

Multi-millennial fire frequency and tree abundance differ between xeric and mesic boreal forests in central Canada

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Summary

1. Macroscopic sedimentary charcoal and plant macroremains from two lakes, 50 km apart, in north-western Ontario, Canada, were analysed to investigate fire frequency and tree abundance in the central boreal forest. These records were used to examine the controls over the long-term fire regime, and vegetative dynamics associated with fire return intervals (FRIs).

2. There were 52 fire events at Lake Ben (surrounded by a xeric landscape) between 10 174 calibrated years before present (cal. year BP) and the present with an average FRI of 186 years with values oscillating between 40 and 820 years. Forty-three fire events were recorded at Lake Small (surrounded by a mesic landscape) between 9972 cal. year BP and the present with an average FRI of 229 years and a range of 60–660 years. FRIs at Lake Small decreased significantly after c. 4500 cal. year BP, whereas at Lake Ben FRIs remained similar throughout the Holocene. Different FRI distributions and independence in the occurrence of fire events were detected between 10 000 and 4500 cal. year BP for the two sites. Between 4500 cal. year BP and the present, similar FRIs were observed, but fires continued to occur independently.

3. Longer FRIs resulted in declining abundance of *Larix laricina* in both landscapes. Longer FRIs resulted in a decline in the abundance of *Picea mariana* in the xeric landscape, but a marginal increase in the mesic landscape. Abundances of *Pinus banksiana*, *Pinus strobus* and *Betula papyrifera* were unrelated to FRI, underlying that these species maintain their local abundance irrespective of fire frequency.

4. *Synthesis.* Our results show contrasting fire regime dynamics between a xeric and mesic landscape in central boreal forests, Canada. These results highlight the influence of local factors as important drivers of fire frequency at centennial to millennial scales. Local site factors, especially soil moisture, need to be incorporated into predictive models of vegetation response to climate change.

Key-words: charcoal, climate, fire history, Holocene, macroremains, Neoglaciatio, palaeoecology and land-use history, Ripley's K-function, Spearman's ρ , vegetation abundance

Introduction

Fire is a critical driver for many forest ecosystems (Bowman *et al.* 2009). In boreal forests of North America, changes in the frequency and extent of wildfires affect vegetation

composition and structure (Bergeron 2000; Bouchard, Pothier & Gauthier 2008; Fauria & Johnson 2008; Chen & Taylor 2012). Fires disrupt the dominant vegetation by consuming large quantities of biomass, thereby providing space and nutrients for colonizing vegetation. Ignition frequency and dry forest fuels are recognised as major contributors in creating the large stand-replacing fires that characterize most boreal fire regimes (Wotton & Martell 2005; Krawchuk *et al.* 2006);

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under natural settings, these factors are primarily controlled by large-scale climatic patterns (Fauria & Johnson 2006; Girardin & Wotton 2009). The area burned by fires in the Canadian boreal forest has increased in the last four decades as temperatures in the summer have increased (Gillett *et al.* 2004), and it is anticipated that further warming and drying throughout the 21st century will increase fire frequency (Wotton, Nock & Flannigan 2010) and extent (Flannigan *et al.* 2005), with severe environmental consequences (Flannigan *et al.* 2009).

Predicting the responses of boreal fire regimes to future climate scenarios is not straightforward. Fire–climate relationships can be counter-intuitive and can vary depending on location; changes in fire frequency have been linked not only to climate but to several regional and local factors including geomorphological context, forest type and fuel characteristics (Girardin *et al.* 2006; Ali, Carcaillet & Bergeron 2009). The relative importance of these biological and physical controls on fire varies across a range of temporal and spatial scales. For instance, Neoglaciation (c. 4500 calibrated years before present, hereafter cal. year BP), a documented climatic trend during the Holocene affecting the onset of cooler and wetter conditions, decreased fire frequency in coniferous boreal forests (Ali, Carcaillet & Bergeron 2009) caused by a reduction in the length of the fire season (Hely *et al.* 2010). However, fire frequency in some forests are unchanged or have increased during the late Holocene under colder/wetter climatic conditions (Lynch, Hollis & Hu 2004; Briles *et al.* 2008; Higuera *et al.* 2009; Blarquez, Bremond & Carcaillet 2010). Differences in fire regimes among landscapes may also be correlated with relative proportion of area under different fire hazards, that is, relative amount of xeric and mesic sites (Heinselman 1981; Romme 1982), or forest type (Hely, Bergeron & Flannigan 2000; Cumming 2001), with the interaction between fuel characteristics and topography generating different fire frequencies (Hellberg, Niklasson & Granstrom 2004; Wallenius, Kuuluvainen & Vanha-Majamaa 2004). In the boreal zone, regional soil characteristics and superficial deposits have also been shown to influence fire regimes (Mansuy *et al.* 2010; Senici *et al.* 2010), and sites with rapid drainage are more prone to fire ignitions (Mansuy *et al.* 2010).

Several paleoecological records (e.g. Lynch, Hollis & Hu 2004; Ali *et al.* 2008) suggest North American boreal forest vegetation compositions have shifted into new arrangements at centennial to millennial time-scales. These shifts are often accompanied by changes in the fire regime, indicating that changes in fire frequency and forest composition coincide over long time-scales (Higuera *et al.* 2009; Johnstone *et al.* 2010). However, throughout the Holocene, the relative influences of climate and non-climatic factors on fire frequency and biomass burning are not fully understood (Gavin *et al.* 2006; Marlon, Bartlein & Whitlock 2006). Although fire frequencies in the current climate determine the relative abundance of trees (Bergeron 2000; Bouchard, Pothier & Gauthier 2008; Chen & Taylor 2012), the centennial and millennial-scale relationship between tree abundance and fire frequency is unclear.

In this study, we used sedimentary macroscopic charcoal and plant macroremains from two lakes in a boreal forest in central Canada to examine how forest vegetation responded to varying levels of fire frequency throughout the Holocene. The two lakes are on different soil types and surficial deposits, and the amount of waterbodies surrounding each site also vary, all of which could affect local fire ignition and propagation and forest vegetation. Our specific objectives were as follows: (i) to examine the temporal variation of fire frequency, expressed in this study as fire return interval (FRI) and fire synchronicity of the surrounding landscapes of the two lakes; and (ii) determine how local species dynamics might be related to FRI through the Holocene.

We expected that the two lakes would display similar fire histories throughout the Holocene based on the relative primacy of climate versus local factors in determining fire regime (Bessie & Johnson 1995; Fauria & Johnson 2008). We also expected increasing FRIs after the onset of Neoglaciation (c. 4500 cal. year BP) (Viau *et al.* 2006) due to its inhibition effect of cooler and moister climate conditions on fire ignition and spread. We expected that local woody and herbaceous species abundance would vary depending on FRI; it was expected that macroremains influx of pioneer species would decrease, whereas late-successional species would increase as FRI increases.

Materials and methods

STUDY AREA

The two kettle lakes, Lake Ben (49°21'25"N; 89°46'10"W; 480 m above sea level [a.s.l]) and Lake Small (49°34'52"N; 90°23'08"W; 478 m a.s.l), are situated in boreal mixedwood forest in north-western Ontario, Canada (Fig. 1). The lakes (Table 1) are located c. 50 km apart within the Moist Mid-Boreal (MBx) ecoclimatic region (Ecoregions Working Group 1989), which is characterized by a strong continental climate with long cold winters and short warm summers. The mean summer temperature is 14 °C, and the mean winter temperature is –13 °C. Mean annual precipitation ranges between 700 and 800 mm. Regional soils are generally thin and coarse-textured over granitic Precambrian bedrock (Rowe 1972). Locally, the regional soils surrounding the Lake Ben site are of the dystic brunisol and humo-ferric podzol soil orders on glaciofluvial deposits with rapid drainage (xeric landscape), whereas the Lake Small site is surrounded by humo-ferric podzol on morainal deposits with moderate drainage (mesic landscape). Local waterbodies make up c. 10% and 27% of the terrestrial area within a 2 km radius from Lake Ben and Lake Small, respectively.

Fires are frequent, with an average regional fire cycle of 150 (126–188) years since 1820 (Senici *et al.* 2010). Regional post-fire regeneration typically includes pioneer species such as *Pinus banksiana* Lamb., *Populus tremuloides* Michx., *Betula papyrifera* Marsh., *Pinus strobus* L., and *Larix laricina* (Du Roi) K. Koch, with slow-growing shade-tolerant *Picea mariana* (Mill.) Britton, *Picea glauca* (Moench) Voss and *Abies balsamea* (L.) Mill. replacing the pioneer species over time (Chen & Popadiouk 2002; Brassard *et al.* 2008). The current vegetation composition and structure at each lake is a result of recent fire histories and local land use, including timber harvesting, over the past 80 years.

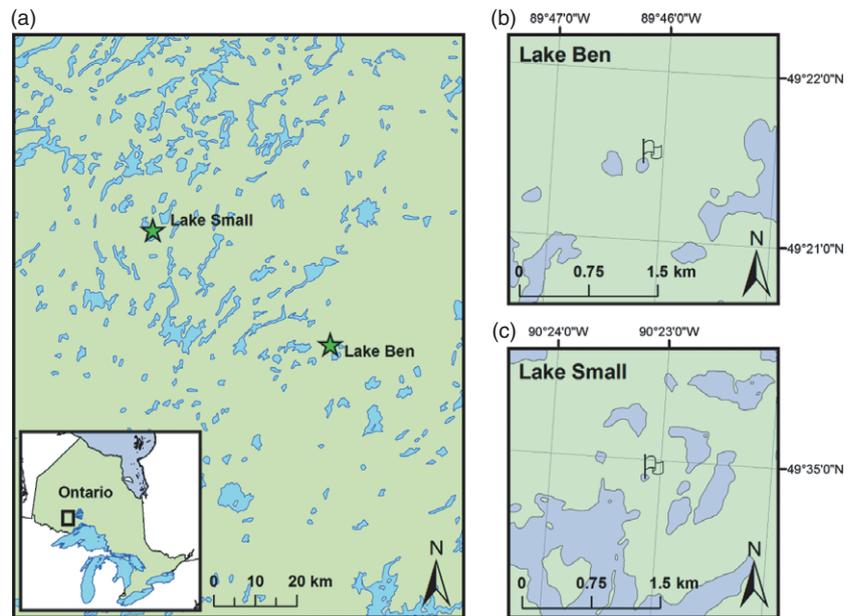


Fig. 1. Location of the study sites in the boreal mixedwood forest.

Table 1. The main characteristics of Lake Ben and Lake Small. Species are listed in order of dominance at each site, with *Pinus banksiana* dominating the current local vegetation composition at Lake Ben and *Picea mariana* dominating the local vegetation at Lake Small

Name (unofficial)	Ben	Small
Latitude (N)	49°21'25.02"	49°34'52.19"
Longitude (W)	89°46'10.36"	90°23'08.34"
Elevation (m.a.s.l.)	480	478
Local woody vegetation	<i>P. banksiana</i> , <i>P. mariana</i> , <i>Larix laricina</i> , <i>Betula papyrifera</i> , <i>Abies balsamea</i>	<i>P. mariana</i> , <i>Abies balsamea</i> , <i>P. banksiana</i>
Hillslopes	Moderate	Moderate
Lake surface (ha)	1.63	0.508
Water depth (m)	5.0	3.9
Core length (cm)	660	390
Sedimentation rate/mean accumulation (cm year ⁻¹)	0.0866	0.0626
Median time-resolution (year per sample)	13	28

SAMPLING

Sediment cores were extracted from the deepest point in each lake from atop the frozen lake surface early spring 2010. A Kajak-Brinkhurst (KB) gravity corer was used to collect the most recently deposited material at the water-sediment interface and was extruded on site in 1-cm sections. A single complete sequence of sediment was collected in the form of 1-m overlapping cores using a Livingston piston corer (Wright, Mann & Glaser 1984). Sediment was wrapped in polyurethane and aluminium foil for preservation and transported to the laboratory. Cores were sliced into discs at contiguous 1-cm intervals.

CHARCOAL ANALYSIS

Subsamples of 1 cm³ were taken from each disc for charcoal analysis. Each subsample was deflocculated in hot 10% KOH solution, bleached in 6% sodium hypochlorite (NaClO) solution, then wet-sieved through a 160 µm mesh. Deflocculation and bleaching were performed to distinguish charcoal from other biological materials present in the sediment. Charcoal fragments larger than 160 µm are produced from fire events occurring 0–3.0 km from the lakeshores (Lynch, Clark & Stocks 2004; Higuera *et al.* 2007); thus, this procedure allowed us to reconstruct fire events at the local scale. Charcoal particles were identified under a ×20 stereo microscope and measured for surface area using a digital camera connected to WinSeedle (Regent Instruments Incorporated, Quebec, QC, Canada). Charcoal measurements (cumulative area per cm³) are multiplied by the estimated sedimentation rate based on the numerical age-depth model to obtain the charcoal accumulation rate (CHAR, mm² cm⁻² year⁻¹).

MACROREMAINS ANALYSIS

Quantification of plant macroremains was performed at 2-cm intervals on sediment sequences from each lake. Samples were chemically treated in hot 5% KOH solution to separate and distinguish biological material. The samples were washed with water and wet-sieved through a 250-µm mesh to extract the macroremains from the sediment. Plant remains were identified under a binocular microscope. Identification of macroremains was based on Cappers, Bekker & Jans (2006) and a reference collection of boreal species at the Herbarium at Université Montpellier 2 (UM2).

AGE-DEPTH MODEL

The chronology is based on radiocarbon dating by ¹⁴C Accelerated Mass Spectrometry (AMS) measurements. Samples were processed by AMS in ¹⁴C laboratories in Poznan, Poland (Poz-) and Miami, Florida (Beta-). The CALIB program (Reimer, Baillie & Bard 2004) was used to calibrate the ¹⁴C ages to dendrochronological years using the IntCal09 (Reimer *et al.* 2009) calibration curve. Ten and seven

ages were obtained for Lake Ben and Lake Small, respectively (Table 2), based on terrestrial plant macroremains and charcoal fragments. Bulk sediment was used in a single case (Beta-293636; Table 2) when plant macroremains and charcoal quantities were insufficient for ^{14}C dating. The age-depth models were constructed using the MCAgeDepth program (Higuera *et al.* 2009) in MATLAB (MathWorks 2005) using a weighted cubic smoothing spline. The number of age estimates in each chronology determined the smoothing parameter used for each spline. The probability distribution of each calibrated age was used to weight the influence of each estimate in the age-depth model (Telford, Heegaard & Birks 2004). Confidence intervals for each age-depth model were derived from 100 Monte Carlo simulations; for each simulation, age estimates used to develop the chronology were randomly selected based on the probability distribution of the calibrated ^{14}C age. The final chronology represents the median age at each depth from the Monte Carlo simulations.

RECONSTRUCTION OF FIRE HISTORY

Charcoal accumulation rate series (Fig. S1 in Supporting Information) were decomposed into background (*Cbackground*) and peak (*Cpeak*) components. A locally defined threshold based on universally applied criteria was used to identify charcoal peaks likely related to the occurrence of one or more local fires (i.e. 'fire events'). These methods are described in detail by Higuera *et al.* (2007, 2009) and summarized below. Prior to decomposition, charcoal data were interpolated to constant 20-year time steps, corresponding approximately to the average of median resolution time per sample of the two lakes.

Low-frequency variations in a charcoal record (*Cbackground*), which represent changes in charcoal production, sedimentation, mixing and sampling, were subtracted to obtain a residual series, *Cpeak* (i.e. *Cpeak* = *Cinterpolated* - *Cbackground*). Consistent with theoretical evidence (Higuera *et al.* 2007) and previous work (e.g. Gavin *et al.* 2006; Higuera *et al.* 2007, 2009), we assume that *Cpeak* is composed of two subpopulations, *Cnoise*, representing variability in sediment mixing, sampling and analytical and naturally occurring noise, and *Cfire*, representing charcoal input from local fires. For each

sample, we used a Gaussian mixture model to identify the *Cnoise* distribution. We considered the 99th percentile of the *Cnoise* distribution as a threshold to separate samples into 'fire' and 'non-fire' events. We estimated *Cbackground* with a locally weighted regression using a 900-year window at Lake Ben and a 700-year window at Lake Small. For each record, we chose the window width that maximized a signal-to-noise index ($\text{SNI} > 3$) and the goodness-of-fit between the empirical and modelled *Cnoise* distributions (KS-test, P -value > 0.05) (Higuera *et al.* 2009). We did not screen peaks based on the original charcoal counts of each peak as in Higuera *et al.* (2007, 2009), because this procedure is specific to charcoal count data only (Ali, Carcaillet & Bergeron 2009). All statistical treatments for charcoal analysis were performed using the program CHARANALYSIS, written by Philip E. Higuera and freely available at <http://sites.google.com/site/charanalysis>.

RECONSTRUCTION OF VEGETATION HISTORY

The plant macroremains counts (Fig. S2) were transformed into influx values ($\# \text{ cm}^2 \text{ year}^{-1}$) for each species or genus based on the numerical age-depth model at each site. Influx transformations minimize the impact of changes in the sedimentation rate. Knowing that the production of macroremains differs among species, those species that dominated the reconstructed influxes were rescaled from 0 to 1 by dividing by the maximum influx value in each species. This procedure allowed comparison between species long-term dynamics to be made efficiently. Selected taxa for analysis include: *B. papyrifera*, *P. banksiana*, *P. strobus*, *P. mariana*, *L. laricina* and a grouping of herbaceous species that includes *Potentilla* spp., *Cyperaceae* spp., *Carex* spp., *Poa* spp. and *Juncus* spp. For a more comprehensive understanding of the temporal dynamics of each species, the influxes were smoothed using a locally weighted regression (LOESS) to highlight the main trends in macroremains dynamics over time.

COMPARISON BETWEEN SITES

To examine whether fire histories differ between the sites, we examined the median fire return intervals (mFRI) using the nonparametric

Table 2. Accelerator mass spectrometry ^{14}C dating of Lake Ben and Lake Small (mean \pm 1 SEM)

Site and depth (cm)	^{14}C year BP	cal. year BP (2 σ)	Materials	Lab. Code
Lake Ben				
30–35	320 \pm 30	387 (309–473)	Plant macroremains	Poz-39543
58–60	605 \pm 30	602 (545–653)	Plant macroremains	Poz-39542
120–122	1670 \pm 30	1573 (1512–1685)	Plant macroremains	Beta-293602
184–185	2720 \pm 30	2814 (2764–2874)	Plant macroremains	Beta-293601
259–260	3780 \pm 40	4155 (4008–4302)	Plant macroremains	Beta-293600
359–360	3930 \pm 40	4364 (4247–4504)	Plant macroremains	Beta-293599
459–460	4940 \pm 40	5663 (5603–5831)	Plant macroremains	Beta-293598
606–610	7310 \pm 40	8107 (8025–8190)	Plant macroremains and charcoal	Poz-39541
631–635	8300 \pm 50	9316 (9134–9440)	Plant macroremains and charcoal	Beta-293597
651–661	8990 \pm 50	10174 (9934–10232)	Plant macroremains	Poz-39891
Lake Small				
47–50	1190 \pm 30	1115 (1014–1221)	Plant macroremains and charcoal	Beta-293608
76–80	2120 \pm 30	2093 (2006–2285)	Plant macroremains and charcoal	Beta-293607
145–150	3490 \pm 40	3764 (3652–3865)	Bulk sediment	Beta-293606
216–220	3750 \pm 40	4110 (3989–4233)	Plant macroremains and charcoal	Beta-293605
287–288	6410 \pm 40	7349 (7349–7419)	Plant macroremains	Beta-293609
356–360	7860 \pm 40	8644 (8563–8917)	Plant macroremains	Beta-293604
380–390	8850 \pm 40	9972 (9972–10150)	Plant macroremains	Beta-293603

Radiocarbon dates have been calibrated using the CALIB 5.0.1 program (Stuiver & Reimer 1993).

two-sample Mann–Whitney *U*-test (MW-test), and the overall FRI distributions using the nonparametric two-sample Kolmogorov–Smirnov test (KS-test) (Clark 1989; Ali, Carcaillet & Bergeron 2009). The complete series, 10 000–0 cal. year BP (BP = 1950 CE), and defined temporal periods of 10 000–4500 cal. year BP and 4500–0 cal. year BP were examined and analysed. These divisions were defined in regard to the Neoglacial climate cooling trend in central Canada (c. 4500–1500 cal. year BP) (Viau *et al.* 2006) and allowed us to examine whether this climatic change had affected the local fire frequency at each site. For the purposes of this study, time periods will hereafter be referred to as complete Holocene (10 000–0 cal. year BP), early Holocene (10 000–4500 cal. year BP) and late Holocene (4500 cal. year BP to present).

To examine whether the recorded fire events occurred simultaneously at each lake over centennial to millennial time-scales, we assessed their synchrony through the bivariate Ripley's *K*-function (Ripley 1977) modified to a single dimension (time) (Doss 1989). The modified bivariate *K*-function allowed us to compare the synchrony of fire events between the two sites within a defined temporal window (± 100 years). This analysis was performed for each temporal division, as well as the complete time series. It is important to note that the analysis of Ripley's *K*-function is more robust for shorter sequences, which allow a better characterization of fire event synchrony (Gavin *et al.* 2006); consequently, results for the temporal partitioning of the sequence (early and late Holocene) are likely more reliable indicators of fire event synchrony. To facilitate interpretation of the results, the *K*-function was transformed into an *L*-function (Gavin *et al.* 2006), which stabilizes the means and variances of the *K*-function outputs. Confidence intervals (95% and 99%) for the *L*(*t*) values were determined by randomization of 1000 fire events. *L*(*t*) values > 0 indicate synchrony between fire events, while values near 0 indicate independence and values < 0 indicate asynchrony. The modified bivariate Ripley's *K*-function and its transformation into *L*(*t*) were performed with the K1D program (Gavin 2010).

Several scenarios may be relevant when interpreting long-term fire history with respect to the relationships between climatic (large-scale) and non-climatic (local scale) factors as driving forces. These scenarios relate to patterns of FRIs as described by the MW- and KS-test results, and fire event synchronicity as described by the modified bivariate Ripley's *K*-function. In Scenario 1, similar FRIs and synchronous occurrence of fire events are observed between sites. These results indicate that large-scale processes, that is, climate or biome transformations are the main factors determining fire frequency. In Scenario 2, the distributions of FRIs are similar, but fire events occur asynchronously or are independent. These results indicate that the time between fire events is similar between two sites, but local non-climatic factors (landscape connectivity, local weather during fire ignition, topography, and watershed size) override the influence of climate at one or both sites. In Scenario 3, the distributions of FRIs are different, but fire events occur synchronously. This scenario indicates that local non-climatic factors cause more (or less) fires events at one site with regional fire occurrence strongly influenced by large-scale processes like climate. In Scenario 4, FRI distributions are different with asynchronous or independent fire events between sites. This scenario indicates that local non-climatic factors strongly influence the regional fire regime.

FIRE AND VEGETATION ANALYSIS

To assess the relationship between local vegetation composition and fire, Spearman's rank correlation coefficient (Spearman's ρ), a non-parametric measure of statistical dependence by assessing the monotonic relationship between two variables was calculated. Spearman's

ρ was calculated for FRI and macroremains influx values of the dominant taxa at Lake Ben and Lake Small throughout the 10 000–0 cal. year BP time period. Macroremains influx values were interpolated to the time-resolution per sample used in the charcoal analysis (20 years), thereby allowing comparison with the FRI output data.

Results

AGE-DEPTH MODEL

The age-depth models represent 10 174 and 9972 years of sedimentation at the Lake Ben and Lake Small sites, respectively. The two age-depth models (Fig. 2a,b) are comparable in sedimentation rate with Lake Ben having a higher mean sedimentation rate at 0.0866 ± 0.0534 cm year⁻¹ to Lake Small's 0.0626 ± 0.0495 cm year⁻¹ (Table 1). Both models exhibit acceleration in the sedimentation rate between c. 5000–3500 cal. year BP, with the maximum deposition occurring at 4310 cal. year BP (0.0291 cm year⁻¹) in Lake Ben and 3785 cal. year BP (0.0333 cm year⁻¹) in Lake Small.

FIRE HISTORY RECONSTRUCTION

In total, fifty-two fire events were identified at Lake Ben between 10 174 cal. year BP and the present, with the first fire recorded c. 9660 cal. year BP. The signal-to-noise index (median SNI = 6.09) ensured a clear separation between the charcoal background and fire event signals allowing accurate reconstruction of local fire history. FRIs range from 40 to 820 years, with an average FRI of 186 ± 23 years (mean \pm SE) and a median FRI (mFRI) of 140 years. FRIs were shortest between 5000 and 4000 cal. year BP (Fig. 3a). FRI length was relatively stable throughout the Holocene with no major changes recorded between time periods (Fig. 3a and Table 3).

Forty-three fire events were identified at Lake Small between 9972 cal. year BP and the present, with the first fire occurring c. 9700 (median SNI = 8.69). FRIs at this site range from 60 to 660 years, with an average FRI of 229 ± 26 years and a mFRI of 170 years. FRIs at the Lake Small site are longer than those at the Lake Ben site throughout the early Holocene (Fig. 3a,b). FRIs decrease markedly c. 4500–4000 cal. year BP (Fig. 3b); the shortest FRIs at the Lake Small site occurred between 4000 and 2000 cal. year BP. FRIs increased between 2000 and 1000 cal. year BP but have been decreasing from 1000 cal. year BP to the present.

BETWEEN-SITE ANALYSIS OF FIRE RECORDS

Over the past 10 000 years, the mFRIs were similar at Lake Ben and Lake Small (MW-test, $P < 0.05$) as were the overall FRI distributions (KS-test, $P < 0.05$) (Table 3). The bivariate Ripley's *K*-function analysis for the same time period suggests that fire events were predominantly independent with limited synchrony for a temporal window of 2500–2800 years ($P < 0.05$, Fig. 4a). These data indicated that regional forest fire history during the last 10 000 years has been controlled by a combination of climate and local factors (Scenario 2).

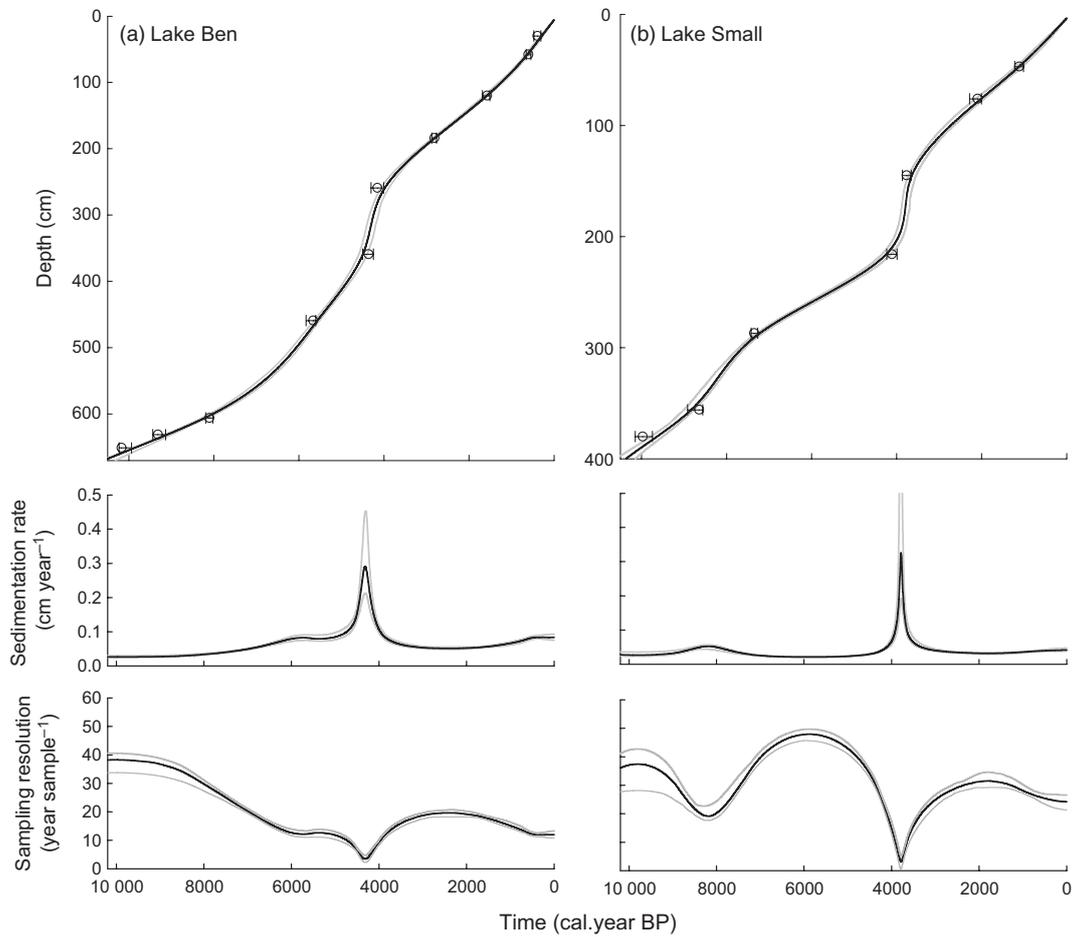


Fig. 2. Age-depth models, sedimentation rate and sampling resolution for Lake Ben and Lake Small. Heavy grey lines correspond to 95% CI.

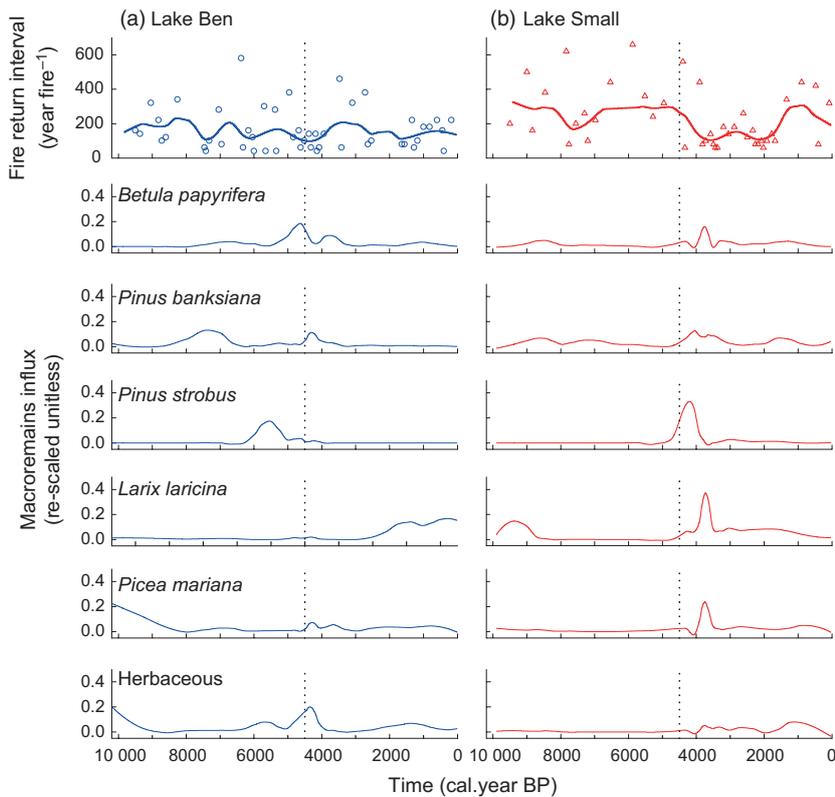


Fig. 3. Fire events and fire return intervals (FRIs) at (a) Lake Ben and (b) Lake Small. Macroremains influxes smoothed by LOESS (sampling proportion of 0.2) of dominant woody plant and herbaceous species at Lake Ben and Lake Small, respectively, in the time period 10 000–0 cal. year BP. The vertical dotted lines indicate the onset of Neoglacial climate cooling in Central Canada (c. 4500 cal. year BP). FRI, fire return intervals.

Table 3. Two-sample MW-test comparisons of median fire return intervals (mFRI, mean \pm 1 SEM) and Two-sample KS-test comparisons of FRI distributions for Lake Ben and Lake Small. The sites display different mFRI (P -value $<$ 0.05) and have different FRI distributions only in the 10 000–4500 cal. year bp time period (in bold)

Time period (cal. year BP)	Lake Ben		Lake Small		KS-test	MW-test
	Average FRI	mFRI	Average FRI	mFRI		
10 000–0	186 \pm 23	140	229 \pm 26	170	0.600	0.095
10 000–4500	190 \pm 35	120	316 \pm 44	260	0.029	0.012
4500–0	183 \pm 36	140	166 \pm 24	120	0.999	0.783

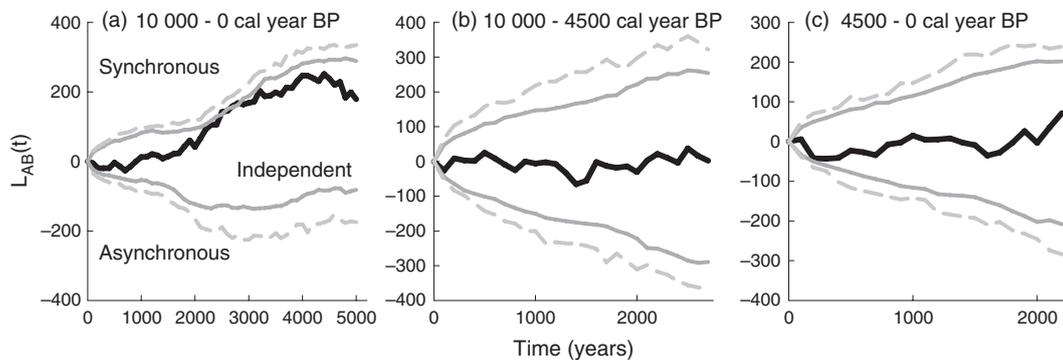


Fig. 4. Bivariate L-function analyses performed on the fire events detected at Lake Ben and Lake Small. Analysis was performed for three time periods (10 000–0, 10 000–4500 and 4500–0). Heavy grey lines correspond to 95% CI and dashed grey lines correspond to 99% CI based on 1000 randomizations of shifting records relative to one another.

In the early Holocene, the median and average FRI distributions between Lake Ben and Lake Small were significantly different (MW-test, KS-test, $P < 0.05$) (Table 3). The analysis of the bivariate Ripley's K-function (Fig. 4b) revealed independent fire events at centennial ($P < 0.05$) and millennial ($P < 0.01$) time-scales between these sites. The data underlined that local scale factors likely influenced the fire regime during this time period (Scenario 4). In the late Holocene, both mFRIs and average FRI distributions were similar between sites (Table 3), with fires events occurring independently (Fig. 4c). The data indicate that local factors likely overrode climatic controls of the fire regime at one (or both) of the sites in these time periods (Scenario 2).

LOCAL VEGETATION HISTORY

In total, 18 taxa were identified in the plant macroremains assemblages at each lake (Fig. S2). The most abundant taxa at Lake Ben were *L. laricina* (needles and seeds), *P. banksiana* (needles, brachyblasts and seeds) and *P. mariana* (needles and seeds). The most abundant taxa at Lake Small were *L. laricina* and *P. mariana*. The main tree assemblages included *B. papyrifera*, *P. banksiana*, *P. strobus*, *P. mariana* and *L. laricina*. Identified shrubs include *Rubus* spp. and *Vaccinium* spp.; however, there were too few macroremains for detailed analysis. Herbaceous species are represented by *Potentilla* spp., *Cyperaceae* spp., *Carex* spp., *Poa* spp. and *Juncus* spp.

At Lake Ben, the oldest period 10 000–9000 cal. year BP was dominated by *P. mariana* transitioning to dominance of *P. banksiana* c. 8000–6500 cal. year BP (Fig. 3a, Fig. S2). The period 6000–4000 cal. year BP was characterized by the maximum influx of macroremains and throughout concomitantly the presence of *P. banksiana*, *P. strobus*, *P. mariana*, *L. laricina* and *B. papyrifera* was recorded. From 2300 cal. year BP to the present, Lake Ben was characterized by a low influx of all macroremains taxa except *L. laricina*.

Lake Small had relatively low macroremains influx for all taxa in the early Holocene (Fig. 3b). *L. laricina* dominates the record between 10 000–9000. Influx of woody species increased considerably at c. 4000 cal. year BP; this trend was not recorded in the herbaceous grouping. The rapid and simultaneous increase in woody macroremains coincided with acceleration in the sedimentation rate recorded c. 4000, suggesting a potential artefact; however, the use of influx transformations to analyse macroremains data had likely minimized the impact of changes in the sedimentation rate. Around 3200 cal. year BP, influxes decreased slightly for all taxa.

FIRE FREQUENCY AND LOCAL TREE ABUNDANCE

Significant correlations were detected between macroremains influxes of both *P. mariana* and *L. laricina* and FRI at each site. Significant correlations were of low-to-moderate ($\rho < \pm 0.4$) strength (Fig. 5). At Lake Ben, *P. mariana*

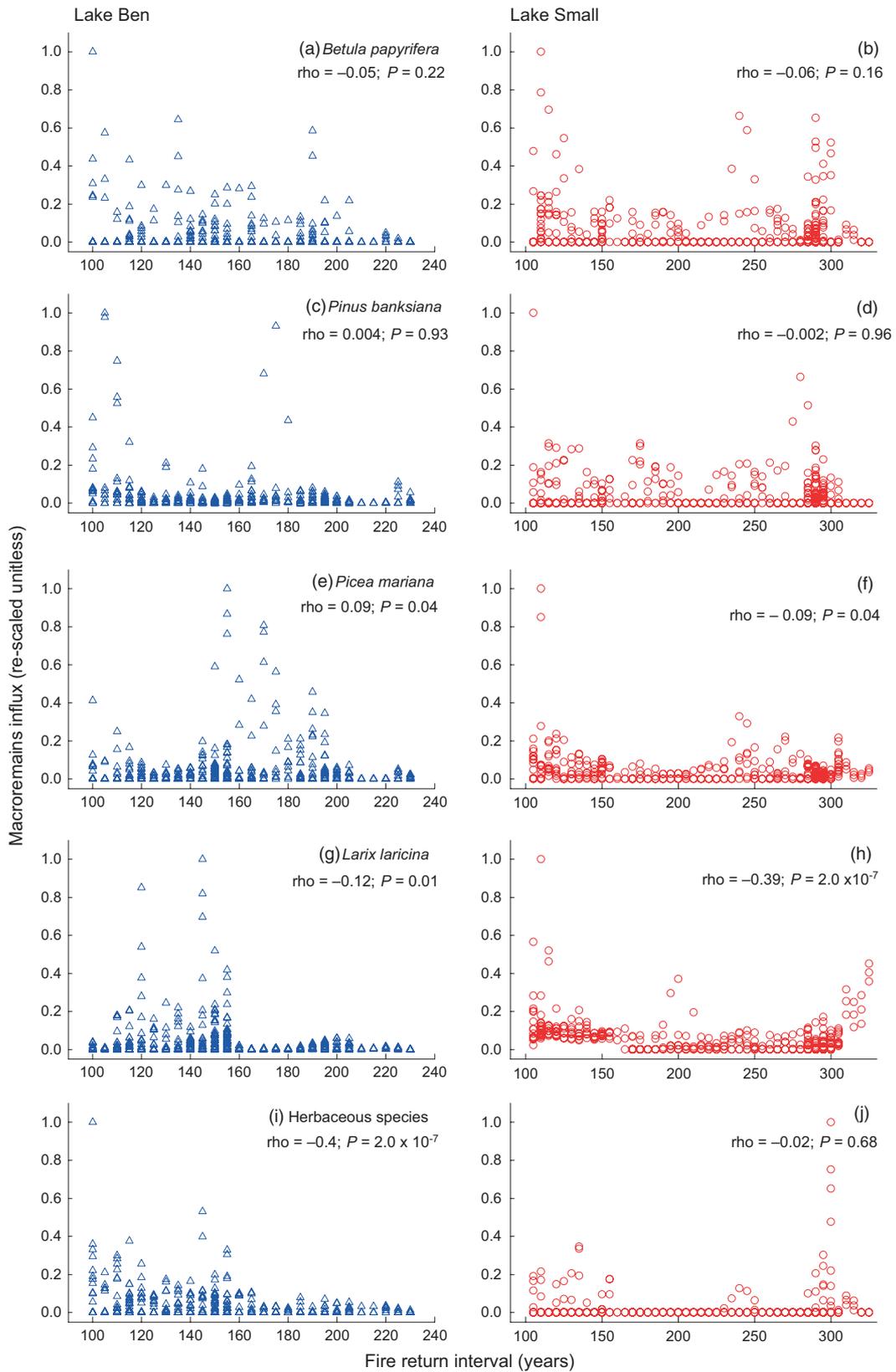


Fig. 5. The relationship between macroremains influx and fire return interval (FRI) for Lake Ben and Lake Small. Spearman's ρ and P -values were calculated for dominant woody species and a grouping of herbaceous plants. FRI, fire return intervals.

(Fig. 5g) was positively ($\rho = 0.1$) correlated with FRI, indicating that this species increased with FRI. At Lake Small, a negative correlation ($\rho = -0.1$) for *P. mariana* (Fig. 5h) indicates that the species was most abundant at this site when FRIs were short (100–150 years), but a high occurrence of its macroremains was also recorded at long FRIs (> 250 years). *L. laricina* influx was highest at Lake Ben when the FRIs were short (Fig. 5i). At Lake Small, a strong negative correlation ($\rho = -0.4$) was found for *L. laricina* (Fig. 5j), and similar to the results for *P. mariana* at this site, this species was most abundant at short FRIs; however, a high occurrence of the macroremains was also recorded when FRIs exceeded 250 years. Herbaceous species were found to be significantly correlated with FRI at Lake Ben (Fig. 5k) but not at Lake Small (Fig. 5l). Herbaceous species at Lake Ben showed a moderate negative correlation; the herbaceous taxa macroremains were most abundant when FRIs were short. At Lake Ben and Lake Small, no significant correlations were detected for *B. papyrifera* (Fig. 5a,b) and *P. banksiana* (Fig. 5c,d), indicating their relative persistence at both sites irrespective of FRI. We note that *P. strobus* (Fig. 5e,f), a relatively minor component of the vegetation at each site displays maximum influx when FRIs were near the complete Holocene average at each lake (Lake Small 229 ± 26 years; Lake Ben 186 ± 23 years).

Discussion

FIRE HISTORY

The general pattern of fire activities at the millennial-scale is counter-intuitive. The climate of the North American boreal forest changed significantly between 6000 and 3000 cal. year BP with conditions becoming cooler and wetter in comparison with the early Holocene (Kerwin *et al.* 2004; Viau *et al.* 2006; Viau & Gajewski 2009). The establishment of cooler and moister environmental conditions during in the late Holocene should not have been favourable for fire ignition, yet the expression of this climatic shift on fire frequency varies between sites, with FRIs at Lake Ben (Fig. 3a) remaining similar to those of the early Holocene and FRIs at Lake Small (Fig. 3b) decreasing significantly. Data from both sites are different from the increased FRIs observed in coniferous boreal forests during the late Holocene (Ali, Carcaillet & Bergeron 2009), likely due to differences in fire regime seasonality between boreal coniferous and mixedwood forests. In boreal mixedwood forests, severe fires occur mainly in the spring (April–June) (Johnson, Miyanishi & O'Brien 1999) prior to the growth deciduous foliage (mainly *B. papyrifera*, and *P. tremuloides*). As decreased fire frequency in the coniferous boreal is associated with a shortened fire season mainly in summer-fall (June–October) under orbital forcing changes (Hely *et al.* 2010), the influence of climatic cooling on fire frequency may be limited at our study sites which are predominantly mixedwood stands. The impact of Neoglacial cooling on fire frequency was apparently limited at Lake Ben.

The difference in local fire frequency between the landscapes surrounding the two lakes can be a result of multiple mechanisms. The Lake Ben site is situated in a landscape with more xeric conditions when compared to Lake Small, as such the area was more prone to fire ignition and propagation as evidenced by the shorter average FRI 10 000–0 cal. year BP. The shorter average FRI at the Lake Ben site in the early Holocene as compared to the Lake Small site might also be explained by the presence of waterbodies in the local landscapes (Cyr *et al.* 2005; Senici *et al.* 2010). There exist abundant lakes that encircle Lake Small (Fig. 1c); these lakes may have acted as natural firebreaks, inhibiting fire spread and preventing some regional fires from reaching sizes or dispersal distances that would be recorded in Lake Small's charcoal palaeo-record. At the Lake Ben site, surrounding waterbodies are few (Fig. 1b) allowing local fires to spread relatively unhindered.

The similar FRIs among sites in the late Holocene could be due to increased water-logging at the Lake Small site (Lynch, Hollis & Hu 2004), induced by a slower rate of decomposition in organic matter due to increased moisture and a cooler climate. Increased mesic conditions at the Lake Small landscape may have favoured the development of *P. mariana* stands as suggested eastward in other sites (Carcaillet *et al.* 2010; Genries *et al.* 2012); the development of *P. mariana* has been shown to increase boreal landscape flammability (Hallett & Walker 2000; Lynch *et al.* 2002). In contrast, the Lake Ben site is surrounded by moderate hillslopes on well-drained sandy soils; as such it is possible that increased moisture had little effect on soil conditions, and *P. mariana* abundance resulting in the stable FRIs at Lake Ben throughout the Holocene.

Different FRIs and independence in fire occurrence were detected in the early Holocene, showing that during this time period, forest fires at each site were primarily controlled by local non-climatic factors (Scenario 4). However, this statement must be considered with caution because during this period, the two sites display significant differences in time-resolution per sample (Fig. 2), even if this impairment was minimized by numerical treatments performed for fire detections. In the late Holocene, FRIs were similar, but independence in fire events was recorded, stressing a combined effect of climate and local factors on forest fire activity. During the last 4500 years, the long-term probability of fire is similar at both sites, but the effect of climate on fire was overridden by local controls at one or both sites (Scenario 2). This period displayed more important climatic controls of fire history over time at the regional scale, even if local factors continued to play a key role in local fire ignition and propagation.

LOCAL TREE ABUNDANCE

As FRI is used as a proxy for fire frequency, our interpretations are based on whether monotonic relationships between species abundance and fire frequency exist. Although we cannot clearly specify the cause and effect (a limitation of Spearman's ρ) in the observed significant monotonic relationships, the

suggested mechanisms by which they might occur are based on differences in the local conditions at each site and the life-history traits and fire adaptations of each species.

At both sites, *L. laricina* is most abundant at short-to-moderate FRIs, consistent with the species status as an early invader that is well adapted for post-fire regeneration (Rowe & Scotter 1973; Johnston 1990). The early development of *L. laricina* at Lake Small at the beginning of the Holocene, that is, c. 10 000 cal. year BP under low fire frequency, could be related to high soil moistures with low drainage processes after the disappearance of the glacial lake Agassiz. *L. laricina* abundance in the vegetation record (Fig. 3, Fig. S2) and significant correlations with FRI might also be partially explained by edge effects. At the Lake Ben site, increased moisture by lakeshore provides mesic conditions. As *L. laricina* grows most commonly on wet to moist organic soils such as peat and woody peat (Johnston 1990), these local microclimate conditions may have allowed the species to exist at a location where it also maximally contributed macroremains to the sediment. Similarly, *L. laricina* is shade intolerant, at the Lake Small site, the increased abundance of *L. laricina* macroremains when FRIs are > 250 years might be explained by increased light availability at the lakeshore permitting species regeneration despite a closed forest canopy.

At the Lake Ben site, *P. mariana* is the only species to have a significant positive correlation with FRI, with peak abundance occurring when FRIs are between 145 and 195 years. At the Lake Small site, *P. mariana* displays a weak negative correlation with FRI. At this site, *P. mariana* abundance is greatest when FRIs are short. The difference in the direction of the correlation between sites for *P. mariana* is likely due to local soil characteristics. The Lake Ben site is more xeric, as such it is probable that post-fire regeneration favoured the growth of colonizers that are better adapted for dry soils with rapid drainage (e.g. *P. banksiana*), with *P. mariana* succeeding them over time. The increase in *P. mariana* abundance at the Lake Ben site with FRI is consistent with the known ecology of the species when fire frequency is low in xeric environments due to their high tolerance to shade and ability to regenerate by seeding or vegetative layering in the understory (Taylor & Chen 2011). By contrast, at the Lake Small site post-fire regeneration in mesic conditions would favour those species that are best adapted to moist organic soil conditions like *P. mariana* and *L. laricina*, with populations declining as FRI increases.

Betula papyrifera, *P. banksiana* and *P. strobus*, the most fire-adapted species of boreal forests, displayed no significant correlation with FRI, contrasting our expectation that influx of these species would be highest at high fire frequencies (short-to-intermediate FRIs). These results suggest that factors other than fire may have controlled the local abundance of these species or that these species maintained their presence at each site irrespective of fire. That *P. banksiana* was able to maintain a near continuous presence at both sites is counter-intuitive because the species is shade intolerant and is near reliant on fire for regeneration (Rudolph & Laidly 1990). However, a recent study of

boreal forest successional pathways show that *P. banksiana* can maintain dominance on xeric and mesic sites well into 300 years post-fire in the boreal forest (Taylor & Chen 2011). Similarly, *B. papyrifera* is well adapted to post-fire regeneration (Brassard & Chen 2006); however, fire itself is not essential for its successful reproduction, and it is likely that the species was able to recruit new individuals in the gaps created by less severe fires and other disturbances (insect defoliation and windthrow) (Bergeron 2000; Chen & Taylor 2012). The presence of *P. strobus* independent of FRI is attributable to the fact that it is long-lived, able to regenerate under its own canopy and able to survive moderate-severity fires due to its thick bark at mature stages (Wendel & Smith 1990).

Herbaceous species were found to be more abundant at Lake Ben when FRI was short. The correlation is consistent with the understanding of post-fire regeneration in the boreal region where herbaceous plants are quick to establish themselves when light is abundant and competitors are absent (Hart & Chen 2006), declining over time as competitive woody species and mosses establish themselves. The absence of a similar trend in Lake Small is likely due to the relative dearth of herbaceous macroremains preserved at this site (Fig. S2).

Conclusions

In central boreal forests, local landscape factors such as soil moisture could overcome the influence of climate on fire frequency. Fire-adapted species like *P. banksiana*, *P. strobus* and *B. papyrifera* can maintain their presence on xeric and mesic sites irrespective of local fire frequency. The abundance of pioneer *L. laricina* generally increases with fire frequency, but the effect of fire frequency on the abundance of slow-growing shade-tolerant *P. mariana* is landscape dependent. These results underline the complexity of climate–fire–vegetation relationships in the boreal forest and emphasise that climate alone cannot explain changes in boreal forest composition over millennia. This corresponds to a key issue in improving the forecasting of fire-induced vegetation dynamics in response to ongoing climate change. The continuous challenge is to differentiate between the influences of climatic and non-climatic factors on fire frequency, and consequences on vegetation composition. Further paleoecological investigations are required to better understand the ecological processes involved in climate–fire–vegetation interactions in the boreal forest.

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Supporting Information

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

Figure S1. Pre-treatment raw charcoal series for Lake Ben and Lake Small.

Figure S2. Macrofossil diagram for local vegetation (trees, herbaceous plants, shrubs (1), and aquatic plants (2)) at Lake Ben and Lake Small.