JOURNAL OF QUATERNARY SCIENCE (2015) 30(4) 365–375 ISSN 0267-8179. DOI: 10.1002/jqs.2790

The effects of forest fuel connectivity on spatiotemporal dynamics of Holocene fire regimes in the central boreal forest of North America

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Received 23 December 2014; Revised 9 April 2015; Accepted 30 April 2015

ABSTRACT: Understanding fire regime dynamics is central to predicting forest structure and the compositional dynamics of boreal forests. Spatial and temporal variations in fire frequency in central Canadian boreal forests over the last 10 000 years were examined to evaluate the influence of bottom-up controls on the regional fire regime. We analysed macroscopic charcoal larger than 160 μm from sediment cores from six lakes to reconstruct fire history and performed GIS analysis of regional landscape features to investigate how fire frequency has changed temporally and how non-climatic factors may have affected long-term fire frequency. Our generalized linear mixed model revealed that temporal changes in fire return intervals (FRIs) were highly dependent on landscape connectivity as inferred through the abundance of natural firebreaks in the form of open water lakes and wetlands. FRIs did not change significantly among highly connected landscapes throughout the Holocene; in contrast, FRIs were significantly longer among poorly connected landscapes in the early Holocene (10–5 cal ka BP), suggesting that the abundant regional firebreaks limited fire spread. All sites had similar FRIs in the late Holocene. The diminishing influence of firebreaks suggests that the regional climate during the late Holocene has overshadowed the influences of the bottom-up controls on fire activities. Copyright © 2015 John Wiley & Sons, Ltd.

KEYWORDS: boreal forest; firebreaks; fire history; forest connectivity; Holocene.

Introduction

Fire is a widespread and key disturbance in many terrestrial ecosystems (Bond and Keeley, 2005; Bowman *et al.*, 2009). In boreal forests, naturally occurring fire is a primary driver of ecosystem dynamics (Weber and Flannigan, 1997; Ryan, 2002; Clemmensen *et al.*, 2013). For several decades, forest fires have been increasing in frequency (Kelly *et al.*, 2013) and size and severity (Kasischke and Turetsky, 2006) in response to ongoing climate change. The potential impacts of altered fire regimes on ecosystem structure and function have driven investigations into the causes and consequences of future changes in fire activity for ecosystems and natural resources management (Littell *et al.*, 2009; Ali *et al.*, 2012).

Climatic factors are considered the predominant top-down control of boreal fire regimes (Johnson, 1992; Power *et al.*, 2008; Marlon *et al.*, 2009), influencing fire at a broad scale (Fauria and Johnson, 2008) by creating a latitudinal gradient in the severity of fire weather conditions, thereby affecting the length of the fire season and proportion of flammable vegetation. Following the end of the Earth's latest ice age, the planet entered an interglacial period known as the Holocene, the warmest portion of which in the central boreal zone of Canada prevailed from about 12 to ~5.5 ka BP after which there was a general progression towards a cooler and moister climate (Viau *et al.*, 2006; Viau and Gajewski, 2009). Several paleofire records (Ali *et al.*, 2009a; Kelly *et al.*, 2013; Senici *et al.*, 2013) from North American boreal forests indicate significant fire frequency changes concurrent with climate cooling trends in the late Holocene, and that the direction and magnitude of such changes differ between regions. Fire frequency has decreased in some eastern coniferous boreal forests (Ali *et al.*, 2009a; Hély *et al.*, 2010) due to reduced fire season length, and increased in some eastern mixedwood (Carcaillet *et al.*, 2010) and western boreal forests (Lynch *et al.*, 2004b; Kelly *et al.*, 2013) due to climate-driven changes in forest fuels and seasonal moisture variability. The contrasting fire frequency responses among boreal regions suggest that differences in both regional climate changes and non-climate factors, i.e. bottom-up controls, are responsible for the different temporal responses throughout the Holocene.

Bottom-up controls, including firebreaks, fuels, surficial deposits and drainage, are increasingly linked to temporal and spatial variability in regional fire regimes (Cyr *et al.*, 2007; Parisien and Moritz, 2009; Mansuy *et al.*, 2010). However, local environmental factors are numerous, variable and interact with climate affecting the ignition, spread and extinction of fires, making their effects on fire regimes difficult to partition (Fauria *et al.*, 2011; Barrett *et al.*, 2013). Dendrochronological approaches to understanding bottom-up controls on fire regime variation confirm that lakes, watercourses and wetlands can disrupt fuel continuity and thereby inhibit fire spread (Larsen, 1997; Hellberg *et al.*, 2004; Cyr *et al.*, 2005) and influence fire frequencies (Heyerdahl *et al.*, 2001). Similarly, surficial deposits and drainage have altered fire cycles in the eastern Canadian boreal forest (Bergeron *et al.*, 2004; Mansuy *et al.*, 2010) by moderating the distribution and growth of vegetation and consequently fuel arrangement, distribution and moisture. Moreover, fuel type influences fire behaviour as coniferous species possess high flammability due to the high volatile content in oils and resin. In contrast, boreal stands dominated by deciduous trees appear to burn at a lower rate, due to decreased ignitions caused by higher foliar moisture content and vertical fuel and canopy arrangement (Hély *et al.*, 2000; Cumming, 2001; Krawchuk *et al.*, 2006). While dendrochronological evidence for the influence of local environmental factors on fire regimes is accumulating, there is a shortage of evidence for the effects of the same environmental factors at

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centennial-millennial timescales. Given that the relative influences of local environmental controls on fire regimes may change over timescales longer than existing observational records, a paleoecological approach to fire history reconstruction can clarify some long-term fire–environment relationships in the boreal forest.

This study describes 10 000-year fire histories reconstructed from high-resolution macroscopic charcoal records obtained from six lakes, two previously published sites (Senici *et al.*, 2013) and four new unpublished records from a mixedwood boreal forest in central Canada (north-western Ontario) (Fig. 1). This region is well suited for exploring the effects of natural firebreaks and surficial geology on fire frequency, because of the highly variable distribution of lakes, wetlands and surficial deposits and relatively homogeneous elevation, slope and aspect. Because forest fuel connectivity is a strong predictor of regional fire frequency (Miller and Urban, 2000; Peters *et al.*, 2004), sites in poorly connected landscapes as inferred through high modern non-forest cover in the form of open-water lakes and wetlands are expected to have longer fire return intervals (FRIs) throughout the Holocene. We predict that the influence of local environmental controls on FRIs might change over time in response to shifting landscape cover, vegetation and ongoing climatic changes following deglaciation.

Materials and methods

Study area

We conducted this study at six lakes, Avril (AVR, 49°22′7″N, 89°25′6″W), Ben (BEN, 49°21′25″N, 89°46′10″W), Beaver (BVR, 49°32′2″N, 90°24′17″W), Dom (DOM, 49°26′22″N, 89°37′55″W), DuBerger (DUB, 49°25′6″N, 90°28′33″W) and Small (SML, 49°34′52″N, 90°23′08″W), in the boreal forest of northw-estern Ontario, Canada (Fig. 1; Table 1). The regional climate is humid continental, with short, warm summers and long, cold winters. The lakes are located within the Moist Mid-Boreal (MBx) ecoclimatic region (Ecoregions Working Group, 1989), characterized by mean summer temperature of 14 °C and mean winter temperature of −13 °C. Mean annual precipitation ranges between 700 and 800 mm. The forest is within the boreal mixedwood region (Baldwin *et al.*, 2012), characterized by a complex mosaic of forest types varying in structure and in relative proportions of coniferous and broadleaved tree species. Regional forests are dominated by conifers (needle-leaved, cone-bearing trees) of the family Pinaceae, mainly *Picea mariana* (Mill.) B. S.P. and *Larix laricina* (Du Roi) K. Koch on wet organic soils and *Pinus banksiana* Lamb. on sandy and loamy soils. Broadleaved trees include *Betula papyrifera* Marsh. and *Populus tremuloides* Michx. These trees tend to be successional, forming pure

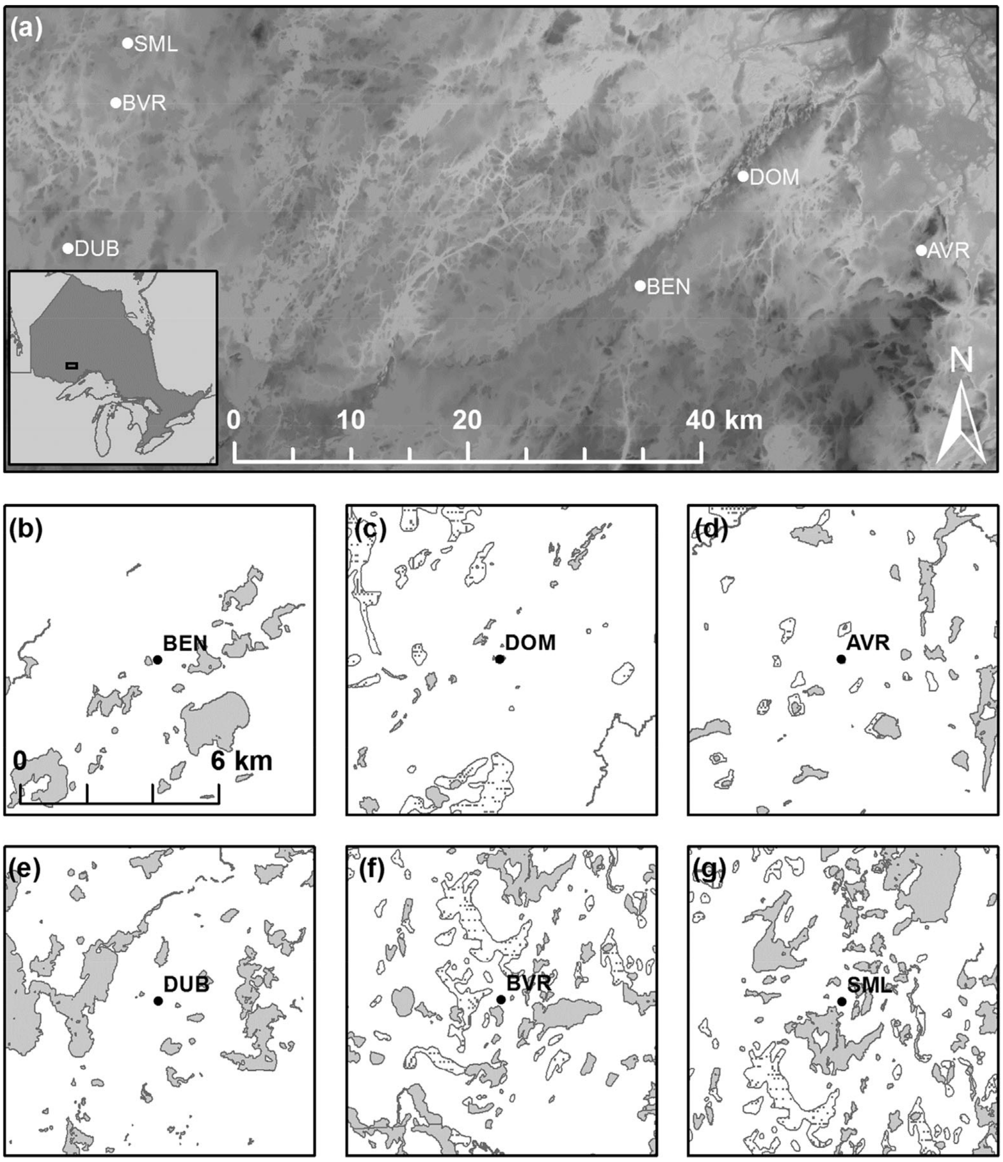

Figure 1. Study region. (a) The six study sites (white dots) in the central boreal forest of north-western Ontario, Canada. Inset is a map of Ontario highlighting the location of the sites. (b) Lake DuBerger (DUB), (c) Lake Beaver (BVR), (d) Lake Small (SML), (e) Lake Ben (BEN), (f) Lake Dom (DOM) and (g) Lake Avril (AVR).

Table 1. Characteristics of study lakes, surrounding landscapes within 5-km radius and charcoal records in the central boreal forest of north-western Ontario, Canada.

	Study site					
	Avril	Ben	Dom	Beaver	DuBerger	Small
Characteristic	(AVR)	(BEN)	(DOM)	(BVR)	(DUB)	(SML)
Latitude (°N)	49°22′7″	49°21′25″	49°26′22″	49°32′2″	49°25′6″	49°34′52″
Longitude (°W)	89°25′6″	89°46′10″	89°37′55″	90°24′17″	90°28′33″	90°23′08″
Lake surface area (ha)	2.7	1.6	3.1	3.2	0.4	0.5
Water depth (m)	5	5	6	4	4	4
Landscape cover						
Connectivity and drainage						
Modern connectivity	High	High	High	Poor	Poor	Poor
Open-water cover (%)	5.3	9.5	1.5	12.3	16.2	16.4
Wetland cover (%)	2.1	3.5	6.7	9.8	7.8	7
Dry drainage cover (%)	85.6	60.8	62.1	71.1	76.1	72.2
Wet drainage cover (%)	7.3	25.9	26.3	6.8	0	4.4
Surficial deposits						
Glaciofluvial landforms (%)	14.7	50.6	39	28.2	16	47.3
Morainal landforms (%)	71.9	19	30.6	42.9	33.2	24.5
Organic terrain (%)	6	13.3	22	6.8	26.8	4.8
Mean (± SD) elevation (m.a.s.l.)	472 ± 19	476 ± 9	469 ± 13	468 ± 6	479 ± 5	473 ± 5
Mean (± SD) aspect (°)	141.9 ± 120.4	113.7 ± 123.9	150.2 ± 112.1	118.3 ± 121.4	84.1 ± 109.8	110.1 ± 118.8
Sediment records						
Core length (cm)	480	660	460	375	415	390
Sedimentation rate (cm a^{-1}, mean ± SD)	0.056 ± 0.036	0.086 ± 0.064	0.051 ± 0.033	0.047 ± 0.046	0.050 ± 0.032	0.063 ± 0.069
Resolution of charcoal analysis (years per sample, mean ± SD)	21 ± 7	16 ± 9	23 ± 9	31 ± 14	25 ± 10	26 ± 12
Median SNI	5.1	8.7	7.5	4.9	4.9	5.9

stands of variable extent following disturbance contingent on pre-disturbance forest cover and substrate ecophysiological characteristics (Brassard and Chen, 2006; Taylor and Chen, 2011).

To evaluate the potential effects of natural firebreaks on fire activity, preliminary regional scouting using topographic maps, satellite imagery and onsite evaluations were conducted to provide qualitative evidence that an equal number of sites would be located in two distinct regional landscapes: one with low lake and wetland density, and one with high lake and wetland density. Furthermore, sites needed to be located relatively close to each other to minimize any variation in regional climate. Among potential sites available for sampling, we choose lakes with small surface areas (<5 ha), deep water (>3 m) and absence of inflowing or outflowing streams (Table 1) (Whitlock and Anderson, 2003).

Sampling

Sediment sequences were extracted in spring 2009 from the deepest point in each lake in the form of 1- m overlapping cores using a modified Livingston piston corer (Wright *et al.*, 1984). A Kajak-Brinkhurst gravity corer was used to collect recent accumulated material at the water–sediment interface, and was extruded on site at 1-cm intervals. Sediment cores were wrapped in polyurethane and aluminum foil for preservation and transported to the laboratory where they were sliced into disks at contiguous 1-cm intervals.

Dating and age–depth models

Chronologies are based on radiocarbon dating by ^{14}C accelerator mass spectrometry (AMS) measurements performed on plant macro-remains and bulk organic sediment when macro-remains were not abundant enough for AMS measurements (Supporting Information Table S1). The CALIB program (Reimer *et al.*, 2004) was used to calibrate radiocarbon ages to calibrated years before present (cal a BP; 1950 CE) using the IntCal09 (Reimer *et al.*, 2009) calibration curve. Age–depth models were created using a cubic smoothing spline, where ages were weighted based on their standard deviation, derived from 1000 bootstrapped samples from the calibrated age distributions using the program MCAgeDepth (Higuera *et al.*, 2009).

Charcoal analysis and fire history reconstruction

Contiguous subsamples (1-cm intervals, 1 cm^3 each) were taken from each sediment sequence for charcoal analysis. To help distinguish charcoal from other biological materials, subsamples were deflocculated in hot 10% KOH solution, bleached in 6% sodium hypochlorite (NaClO) solution and then wet-sieved through a 160-μm mesh. Charcoal fragments larger than 160 μm were identified, counted and measured for surface area under a 20$\times$ stereo microscope using an attached digital camera connected to WinSeedle (Regent Instruments, Quebec, Canada).

Peaks in the charcoal accumulation rate (CHAR, mm^2 cm^{-2} a^{-1}) in lake sediment records have been shown empirically (Lynch *et al.*, 2004a; Ali *et al.*, 2009b) and through simulation models (Higuera *et al.*, 2007) to be associated with the occurrence of local (0–1.0 km) single or multiple high-severity fires (hereafter referred to as a 'fire event'). Fire events at each lake were identified through peak analysis of its sedimentary charcoal record using CharAnalysis 1.1 (Higuera, 2009), available online at charanalysis.googlepages.com. To account for uneven sampling intervals resulting from variable sediment accumulation rates among sites, before decomposition all charcoal data were interpolated to a temporal resolution of 25 years per sample, corresponding to the approximate median sample resolution (23.5) of the six records (Table 1). Each CHAR series was decomposed into 'background' (C*back*), and 'peak' (C*peak*) subpopulations. C*back* is composed of low-frequency variations in the charcoal record and represents changes in charcoal production (regional biomass burning), sedimentation mixing and secondary charcoal transport (Clark *et al.*, 1996); we estimated *Cback* with a locally weighted regression using a 1000-year moving median applied to the raw charcoal series. *Cback* values were subtracted to obtain a residual series, *Cpeak*. 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 fire events (Higuera *et al.*, 2010). *Cfire* and *Cnoise* distributions were estimated in a 1000-year moving window using a Gaussian mixture model and at the centre of each window a threshold was defined as the 99th percentile of *Cnoise* to separate samples into 'fire' and 'non-fire' events. For each record, we chose the window width that maximized a signal-to-noise index (SNI $>$ 3) and the goodness-of-fit between the empirical and modelled *Cnoise* distributions (KS-test, $P >$ 0.05) (Higuera *et al.*, 2009). We did not screen peaks based on charcoal counts of each peak as in Higuera *et al.* (2008, 2009) because this procedure is specific to charcoal count data only (Ali *et al.*, 2009b).

FRIs were calculated as the number of years between two consecutive fire events. Mean FRIs (mFRIs) occurring between 10 and 5k cal a BP (early Holocene), during the Neoglacial and modern period of 5–0k cal a BP (late Holocene) and the complete reconstruction (10–0k cal a BP), were calculated for all sites and between pooled highly and poorly connected sites. To test whether fire events occurred synchronously ($\pm$100 years) between highly and poorly connected sites in these periods, we used the L function, a modified version of Ripley's K-function (Ripley, 1977) in the program K1D (Gavin *et al.*, 2006; Gavin, 2010).

Landscape analysis

We analysed landscapes at spatial scales larger than local fire event detection inferred from charcoal peaks (~1-km radius) to evaluate the regional bottom-up environmental factors that may influence fire spread and consequently fire event occurrence (Barrett *et al.*, 2013). We characterized the local environment at radiuses of 2–5 km around each lake using ESRI's ArcMap version 10.1 (ESRI., 2012). We present the 5-km results (Table 1). Land cover types and area were assessed using data from Digital Northern Ontario Engineering Geology Terrain Study (Ontario Geological Survey, 2005); existing surficial deposits >5% cover in each radius were organized into three broad types: glaciofluvial, encompassing glaciofluvial outwash, delta and esker; morainal, which included ground moraine and mixed moraine–bedrock terrain; and organic terrain (peatlands) (Table 1). Modern open-water lake and wetland cover were assessed using data from CanVec (Natural Resources Canada, 2007). In this paper we make a distinction between wetlands and peatlands; wetlands include only riparian fens or bog dominated by graminoid non-woody vegetation, marshes and shallow water wetlands (<2 m deep); peatlands encompass terrain where organic substrate is >40 cm, drainage is poor, and dominant vegetation is *Picea mariana* and *Larix laricina*. Wetland and peatland types and extent were verified on site using the Canadian Wetland Classification System (National Wetlands

Working Group, 1997). Area calculations were converted to per cent cover. Topographic indices of elevation, slope and aspect were calculated using an 8–23-m resolution digital elevation model (Natural Resources Canada, 2007).

The open-water lake and wetland features at the 5-km radius were then clustered by the K-means clustering method (MacQueen, 1967) to divide lakes into two classes: highly connected, including lakes AVR, BEN and DOM, and poorly connected, including lakes BVR, DUB and SML (Table 1).

Statistical analysis

To examine how FRIs changed temporally and whether the changes were influenced by bottom-up factors, we analysed relationships between FRIs, time and landscape connectivity using generalized linear mixed effect models (GLMMs) from the package *arm* (Gelman *et al.*, 2013) in the statistics program R (R Development Core Team, 2013). Our response variable was FRI. Forest connectivity was assessed using groupings from our cluster analysis of open-water lake and wetland features. We used calibrated years before present (cal a BP) as a predictor for FRI change over time. As we are also interested in the difference in FRI between the early Holocene (10–5k cal a BP) and late Holocene (5–0k cal a BP), we included Holocene (early vs. late) as a predictor. Continuous variables were centered before analysis. We used an information-theoretic approach based on corrected Akaike Information Criterion (AIC_c) (Burnham and Anderson, 2002; Stauffer, 2008) to select the most parsimonious model. Our final model was:

$$\mathrm{FRI_{ijkl}} = \mu + \mathrm{G_i} + \mathrm{H_{j(i)}} + \mathrm{T_{k(i)}} + \mathrm{H_{j(i)}} \times \mathrm{T_{k(i)}} + \pi_\mathrm{l} \quad (1)$$

where FRI_{ijkl} is fire return interval (years), μ is the mean, G_i is group, $H_{j(i)}$ is Holocene time period nested within group, $T_{k(i)}$ is time (cal a BP) nested within group and π_k is random effect of sampling lake.

Model goodness of fit was assessed by R^2, calculated using the methodology presented by Nakagawa and Schielzeth (2013). For mixed-effects models, R^2 is evaluated as marginal R^2 and conditional R^2 (Vonesh *et al.*, 1996) where marginal R^2 represents variance explained by fixed factors, and conditional R^2 represents variance explained by both fixed and random factors.

Results

Dating and age–depth models

The age–depth models represent 10 004 years of sedimentation at AVR, 11 700 at BVR, 10 212 at BEN, 10 299 at DOM, 10 108 at DUB and 10 007 at SML. The models (Fig. 2) are comparable in sedimentation rate, with BEN having the highest mean sedimentation rate at $0.0866 \pm 0.0534\,\mathrm{cm\ a^{-1}}$ and BVR having the lowest at $0.0468 \pm 0.0495\,\mathrm{cm\ a^{-1}}$ (Table 1). Models for BEN, BVR and SML exhibit acceleration in the sedimentation rate between *c.* 5 and 3.5k cal a BP.

Charcoal analysis and fire history reconstruction

Global SNI values for all charcoal records are high (median SNI >3.0) (Fig. 3) and show a clear separation between background charcoal and fire event signals, indicating that

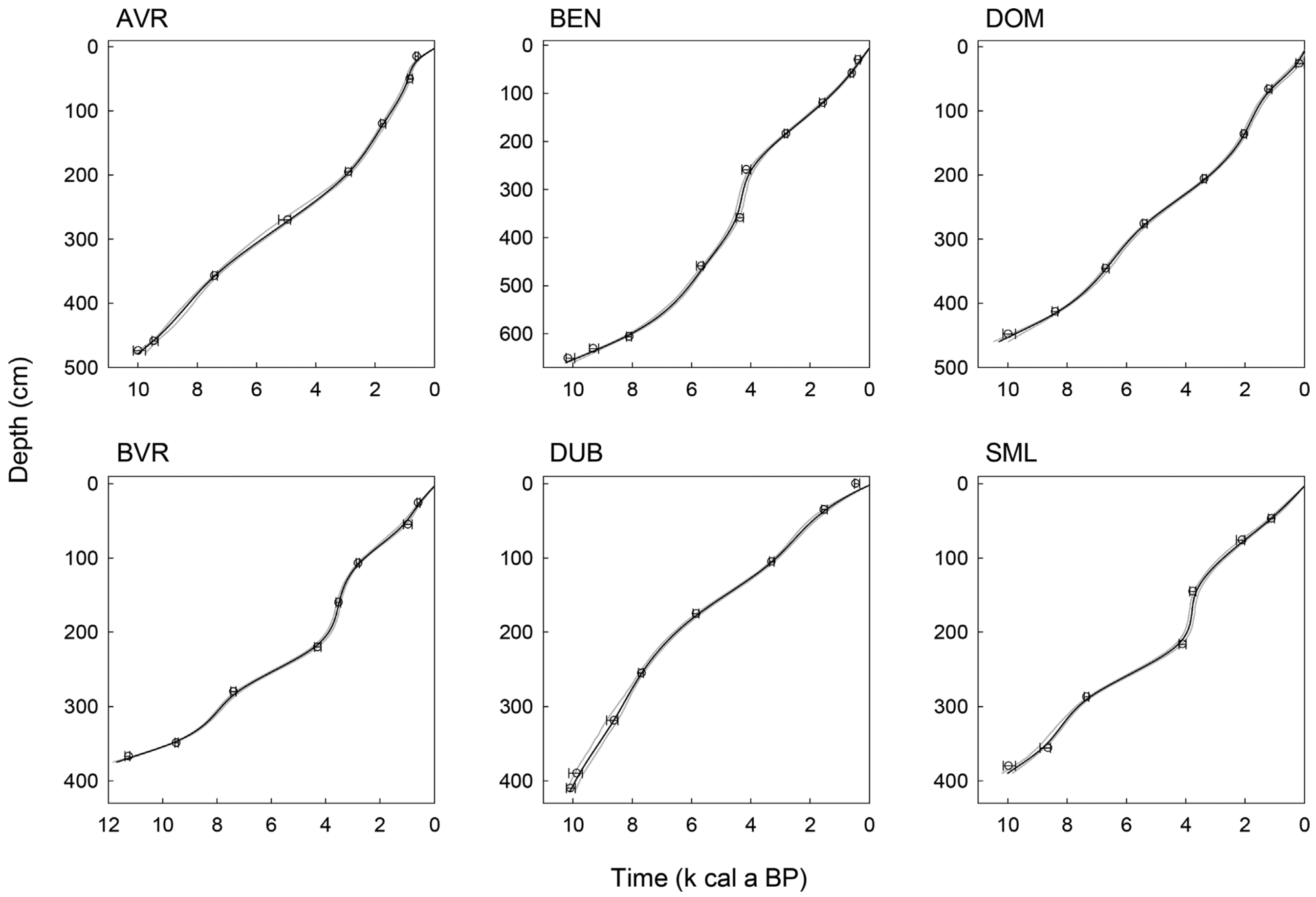

Figure 2. Age–depth models for sediment cores from the six lakes calculated using a cubic spline. Open circles are ^{14}C ages, and error bars represent estimated 95% confidence intervals based on 1000 bootstrapped samples of the calibrated dates.

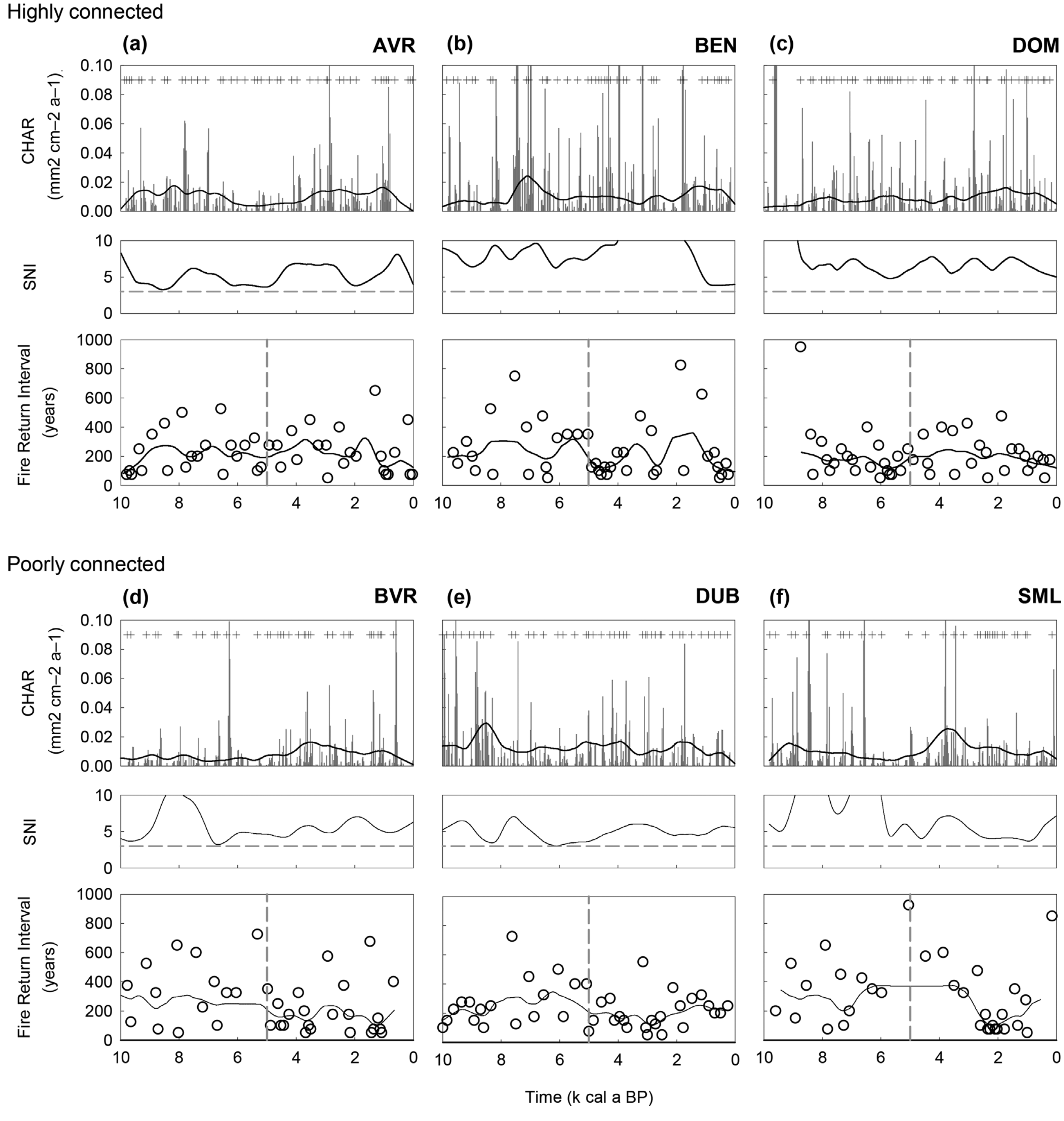

Figure 3. Charcoal peak and background records, signal-to-noise index (SNI) and fire return intervals (FRI) over time for (a) AVR, (b) BEN, (c) DOM, (d) BVR, (e) DUB and (f) SML. The first panel displays the charcoal records, where vertical gray lines are the interpolated CHAR peaks, the black curve represents CHAR background and the crosses indicate identified fire events. In the second panel, the solid black curve represents the SNI and the dashed gray line indicates the minimum threshold (SNI = 3) used to evaluate the suitability of the charcoal record for peak detection. The third panel shows FRI distributions, where circles represent identified fire events and the corresponding fire interval, and the black curve represents LOESS-smoothed FRIs through time.

these records are suitable for fire history reconstructions using peak analysis (Kelly *et al.*, 2011).

In total, 50 fires were detected at AVR, 46 at BEN, 47 at DOM, 39 at BVR, 39 at DUB and 36 at SML (Fig. 3). FRI reconstructions (raw FRIs interpolated to annual values and smoothed with the program LOESS) indicate that fires were most frequent in the late Holocene among all sites except DOM (Fig. 3c). Among highly connected sites, fires recur at relatively even intervals throughout the reconstruction; fires occur most frequently between *c.* 10 and 8k cal a BP at AVR (Fig. 3a), between *c.* 6 and 4k cal a BP at BEN (Fig. 3b) and between *c.* 8 and 6k cal a BP at DOM (Fig. 3c). Among poorly connected sites fire occurrence was somewhat irregular following deglaciation but increased with time; fires were most frequent between *c.* 4 and 1k cal a BP at BVR, between *c.* 4 and 2k cal a BP at DUB and between *c.* 3 and 1k cal a BP at SML.

Mean FRIs were longer among poorly connected sites throughout the Holocene (Table 2); differences were prominent in the early Holocene where mFRI variation between highly and poorly connected sites was >100 years. In the late Holocene, all sites have comparable mFRI distributions. Fire

Table 2. Mean fire return intervals (years) with 95% confidence intervals in the early (10–5k cal a BP), late (5–0k cal a BP) and complete (10–0k cal a BP) Holocene time periods at each site and for clustered connectivity classes.

	Early Holocene	Late Holocene	Complete
Highly connected	216 (177–255)	203 (165–241)	209 (182–236)
AVR	189 (156–222)	212 (144–280)	201 (162–240)
BEN	236 (158–314)	191 (125–257)	211 (160–262)
DOM	226 (145–307)	208 (145–271)	217 (165–269)
Poorly connected	319 (267–371)	229 (184–275)	267 (232–302)
BVR	345 (232–458)	222 (150–294)	267 (203–331)
DUB	300 (214–386)	226 (154–298)	259 (202–316)
SML	312 (240–384)	240 (149–331)	275 (215–335)

event occurrence was independent among highly connected sites in both periods (Fig. 4a,b). Similarly, fires occurred independently in both early and late Holocene periods among poorly connected sites (Fig. 4c,d).

Landscape analysis

The spatial distributions of land cover are dissimilar between highly and poorly connected groups (Table 1). The percentage of open-water coverage was highest at SML (16.4%) and lowest at DOM (1.5%). Wetland coverage was highest at BVR (9.8%) and lowest at AVR (2.1%). Total organic material was highest at DOM (28.7%) and lowest at AVR (8.1%). Dominant surficial deposits include glaciofluvial deposits in the form of eskers, ice-contact deltas and outwash plains, and ground moraine. At DUB a large portion (26.8%) of the regional landscape is classified as organic terrain (Table 1), but this area is a heterogeneous mixture of peat, sand and gravel in glaciofluvial outwash with subordinate landforms of till and sand in ground moraines with overall dry drainage; accordingly, this area was not considered peatland. Elevation, slope and aspect were relatively homogeneous among all sites.

Temporal and spatial effects on FRI

Signs of *z*-values and significance of the predictor variables in the GLMM showed that FRIs were strongly affected by landscape connectivity and their interactions with time (Table 3). Overall, FRIs were longer among poorly connected sites (Table 3). There were no significant differences in FRIs among highly connected sites between different Holocene time periods (Table 2; Fig. 5a); similarly, among these sites there were no significant differences in FRIs over time in each period (Table 3; Fig. 5a). Among poorly connected sites FRIs were significantly shorter in the late Holocene (Table 2; Fig. 5b). In the early Holocene there was a gradual increase in FRIs following deglaciation to *c.* 5k cal a BP (Fig. 5b), after which fires occurred much more frequently. The marginal R^2 for this model was 0.72 and the conditional R^2 was 0.89.

Discussion

There are clear differences in fire activity between highly and poorly connected sites in the early Holocene, although in the late Holocene all charcoal records have similar peak frequencies and FRI distributions, suggesting broadly similar fire regimes over the last 5000 years. Our model indicates that FRIs were significantly longer in the early Holocene near sites with abundant natural fire breaks (Fig. 5b; Table 2), which suggests that the expression of long-term climatic changes on fire regimes may be moderated by the presence of open-water lakes and wetlands in the regional landscape. The temporal changes in FRIs associated with these sites supports the idea that while top-down controls, sich as climate, influenced regional centennial- to millennial-scale fire frequency dynamics, bottom-up controls probably affected fire ignitions and spread, generating variable fire event timing and FRI distributions (Barrett *et al.*, 2013; Lynch *et al.*, 2014; Mustaphi and

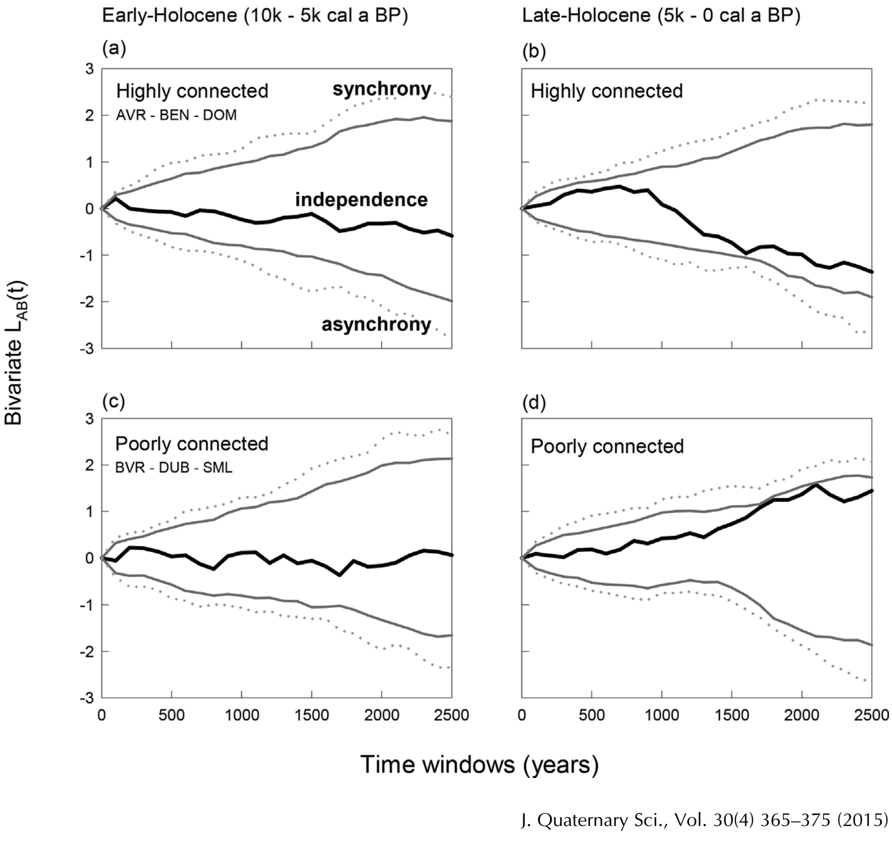

Figure 4. Temporal synchrony analysis of fire occurrence between poorly connected (a, b) and highly connected (c,d) sites in the early and late Holocene. In each plot, fire event synchrony is assessed by comparing the bivariate L function (black line) with a bootstrapped 95% (gray lines) and 99% (dotted gray line) confidence envelope. Fire occurrence within a specified time window is considered significantly synchronous if the L function exceeds the upper confidence interval (CI), asynchronous if the L function exceeds the lower CI, or occurring independently if no CIs are exceeded.

Table 3. Estimates of *z*-value and standard error of the fixed effects from a generalized linear mixed model with fire return intervals as dependent variable (Poisson distribution; log-link).

Term	Estimate	SE	*z*-value	*P*
(Intercept)	5.413	0.050	107.780	<0.001
Group (poor)	0.752	0.071	10.600	<0.001
Group (high): Holocene (late)	−0.009	0.023	−0.390	0.698
Group (poor): Holocene (late)	−0.796	0.024	−33.180	<0.001
Group (high): Time	0.056	0.017	3.260	0.001
Group (poor): Time	−0.388	0.016	−23.700	<0.001
Group (high): Holocene (late): Time	−0.011	0.023	−0.480	0.630
Group (poor): Holocene (late): Time	0.351	0.025	14.110	<0.001

Pisaric, 2014). Our observations are consistent with recent studies that demonstrate divergent fire regimes between areas with abundant lakes and wetlands and those without (Hellberg *et al.*, 2004; Barrett *et al.*, 2013; Lynch *et al.*, 2014); however, our results suggest that some of the observed FRI differences may be restricted to particular climates or periods where differences among sites may have been more pronounced, i.e. the immediate postglacial period of the early Holocene.

As heat transfer is reduced by fuel breakages, the observed differences in FRIs among sites may simply be a consequence of diminished fire ignitions and spread in landscapes with abundant firebreaks. However, our significant model results for temporal period (Table 3) and the broadly similar mFRIs (Table 2) in the late Holocene regardless of firebreaks suggest that the differences in fire histories may be related to climatic factors. Although climatic influences on wildfire behavior in the boreal forest are well documented (Wotton *et al.*, 2010; Parisien *et al.*, 2014), the long-term influences on fire occurrence and extent in central Canada are uncertain because of limited data on paleo-fire occurrence and Holocene-scale regional paleoclimate reconstructions. Among poorly connected sites, in the early Holocene when it was warmer and drier (Viau and Gajewski, 2009) mFRIs were approximately 30% longer than those of the last 5000 years when the regional climate was cooler and wetter (Table 2; Fig. 5b). These results differ from the highly connected sites where mFRIs did not change significantly between temporal periods (Table 2). Overall, these results are consistent with studies showing higher fire frequencies in boreal forests under wetter climates of the late Holocene (Lynch *et al.*, 2004b; Genries *et al.*, 2012), although this interpretation is complicated because the decreased FRIs were driven primarily by the poorly connected sites. Additionally, given the relative proximity among sites, it is unlikely that the fire frequency differences between temporal periods and our connectivity classes are a direct result of climatic conditions. The non-uniform fire frequency responses between connectivity classes over time and ubiquitous independence in fire event occurrence suggests complex temporal and spatial fire regime variations that may reflect interactions between a changing climate and shifting land cover following deglaciation.

When compared with lakes, wetlands are highly dynamic firebreaks as hydrology and vegetation varies over time scales much shorter than those of these paleoecological reconstructions, complicating our understanding of their long-term potential in stopping fires (Hellberg *et al.*, 2004). Consequently, the significant results for temporal period and connectivity class may reflect differences in land cover of the early Holocene versus the late Holocene, by which the pattern and timing of wetland and peatland formation and development may have contributed to the increased fire frequency among poorly connected sites. Many peatland successional pathways originate from the gradual in-filling of water bodies (Harris *et al.*, 1996; Rydin and Jeglum, 2006), moreover there is an average 4000–5000-year (Gorham *et al.*, 2007; Ruppel *et al.*, 2013) lag time between deglaciation and peak peat development due to the time it takes for land to become amenable for peat formation (Halsey *et al.*, 2000). Consequently, the terrestrial cover designated wetland may have been open-water in the early Holocene, and the increased fire activity in the late Holocene may have resulted from wetland cover becoming a viable source of forest fuels thereby facilitating

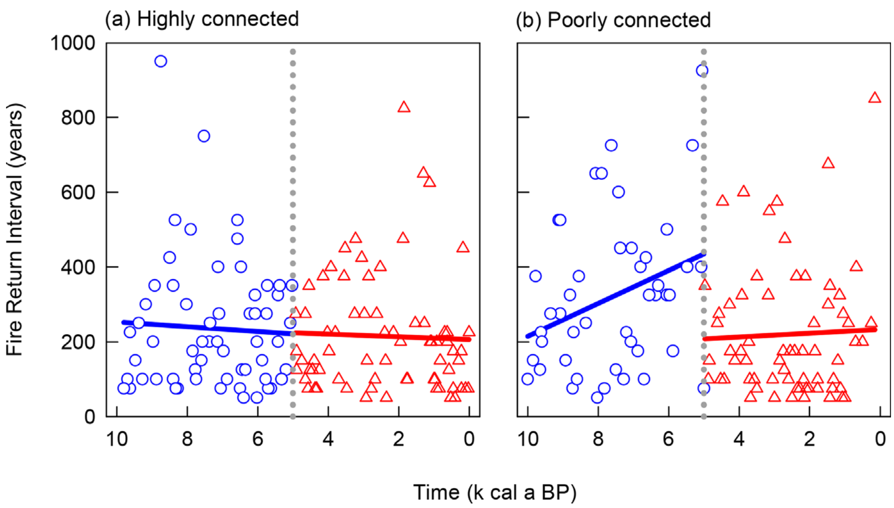

Figure 5. Scatterplots and fitted fire return intervals (FRIs) of significant fixed effects from the generalized linear mixed model. For illustrative purposes we present simple linear regression lines through FRIs in the early and late Holocene time periods at (a) highly connected and (b) poorly connected sites. The vertical dotted gray line marks the Holocene boundary (5k cal a BP). This figure is available in colour online at wileyonlinelibrary.com.

the spread of fire. We acknowledge the limitations in using modern metrics for landscape features throughout the Holocene, specifically before *c.* 5–6k cal a BP, given that the arrangement and development of soils (Liu, 1990) and peatland initiation and expansion (Ruppel *et al.*, 2013) may have been spatially more limited in the immediate postglacial period.

The increased fire frequency after *c.* 5k cal a BP may be a result of positive vegetative feedbacks between highly flammable vegetation and frequent crown fires (Johnstone *et al.*, 2010; Minckley *et al.*, 2012; Lynch *et al.*, 2014). Lower temperatures and increased precipitation in the late Holocene may have been advantageous for the growth and development of coniferous vegetation (Brooks *et al.*, 1998). In the late Holocene, *Picea mariana* has expanded in eastern mixedwood boreal forests (Carcaillet *et al.*, 2001 2010), and in boreal forests of Alaska (Lynch *et al.*, 2002; Brubaker *et al.*, 2009; Higuera *et al.*, 2009) and is linked to increased fire frequency. Additionally, recent paleoecological vegetation reconstructions in the same ecoregion (Genries *et al.*, 2012) indicate increased *Picea*, *Pinus banksiana* and *Betula papyrifera* in the late Holocene with a concomitant decrease in mFRIs. Furthermore, the cooler moister prevailing climate of the late Holocene would not have precluded the incidence of extreme short-term fire weather (De Groot et al., 2013) capable of sustaining very large, high-intensity wildfires able to overcome natural firebreaks, contributing to the decreased FRIs among poorly connected sites.

One surprising outcome of this study was the relative complacency of fire regimes among highly connected sites. These results contrast with other boreal fire records that show substantial fire regime variability at centennial–millennial timescales (Ali *et al.*, 2012; Genries *et al.*, 2012; Kelly *et al.*, 2013; Mustaphi and Pisaric, 2014), which suggests that forest ecosystems at our highly connected sites were better able to sustain fundamental function, structure and feedbacks when confronted with perturbations such as climate changes or fire (Chapin *et al.*, 2010). As bottom-up controls on fire regimes are inherently spatially heterogeneous, their spatial arrangement in the landscape largely determines their relative influence on fire regime, whereby greater spatial variability in a factor turns into more variable fire patterns (Parks *et al.*, 2012). As our highly connected sites possess fewer landforms sensitive to changes in climate (i.e. open-water and wetlands) in both count and per cent cover, these regions may have been comparably more resilient to late Holocene changes in soil moisture and lake and wetland hydrology than our poorly connected sites, thereby maintaining similar land cover and comparable levels of fire activity between temporal periods. The relatively continuous intermediate level of fire frequency (mFRI $\sim$ 200 years) suggests additional mechanisms that may have contributed to fire regime complacency at these sites. This region of the boreal forest may be resistant to very high burn rates because continuous fire recurrence and overlap can lead to an overabundance of young forest stands in the regional landscape, thereby creating a fuel-mediated negative feedback on increased fire activity (Héon *et al.*, 2014). Alternatively, potential late Holocene fire frequency increases may have been constrained by increased broadleaved growth (Chen *et al.*, 2009; Kelly *et al.*, 2013), thereby producing a potential negative feedback to increased regional burning (Beck *et al.*, 2011; Johnstone *et al.*, 2011; Girardin *et al.*, 2013). A high-resolution pollen analysis from these sites could help resolve some of these possibilities.

Current global climate models and climate change scenarios suggest that fire regimes will be characterized by increased fire activity and area burned across the boreal region throughout the 21st century (Flannigan *et al.*, 2009, 2013). The impacts of climate changes on fire regimes will not be consistent across boreal regions; our results imply there may be significant variation within regions not only due to the direct effects of climate change but indirect effects mediated through bottom-up factors sich as firebreaks and land cover changes. More specifically, landscapes with abundant lakes and wetlands may be more vulnerable to land cover transformations through shallow lake and wetland shrinkage and drying leading to increases in forest connectivity and burning.

Conclusions

This study demonstrates complex spatial and temporal variability in fire regimes over the past 10 000 years. Throughout the Holocene, FRIs did not vary significantly near sites with few natural firebreaks in the regional landscape. In contrast, from 10 to 5k cal a BP, FRIs were significantly longer near sites with abundant natural firebreaks, with FRIs decreasing in the last 5000 years to equal those of the highly connected sites. The decrease among poorly connected sites was probably in response to the indirect effects of climate change, characterized by a wetter and cooler climate, influencing land cover and forest fuels. In contrast, fire regimes at highly connected sites were insensitive to changes in centennial- to millennial-scale climate, which suggests greater resilience to perturbations and potential negative feedbacks constraining increased fire activity. Our results show divergent fire regimes between highly and poorly connected landscapes and highlight the importance of considering the effects of bottom-up factors when interpreting Holocene-scale paleofire records. These results clarify some patterns and controls of central boreal forest fire regime variations, and imply that landscapes with abundant lakes and wetlands may be more vulnerable to future climate changes with far-reaching implications for forest ecology and wildfire management. We stress the need for more studies investigating the role that bottom-up controls play in affecting boreal fire regime variation.

Supporting Information

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

Table S1: AMS ^{14}C dating of the study lakes.

Acknowledgements. We thank Loc̈ Bircker, Benot̂ Brossier, Etienne DuBerger and Raynald Juliens for their assistance in data collection. Financial support was provided to H.Y.H.C. by the Natural Sciences and Engineering Research Council of Canada (NSERC DG283336-09), Ontario Early Researcher Award, and Northern Ontario Heritage Foundation Corporation, to Y.B. by NSERC and to A.A. by the CNRS (BOREOFIRE, PALEO2, INSU). The lead author acknowledges NSERC, Forest Ecosystem Science Co-operative, Inc. and Resolute Forest Products for an Industrial Postgraduate Scholarship.

Abbreviations. AMS, accelerator mass spectrometry; CHAR, charcoal accumulation rate; FRI, fire return interval; mFRI, mean fire return interval; SNI, signal-to-noise index.

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