two sites are part of a network of lakes selected to study the stocks of subfossil logs in boreal lakes and their fluxes across the forest–lake interface (Gennaretti, Arseneault & Bégin 2014b), as well as to develop a dendroclimatic reconstruction of the summer temperatures of Eastern Canada over the last millennium (Gennaretti *et al.* 2014). The lakes were selected because they comprise a littoral segment with abundant subfossil logs facing old-growth lakeshore forest vegetation (i.e. time since last fire of about 300–400 years) on a well-drained glacial deposit and on the lakeside protected from dominant winds.

To characterize the structure and composition of the present-day lakeshore forest stands, we sampled 39 and 33 plots (10 × 10 m) spaced at 20-m intervals along and adjacent to the selected shore segments at L18 and L20, respectively (Fig. 1). Within each plot, we recorded the diameter at breast height (DBH) by species (spruce, fir or tamarack) of all living trees and snags ≥ 2 cm DBH. We also recorded the maximum diameter of all stumps and coarse woody debris pieces on the forest floor, excluding specimens with a maximum diameter < 4 cm. Snags were defined as standing dead trees connected to their roots and taller than breast height, stumps as dead trees connected to their roots and lower than breast height, and coarse woody debris pieces as dead trees on the floor not connected to their roots. The two or three tallest living trees (depending on species diversity) at each plot were cored as close to the collar as possible using a Haglöf increment borer. In the laboratory, tree-ring counting on the increment cores (No. = 165) allowed the minimum time since the last stand-replacing fire at each plot to be determined (i.e. maximum number of tree-rings per tree after applying a correction for coring height). Seedlings and saplings (< 2 cm DBH) were counted within two subplots (1 × 10 m) perpendicular to the lakeshore, nested within and on the two opposite edges of each main plot.

In the littoral zone facing the lakeshore segments, all subfossil logs with diameter ≥ 4 cm were sampled in the water or in the superficial sediments within 15–20 m from the shores, using the method described by Arseneault *et al.* (2013). In total, 627 and 848 logs were sampled along 1170 and 990 m of shoreline at L18 and L20, respectively. For each subfossil log, the sampling location was mapped with a total station and a cross-section was collected at its maximum diameter for dendrochronological analysis. In the laboratory, the tree species were identified using wood anatomy characteristics (spruce, fir or tamarack) and tree-ring width measurements and dendrochronological dating were performed with standard procedures as described by Gennaretti, Arseneault & Bégin (2014b). In total, 426 (all black spruce) and 611 (595 black spruce and 16 balsam fir) logs could be crossdated over the last ~1400 years at L18 and L20, respectively. Whereas fir and spruce individuals could be crossdated together, no master chronology could be developed for tamarack.

These subfossil logs have not been significantly redistributed along the littoral zone after recruitment into the water as proven by the relatively high proportion of specimens oriented perpendicularly to the shore with their base towards the forest and by the contrasting recruitment patterns of logs between consecutive shore segments with different fire histories (Gennaretti, Arseneault & Bégin 2014b). Thus, the logs can be used to reconstruct the long-term dynamics of the facing forest stands (i.e. past fire years, past fire impacts on tree mortality and regeneration and past changes in stem density and spruce growth; see 'Data analysis' below). However, these data do not allow reconstructing past variations in species abundance within the lakeshore forests because very few fir and no tamarack logs were crossdated (Fig. S2). This is due to the fact that fir and tamarack are much less abundant than spruce stems in the studied lakeshore forests, especially within the first line of tall dominant trees near the shoreline, which can generate persistent subfossil samples with a sufficient number of tree-rings for the crossdating procedure (Gennaretti, Arseneault & Bégin 2014b).

DATA ANALYSIS

The data used in this study (living plots and subfossil logs) and the analysis workflow are summarized in Fig. S2. First, triplets of consecutive neighbouring plots in the lakeshore forests were considered, so as to obtain 37 and 31 triplets at L18 and L20, respectively (e.g. triplet 1 comprises plots 1, 2 and 3; triplet 2 comprises plots 2, 3 and 4). Using triplets allowed compiling data within larger and more representative portions of the lakeshore forests and smoothing out the background noise among plots. Several variables were then developed to characterize the forest structure and composition of each triplet (Table 1). When two variables were strongly correlated ($r > 0.8$ or < -0.8), one of them was excluded from the subsequent analyses to limit redundancy (Tables S3 and S4 in Supporting information). In this way, 'Nliv', 'Ntot', 'F%reg', 'BAliv' and 'a' were excluded for L18, while 'Nliv', 'Ntot', 'Nliv6', 'BAliv' and 'a' where excluded for L20. Correlation between 'F%' and 'Ndead' was slightly higher than 0.8 at L18, but the two variables were retained as their association is not straightforward.

We performed a principal component analysis (PCA) on the triplets of each lake using our set of descriptive variables. All variables were scaled to unit variance. Only principal components with eigenvalues > 1 were retained (Figs 2 and S3–S6). A hierarchical cluster analysis was subsequently used to detect associations among triplets at each site based on a Euclidean distance matrix obtained from the component scores scaled so as to have variance proportional to their corresponding eigenvalues. Euclidean distance was chosen because it is appropriate with quantitative descriptors and enhances differences among objects by squaring (Legendre & Legendre 1998). Ward's method was applied in clustering because it minimizes variance

Table 1. Variables used to describe present-day forest structure and composition in triplets of sampling plots at the sites L18 and L20

Variable ID	Unit	Description
Nliv	No. ha^{-1}	Density of living trees comprising saplings and seedlings
Ntot	No. ha^{-1}	Density of living trees comprising saplings and seedlings plus snags and stumps
Nreg	No. ha^{-1}	Density of saplings and seedlings
Nliv2	No. ha^{-1}	Density of living trees ≥ 2 cm DBH
Nliv6	No. ha^{-1}	Density of living trees ≥ 6 cm DBH
Nliv12	No. ha^{-1}	Density of living trees ≥ 12 cm DBH
Ndead	No. ha^{-1}	Density of snags and stumps
Ncwd	No. ha^{-1}	Density of coarse woody debris pieces on the floor
BAliv	m^2 ha^{-1}	Basal area of living trees ≥ 2 cm DBH
MeanBAliv	m^2 tree^{-1}	Average basal area per living tree ≥ 2 cm DBH
BAdead	m^2 ha^{-1}	Basal area of snags and stumps
MeanBAdead	m^2 tree^{-1}	Average basal area per snag or stump
F%reg	%	Percentage of fir in the saplings and seedlings
F%	%	Percentage of fir among living trees ≥ 2 cm DBH
T%	%	Percentage of tamarack among living trees ≥ 2 cm DBH
Age	Years	Average minimum time since the last stand-replacing fire of the three plots
a	–	Coefficient 'a' of the power function model describing the stand size structure of living trees*
b	–	Coefficient 'b' of the power function model*

*$y = a*x^{(-b)}$ where y is the number of individuals per hectare and x is the central value of 2-cm size classes (Tables S1 and S2).

intraclusters and maximizes variance inter-clusters. Homogeneous clusters of triplets were then defined for each lake by cutting dendrograms at distance two (Figs S7 and S8). Sensitivity of clustering results to the choice of the method is evaluated in Table S5. Each lakeshore forest plot was finally considered as a part of a cluster if the majority of the triplets in which it was included belonged to that cluster. Two plots (one per lake) could not be assigned to any cluster because their corresponding triplets were equally distributed among more than one cluster (Fig. 1).

Crossdated spruce and fir logs were subsequently assigned to the nearest lakeshore plot and then to the corresponding cluster. To limit data fragmentation along the shoreline, logs assigned to a series of less than three contiguous plots belonging to the same cluster were discarded from the subsequent analyses (i.e. logs facing plots 9 and 10 at L18, and those facing plot 1 at L20; Fig. 1). Cluster 3 at L18 was also divided into two subclusters for the analysis of the subfossil logs as, even if today the lakeshore plots are characterized by a similar forest, their histories showed some differences (cluster 3A contains logs assigned to plots 6–8 and 11–15, while cluster 3B contains those assigned to plots 24–32; see Figs 1 and 3).

Tree-ring dating of charred subfossil logs (see Fig. S9 for some examples), along with concurrent variations of log abundance, allowed us to determine when wildfires affected the lakeshore forest of each cluster during the last millennium. Each identified fire was assigned to the date of its most recent evidence considering that some subfossil logs may have lost their charred marks and may have been more or less eroded. Fire evidences are the outermost tree-ring dates of charred logs or of subfossil logs in proximity of a charred specimen and preceding a clear discontinuity in the temporal sequence of outermost tree-ring dates. A detailed analysis of more than 1600 logs from five lakes indicates that our estimated fire dates may precede the actual dates by a few years because an average of three outermost tree-rings per century is lost through decay per log (Gennaretti, Arseneault & Bégin 2014b). The relative severity of the detected wildfires was evaluated from their impacts on the number of subfossil logs produced by the lakeshore forest and preserved in the adjacent littoral zone. A typical response to fire includes a peak in subfossil log recruitment (this peak may be attenuated if several killed trees on the shore decompose in an upright position), followed by a recruitment reduction as trees grown up after fire have to reach a minimum height before being available to generate subfossil logs from their upper stem portions (Gennaretti, Arseneault & Bégin 2014b). Here, a complete interruption or a strong reduction of log recruitment for several years after a fire were used as an indicator that most of the trees were killed and that the stand developed as an even-aged post-fire cohort.

The subfossil records of both sites were divided into discrete fire-free intervals delineated by the estimated wildfire dates. Three fire-free intervals were identified at both sites: AD 682–1251, 1251–1624 and 1729–1994 at L18, and 728–1207, 1207–1592 and 1592–2002 at L20. The recruitment rates of subfossil logs (number recruited per 100 years per 100 m of shoreline based on their outermost tree-ring dates) were computed for each of these intervals to compare the relative openness of the lakeshore forest cover between clusters at each site (Figs 3 and 4). Assuming that the number of subfossil logs

Fig. 2. Biplots of the first two principal components of the L18 (left) and L20 (right) principal component analysis. Variables (see Table 1) are in grey and triplets of plots are in black. Triplets belonging to the same cluster are enclosed in minimum spanning ellipses (solid: cluster 1; dashed: cluster 2; dotted: cluster 3).
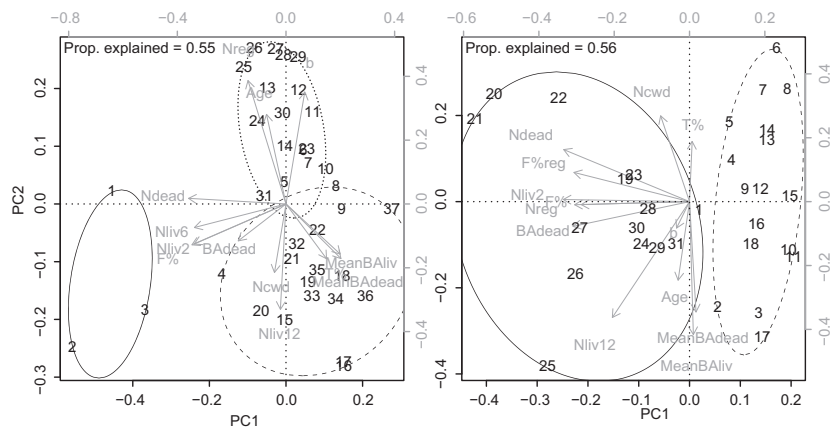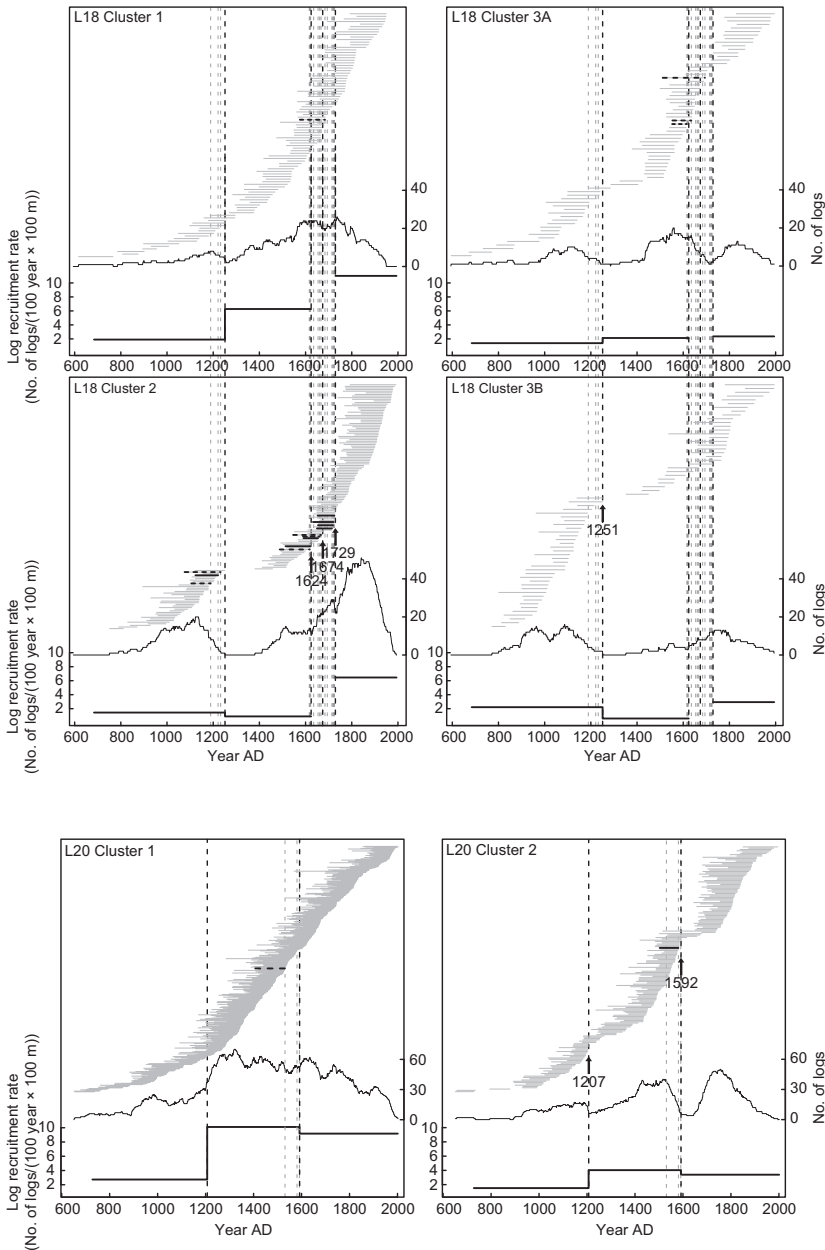
Fig. 3. Life spans, abundance and recruitment rate of L18 subfossil logs crossdated to the calendar year and assigned to the corresponding cluster according to their location. Each horizontal grey solid line refers to the life span of one log. Charred logs facing plots at the boundary between two cluster (horizontal black dashed lines) and other charred logs (horizontal black solid lines) are also shown, as well as the recruitment date of all charred logs in the littoral zone (based on their outermost tree-ring date; vertical grey dashed lines) and the estimated wildfire dates (vertical black arrows on the most recent fire evidence and vertical black dashed lines). The thin black line at the middle of each panel shows the number of logs that were living each year. The thick black line at the bottom of each panel shows the average recruitment rate of logs during the identified fire-free interval (number recruited per 100 years per 100 m of shoreline based on the outermost tree-ring dates).

Fig. 4. Life spans, abundance and recruitment rate of L20 subfossil logs crossdated to the calendar year and assigned to the corresponding cluster according to their location. All symbols are as in Fig. 3.

produced by the lakeshore forest in a cluster is directly related to the density of large trees during a fire-free interval, which in turn depends on the pathway of forest recovery following the last fire, regular and high recruitment rates were attributed to a dense mature forest cover and low rates to an open cover. However, because subfossil logs progressively decay, these recruitment rates fade out when moving backward in time and cannot be compared among different fire-free intervals. To allow this comparison, we used the presence at each site of a cluster that has escaped severe fires over the entire study period (see Results). For each site, we standardized the number of subfossil logs that were living each year per 100 m of shoreline in each fire-affected cluster by dividing it with the number of logs in the cluster that had escaped severe fires. These ratios show the relative openness of the lakeshore forest cover among fire-free intervals and clusters (Fig. 5).

The smoothed average age-related growth curves of the black spruce subfossil logs recruited during different fire-free intervals were compared among clusters and fire-free intervals at each lake. For each

interval and cluster, all individual ring width series were aligned according to cambial age and averaged. Firs (16 logs at L20) and specimens with missing pith (7 and 14 logs at L18 and L20, respectively) were discarded. A spline with a 50% frequency cut-off and time-varying response (starting from 10 years and increasing by one each year; Melvin *et al.* 2007) was then used as smoothing algorithm to generate the smoothed growth curves. These growth curves allowed us to detect the most important temporal and spatial shifts of lakeshore forest growth in response to disturbances and climate change (Figs 6, 7, S10 and S11).

Results

PARTITIONING OF THE PRESENT-DAY FOREST

Principal component and cluster analyses identified three and two clusters of homogeneous lakeshore forest stands at L18
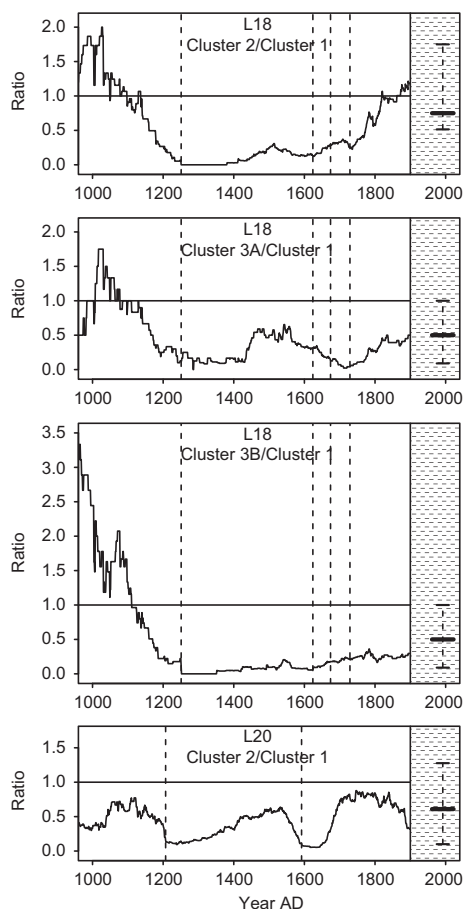
Fig. 5. Ratio between the number of subfossil logs that were living each year per 100 m of shoreline in the cluster 2 or 3 and the number of logs living in the cluster 1 at L18 (three upper panels) and L20 (bottom panel). Values older than AD 1000 or more recent than AD 1900 are not shown because they are influenced by relevant losses of subfossil logs through decomposition and burial (Gennaretti, Arseneault & Bégin 2014b) or by the fact that the recruitment of subfossil logs in the littoral zones is still ongoing, respectively. The estimated wildfire dates at each lake (vertical dashed lines) and the 5th, 50th and 95th percentiles of the ratios between the density of living trees ≥ 12 cm diameter at breast height (Nliv12) in the triplets of sampling plots belonging to the corresponding clusters (bold horizontal line and whiskers) are shown.

and L20, respectively (Figs 1 and 2). At L18, the first principal component (31% of the variance explained) differentiated cluster 1 from clusters 2 and 3, based on its higher percentages of fir, higher densities of snags and stumps, and higher densities of living trees, especially of small size classes (Figs 2 and S3 and Table 2). The second principal component (24% of the variance explained) differentiated cluster 3 from clusters 1 and 2, based on its lower densities of large-sized trees (≥ 12 cm DBH) and higher densities of saplings and seedlings that together influenced the coefficient 'b' of the power function models (Figs 2 and S3 and Table 2). Compared to cluster 1 and 3, cluster 2 displayed intermediate characteristics and lower densities of saplings and seedlings. At L20, the two clusters differed mainly by their first principal component scores (35% of the variance explained). In

comparison with cluster 2, cluster 1 was associated with higher fir percentages, higher basal areas of dead trees and higher densities of regeneration, dead trees and living trees ≥ 2 cm DBH (Figs 2 and S4 and Table 2).

PAST FIRES, SUBFOSSIL RECRUITMENT AND LAKESHORE TREE DENSITY

At least four wildfires of varying severities affected the lakeshore forest at L18 during the last millennium (Fig. 3). Cluster 1, which is today characterized by denser forest with more abundant fir, was clearly less severely affected by these wildfires than clusters 2 and 3 and escaped stand-replacing fires over at least the last 1200 years. A fire event completely interrupted the recruitment of subfossil logs in clusters 2 and 3B and strongly reduced the recruitment in cluster 3A at AD 1251, indicating severe tree mortality in the lakeshore environment. The fire may have partially burned the forest of cluster 1, where the recruitment of subfossil logs slightly decreased, but several individuals survived. Because fires generally reduce the recruitment of subfossil logs for about 120 years in these boreal lakes (Gennaretti, Arseneault & Bégin 2014b), the interruption/reduction that lasted for at least 200 years at clusters 2 and 3 after the AD 1251 event suggests the occurrence of a second fire before about AD 1400. This presumed fire most likely killed trees established after AD 1251 before they could become tall enough to generate subfossil logs with diameters ≥ 4 cm. Three subsequent closely spaced fires burned across the lakeshore forest of clusters 2 and 3 during the 17th and the first part of the 18th century. The AD 1624 fire was identified from charred subfossil logs preceding a discontinuity in the temporal sequence of *innermost* tree-ring dates (i.e. several lakeshore trees established after this fire), while the AD 1674 and 1729 fires were identified from charred subfossil logs and discontinuities in the sequence of *outermost* tree-ring dates (i.e. a break and a sudden increase in log recruitment indicating that several lakeshore trees died during these fires; see cluster 2 in Fig. 3). All these wildfires were less severe than the AD 1251 fire, as the recruitment of subfossil logs was altered but not interrupted. Despite the fact that a charred log with an outermost tree-ring in 1684 was found at the boundary between clusters 1 and 2, the recruitment of subfossil logs remained high and constant in cluster 1, indicating uninterrupted forest development and negligible fire impact.

Although all clusters at L18 exhibited similar recruitment rates of subfossil logs prior to the AD 1251 fire, cluster 1, which escaped severe fire disturbances during the last millennium, has been subsequently characterized by much higher and constant rates of recruitment of subfossil logs than clusters 2 and 3 (Fig. 3). This suggests that the density of lakeshore trees was similar among clusters before AD 1251 and that the fires produced a long-lasting decrease of stem density at clusters 2 and 3. These two clusters seem to have diverged from each other following the fires of the 17th and 18th centuries because cluster 2 has exhibited
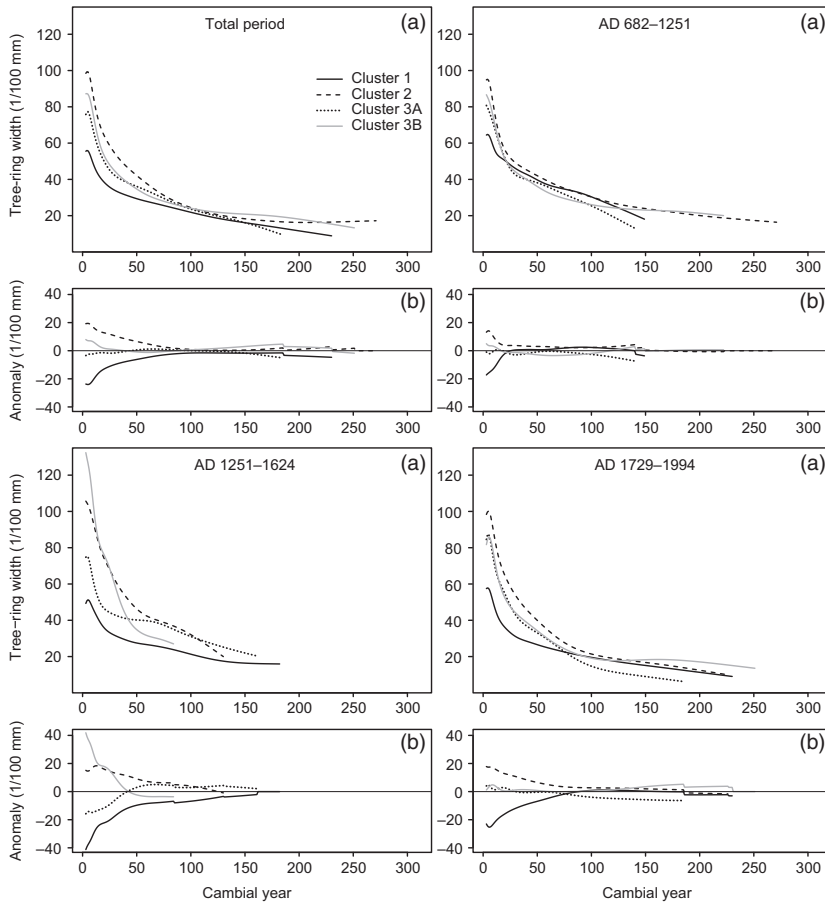
Fig. 6. Comparison among all clusters at L18 of the smoothed average growth curves for the subfossil logs recruited during different fire-free intervals. The 'a' plots show the smoothed average growth curves, while the 'b' plots show the growth anomalies calculated by subtracting the average of all clusters from the curve of each cluster. The legend in the first 'a' plot refers to the other plots as well.

higher recruitment rates than cluster 3 since the mid-18th century (6.5 vs 2.4 to 2.9 logs per 100 years per 100 metre of shoreline). These higher rates are consistent with the higher present-day density of large-sized trees ($\geq$ 12 cm DBH) in the lakeshore plots of cluster 2 as compared to cluster 3 (Table 2).

Fires were less frequent at L20 than at L18, as we detected only two fire events over the last millennium (Fig. 4). The only fire confirmed by charred marks on the logs occurred at AD 1592 and almost completely burned the lakeshore forest of cluster 2, as based on a severe reduction in subfossil log recruitment. The fire probably stopped near plot 20, at the border between clusters 1 and 2, where we found a charred subfossil log. The remaining plots of cluster 1 escaped the fire, as indicated by the very regular and high recruitment rates of subfossil logs. A peak of tree mortality in cluster 2 most likely indicates a previous moderate severity fire at about AD 1207, even if no charred log was discovered.

Similarly to L18, dense present-day forest stands with high fir percentages at L20 have escaped stand-replacing fires over the last millennium (over at least the last 1400 years at cluster 1 of L20). Recruitment rates of subfossil logs have always been higher at cluster 1 than at cluster 2, denoting that stem density has probably been higher at cluster 1 over the entire time period covered by our study (Fig. 4).

The yearly ratios of subfossil log abundance in burned relative to unburned clusters at each lake indicate that each

fire triggered a specific trajectory of stem density in the burned lakeshore clusters with varying post-fire density alterations and rates of recovery (Fig. 5). These effects included prompt and complete recovery to pre-fire stem density (e.g. cluster 2 at L20 after the AD 1592 fire), full but progressive recovery over several centuries (e.g. cluster 2 at L20 after the AD 1207 fire), extremely slow and partial recovery (e.g. clusters 2 and 3A at L18 following the two successive AD 1251 and ~1400 fires), persistent shift to low stem densities (e.g. cluster 3B at L18 following the two successive AD 1251 and ~1400 fires), as well as increased stem densities relative to pre-fire conditions (e.g. cluster 2 at L18 after the three fires between AD 1624 and 1729).

AGE-RELATED GROWTH CURVES OF THE SUBFOSSIL LOGS

The analysis of the average growth curves of the subfossil logs showed important climate- and fire-induced impacts on the lakeshore forest growth during the last millennium. Fires reduced lakeshore stem density and, as a consequence, the juvenile growth of trees (i.e. for young cambial ages) was faster in the burned lakeshore clusters than in the unburned ones (i.e. cluster 1 at both sites) during the subsequent fire-free intervals (see the juvenile growth of the subfossil logs of clusters 2 or 3 in comparison with that of logs of cluster 1 in
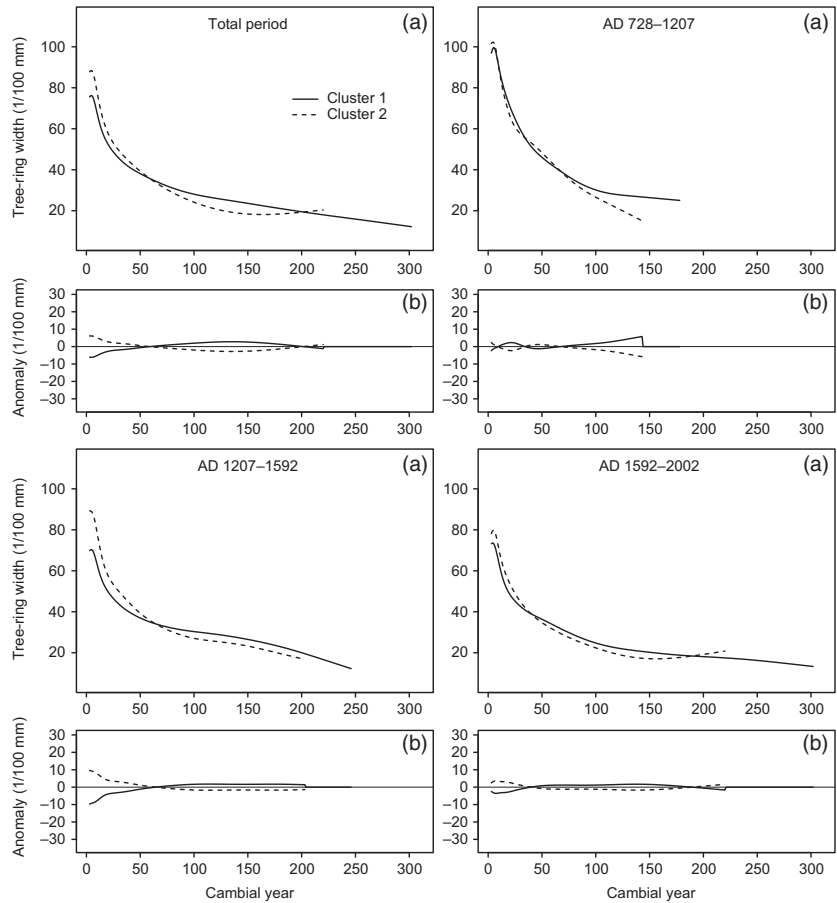
Fig. 7. Comparison between the two clusters at L20 of the smoothed average growth curves for the subfossil logs recruited during different fire-free intervals. The plots 'a' and 'b' are as in Fig. 6.

Table 2. Description of the lakeshore forest of each cluster at L18 and L20. Distinguishing traits are in bold (i.e. values of the variables contributing the most to the discrimination of the clusters of homogeneous lakeshore forest according to our multivariate analysis; see Figs 2, S3 and S4). Standard deviations (SD) refer to variability among triplets of sampling plots. Variables are described in Table 1

Variable	L18			L20	
	Cluster 1 (mean ± SD)	Cluster 2 (mean ± SD)	Cluster 3 (mean ± SD)	Cluster 1 (mean ± SD)	Cluster 2 (mean ± SD)
Nliv (No. ha^{-1})	22578 ± 9255	11671 ± 2640	25806 ± 6088	24393 ± 5432	15396 ± 4337
Ntot (No. ha^{-1})	23778 ± 9103	12171 ± 2714	26457 ± 6120	25671 ± 5672	16135 ± 4370
Nreg (No. ha^{-1})	17889 ± 9083	9225 ± 2367	**23500 ± 5931**	**19964 ± 5156**	12608 ± 4197
Nliv2 (No. ha^{-1})	**4689 ± 435**	2445 ± 758	2306 ± 548	**4429 ± 418**	2788 ± 488
Nliv6 (No. ha^{-1})	**2244 ± 271**	1182 ± 262	1237 ± 308	2036 ± 385	1351 ± 250
Nliv12 (No. ha^{-1})	544 ± 19	482 ± 207	**296 ± 142**	421 ± 103	273 ± 123
Ndead (No. ha^{-1})	**1200 ± 219**	500 ± 166	651 ± 95	**1279 ± 379**	739 ± 166
Ncwd (No. ha^{-1})	811 ± 84	757 ± 335	580 ± 254	610 ± 100	590 ± 116
Baliv (m^2 ha^{-1})	18.6942 ± 1.9140	14.8115 ± 4.9150	10.8277 ± 2.6050	18.1739 ± 2.8759	11.4771 ± 2.4030
MeanBAliv (m^2 tree^{-1})	0.0040 ± 0.0001	0.0067 ± 0.0031	0.0049 ± 0.0013	0.0041 ± 0.0005	0.0041 ± 0.0006
Badead (m^2 ha^{-1})	10.8140 ± 1.6916	6.7733 ± 1.7550	6.9507 ± 2.1521	**10.4133 ± 2.4791**	6.0797 ± 1.9972
MeanBAdead (m^2 tree^{-1})	0.0090 ± 0.0002	0.0142 ± 0.0037	0.0109 ± 0.0038	0.0085 ± 0.0020	0.0085 ± 0.0027
F%reg (%)	3 ± 3	0 ± 0	0 ± 0	**42 ± 21**	9 ± 16
F% (%)	**22 ± 4**	1 ± 2	0 ± 0	**28 ± 13**	8 ± 9
T% (%)	0 ± 0	2 ± 2	1 ± 1	1 ± 2	2 ± 1
Age (years)	245 ± 32	226 ± 15	**252 ± 13**	217 ± 15	207 ± 17
a	17871 ± 9090	9220 ± 2367	23497 ± 5932	19949 ± 5159	12597 ± 4201
b	2.0 ± 0.4	2.2 ± 0.5	**3.1 ± 0.5**	2.2 ± 0.2	2.2 ± 0.4

Figs 6 and 7). Furthermore, the average growth curves showed that, in clusters that escaped severe fire disturbances over the entire time period covered by the study (i.e. cluster 1 at both sites), trees grew faster during Medieval times than afterwards, suggesting the influence of a warmer climate (Figs S10 and S11).

Discussion

FIRE VS. TRAJECTORIES OF FOREST STRUCTURE AND COMPOSITION

The long-term perspective, along with the high spatial and temporal resolutions provided by this study, allowed the verification of whether or not variations in the present-day structure and composition of contiguous lakeshore forest stands in the Eastern Canadian taiga correspond to their respective fire histories during the last millennium. Our multivariate analysis of the current lakeshore forest vegetation revealed three and two homogeneous clusters with different forest compositions and structures at L18 and L20, respectively, even if these forests only face 1170 and 990 m of shore (Figs 1 and 2 and Table 2). The dendrochronological analysis of the subfossil logs collected in the littoral zone facing these clusters confirmed that they experienced site-specific fire histories over the last millennium that locally influenced tree density and tree growth (Figs 3–7), thus shaping the present-day landscape diversity. Unfortunately, our results do not allow reconstructing past variations in species abundance within the studied lakeshore forests (see 'Study sites and sampling'). However, all the lakeshore segments that were affected by fire during the last millennium are today characterized by more open forests with less dead wood and lower percentages of balsam fir than the unburned stands (Table 2), even despite the most recent fire occurring about 300 to 400 years ago. Consequently, our results support the hypothesis that fire impacts may persist for several centuries in the Eastern Canadian taiga and that present-day landscapes are the outcome of the progressive fire-induced breakup (i.e. forest cover opening and balsam fir exclusion) of a previously closed-crown spruce-fir vegetation zone (Sirois 1997; Arseneault & Sirois 2004; Ali *et al.* 2008; de Lafontaine & Payette 2010).

An important result of this study is the large variability in the post-fire forest structure trajectories in the lakeshore environment over the last millennium. Although it is generally assumed that black spruce is a fire-adapted species due to its serotinous cones, our results suggest that the classical model of post-fire forest recovery in black spruce forests (i.e. fast recovery to pre-fire stem densities) is over-simplistic because each fire can trigger a specific forest structure trajectory characterized by a different stem density reduction and a different rate of recovery. Despite the fact that an increase in stem density relative to pre-fire conditions occurred at cluster 2 of L18 following the three low- to moderate-severity fires between AD 1624 and 1729, all other fires decreased stem densities or maintained the low densities triggered by previous fires and the rates of recovery were extremely variable (Fig. 5). All time periods of fire-induced low stem densities reconstructed from low recruitment rates of subfossil logs (i.e. AD 1207–1592 at cluster 2 of L20 and AD 1251–1994 at clusters 2 and 3 of L18) are confirmed by concomitant faster juvenile growth of spruce trees in burned clusters (Figs 6 and 7). Indeed, black spruce grows faster in open post-fire woodlands than in dense post-fire or old-growth forests

stands due to less intense competition (Fourrier, Pothier & Bouchard 2013).

Although we could not identify the processes that have influenced the variability of the post-fire forest trajectories, several circumstances may have contributed to hamper rapid post-fire recovery to pre-fire stem densities, especially in the taiga context where severe climate conditions may limit spruce growth and reproduction and may lead to significant tree mortality events (Bond-Lamberty *et al.* 2014). For example, high fire severity and a short time interval between the severe AD 1251 fire and the subsequent supposed fire prior to AD 1400 may explain the low stem densities that have characterized the last 750 years in the clusters 2 and 3 of L18 (Fig. 5). Unfavourable conditions for seed maturation during the Little Ice Age may also have contributed to these low post-fire tree densities. Once such open stands are initiated due to insufficient post-fire regeneration, tree density is probably to remain low until at least the next fire because a continuous lichen mat subsequently develops at the soil surface and inhibits seedling establishment (Morneau & Payette 1989).

Contrary to black spruce, balsam fir does not retain its seeds in serotinous cones and thus must re-establish from fire survivors outside burned areas (Asselin, Fortin & Bergeron 2001). Consequently, balsam fir abundance and dominance increase with decreasing fire recurrence across its distribution range. Our results did not allow the reconstruction of past variations in fir abundance from direct field evidence because very few firs were found among the subfossil logs (see 'Study sites and sampling' and Fig. S2). However, at both of our study sites, all lakeshore clusters that experienced at least one severe fire exhibited low fir percentages (0–8%) and all clusters with abundant fir (i.e. more than 20%; Table 2) had escaped fire or were only marginally affected by fire over remarkably long time intervals of more than 1200 years (Figs 3 and 4). This exclusive and systematic high fir abundance in the present-day unburned forest remnants strongly supports the idea that balsam fir is out of phase with the late Holocene fire regime and the associated climate and that fir has persisted mainly in unburned refugia (Sirois 1997; Arseneault & Sirois 2004; Boucher, Arseneault & Hétu 2006; Ali *et al.* 2008; de Lafontaine & Payette 2010).

LONG-TERM FIRE IMPRINTS ON LANDSCAPE DIVERSITY

Our study provides a long-term perspective that helps explain how fire disturbance and time since fire have shaped the present-day landscape diversity in the Eastern Canadian taiga, in the context of the generalized decrease in conifer stem density that has characterized the northern boreal zone over the last 600–900 years (Payette & Gagnon 1985; Sirois & Payette 1991; Payette & Morneau 1993; Lavoie & Sirois 1998; Girard, Payette & Gagnon 2008; Payette, Filion & Delwaide 2008). The high variability in the post-fire stem density reduction and in its rate of recovery displayed by our lakeshore clusters since the first detected fire at about AD 1207

(Fig. 5) suggests that present-day landscapes (see Fig. S1) are mosaics of forest patches representing different times since fire along specific post-fire forest structure trajectories. In the taiga, open woodlands would have experienced at least one severe fire since the Medieval Climate Anomaly, often reducing tree densities or maintaining low densities triggered by previous fires and excluding balsam fir from stands where the species was still present. In addition, some important implications can be deduced from the fact that present-day forest stands reflect the past fire history even if the last fire occurred at least 300–400 years ago. First, it indicates that several centuries are needed for stem density and forest composition to converge between forest stands that experienced or escaped fire. Second, it proves that the taiga contains two types of old-growth forest stands (i.e. some centuries old) on well-drained soils (dense vs. open old-growth forest stands) depending on whether or not they burned during the last 800 years.

It has already been observed that the long-term absence of severe disturbances can lead to the decline of forest ecosystems and to the reduction of forest biomass in several biomes (Wardle, Walker & Bardgett 2004). In this study, we observed rather that sites that did not severely burn during the last 1200 years had higher stem density, tree basal area and tree species diversity than sites that burned 2–5 times over the same time period. Even if these dense stands are relict from previous more favourable climate conditions, they nevertheless indicate that relatively high stem densities can be maintained over at least a millennium in absence of fire. Extrapolating the recent regional burn rate of about 0.2% per year (based on the 1980–2010 fire data; Boulanger *et al.* 2012) to the last millennium, and assuming that stand age distribution is negative exponential (Johnson 1992), stands older than 1000 years would represent only about 15% of the present-day landscape. We conclude that the forest decline stage linked to the absence of disturbances is uncommon in the northern taiga of Eastern Canada.

The increase in fire occurrence and area burned that is expected for the Eastern Canadian taiga over the 21st century (Boulanger *et al.* 2013) is probably to impact landscape diversity in our study area. Our data suggest that higher burn rates will accelerate the regression of balsam fir and will increase the abundance of more open woodlands, unless climactic thresholds that once allowed the development of dense spruce-fir stands are surpassed, improving the forest regeneration processes (Sirois, Bonan & Shugart 1994). In addition, considering that the jack pine eastern range limit is located only 10 km west of site L18, and that pine has faster juvenile growth, earlier sexual maturity, and higher seed retention in serotinous cones than black spruce (Rudolph & Laidly 1990), jack pine is probably to expand into our study region with an increased fire frequency. If a pine expansion occurs, then open spruce woodlands will be probably shift to denser pine-spruce stands after fire with pine abundance increasing after repeated fires, as observed within the current pine range limit (Lavoie & Sirois 1998; Le Goff & Sirois 2004).

Data accessibility

All data from the manuscript are archived in 'Figshare' (Gennaretti, Arseneault & Bégin 2014a).

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Figure S1. Photo from a helicopter of a typical area of the taiga zone.

Figure S2. Flowchart highlighting data and analyses.

Figure S3. Component loadings for L18 PCA.

Figure S4. Component loadings for L20 PCA.

Figure S5. L18 PCA biplots.

Figure S6. L20 PCA biplots.

Figure S7. Cluster dendrogram for L18 triplets of plots.

Figure S8. Cluster dendrogram for L20 triplets of plots.

Figure S9. Examples of charred subfossil logs.

Figure S10. Comparison among fire-free intervals of the growth curves of the subfossil logs for each cluster at L18.

Figure S11. Comparison among fire-free intervals of the growth curves of the subfossil logs for each cluster at L20.

Table S1. Power function models describing the stand size structure of triplets of plots at L18.

Table S2. Power function models describing the stand size structure of triplets of plots at L20.

Table S3. Correlation matrix of the variables used to characterize the lakeshore forest at L18.

Table S4. Correlation matrix of the variables used to characterize the lakeshore forest at L20.

Table S5. Sensitivity of clustering results to the choice of the method.