Holocene fire-climate-vegetation dynamics in Central Canadian Shield boreal forests of Northwestern Ontario, Canada

by
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Abstract

The boreal forest is the largest terrestrial ecosystem in North America, one of the least disturbed by humans, and most disturbed by fire. This combination makes it an ideal system to explore the environmental controls on fire frequency, the relative importance of climatic and non-climatic factors, and the importance of fire in governing ecosystem processes at a large scale. Multiple vegetation and forest fire history records were established by analyzing Holocene-aged lake sediment stratigraphies collected in the central boreal shield region of northwestern Ontario, Canada. The stratigraphies were dated using ^{14}C AMS. In the first research chapter macroscopic sedimentary charcoal and plant macroremains were analysed in order to investigate local fire frequency and tree abundance. The results show contrasting fire regime dynamics between a xeric and mesic landscape and highlight the influence of local factors as important drivers of fire frequency at centennial to millennial scales. The second research chapter examines spatial and temporal variations in fire frequency to evaluate the influence of some local non-climatic factors on the regional fire regime. The results show that sites within landscapes fragmented by high open-water lakes and wetland cover tended to have lower fire frequencies, and that this trend was stronger in the past. Results clarify some regional fire regime controls and imply climate-vegetation interactions will significantly affect future boreal fire regime dynamics. The third research chapter examines regional fire-vegetation interactions. The results show that millennial-scale species community diversity may not be driven by fire frequency variations. This study contributes to our knowledge of the varying spatial controls forest fire regimes in the central boreal forest region.

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Preface

This integrated article format thesis dissertation is comprised of a chapter detailing the methodological context of the work and three original research chapters that have been/will be submitted to peer-reviewed scientific journals. Each original research chapter has been edited and modified from the submitted versions for formatting and figure and table numbering.

A version of Chapter 2 was published in the *Journal of Ecology*.

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Where D.S., H.Y.H.C., Y.B., and A.A.A., conceived the study; D.S. and A.A.A. led the field work; D.S. performed lab work on charcoal; A.Lu. performed lab work on macrofossils; D.S. led the data collection and data analysis; D.S., and A.A.A. led the writing; and all co-authors contributed in reviewing the manuscript.

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Acronyms and Definitions

a (unit)	*annus* (year)
AMS	accelerator mass spectrometry
BP	Before Present (CE 1950)
Cal a BP, cal yr BP	calibrated years Before Present
CE	Common Era
CHAR	charcoal accumulation rate
Charcoal	charred particles
CONISS	constrained incremental sums of squares cluster analysis
FI	fire interval
Fire regime	long-term description of fire activity in a region; multiple components.
FRI	fire return interval
LIA	Little Ice Age (1350 - 1850 CE)
LOESS/LOWESS	locally weighted (regression) and scatterplot smoothing
mFRI	median fire return interval
mFI	median fire interval
PCA	Principal Components Analysis
ROC	Rate of Change
SNI	signal-to-noise index

CHAPTER ONE General Introduction

Research context & background

Paleoecology refers to the study of past organisms in relation to their past environment. Paleoecological and paleoenvironmental research use physical, chemical, geological and biological evidence from fossil deposits to investigate the past occurrence, distribution and abundance of different ecological units (species, populations, communities), events (natural disturbances) and environmental states (climate) on a variety of timescales (Birks and John 2008). While it encompasses any time interval in which life existed on Earth, most paleoecologists are concerned with investigating past ecosystem dynamics in the Quaternary period (the last 2.58 million years), with the bulk of research concentrated in the last 20,000 years. The field is multidisciplinary in nature with researchers often combining techniques from paleontology, sedimentology, and geochemistry in order to reconstruct past environmental dynamics and investigate biotic responses to environmental change.

Layers of sediments that accumulate on the bottoms of lakes are an archive of environmental variability that can be used to understand how local terrestrial ecosystems have responded to natural and anthropogenic influences at multi-millennial scales (Last and Smol 2001). The accumulated sedimentary material can be quantified through various physical and chemical processes to reconstruct previous environmental conditions via preserved fossil proxies; charred particles (hereafter charcoal), plant macroremains and pollen can be used to reconstruct high-resolution records of wildfire and vegetation dynamics at local and regional scales (Faegri and Iversen 1989; Whitlock and Larsen 2001). Paleoecological research continues to enjoy tremendous interest and progress in the scientific community as it can be used to

identify ecological thresholds for historical "natural" rates of change and can therefore be of use in environmental and socioeconomic planning for conservation, resource development and model building (Birks and John 2008; Brubaker *et al.* 2009).

The North American boreal forest constitutes the largest biome in most Canadian provinces and territories and in Alaska. Boreal regions have a history of repeated glaciation and glacial displacement and the last 10,000 years of post-glacial recovery have generated a forested landscape developed on a mosaic of bedrock outcrops, glacial till, lacustrine deposits and organic soils in poorly drained depressions with the entirety interspersed with lakes, wetlands, fens and bogs. In the boreal forest, fires are a major driver of the carbon cycles and is a significant contributor to ecosystem functioning and biodiversity (Rowe and Scotter 1973; Harden *et al.* 2000; Bowman *et al.* 2009). The combination of heterogeneous mosaic of terrain differences and active fire regime has generated a diversity of ecosystem compositions, structures and productivities throughout the boreal biome (Johnson *et al.* 1998; Weir *et al.* 2000; Mansuy *et al.* 2010; Barrett *et al.* 2013). Examining the natural variability and complex interactions occurring at various spatiotemporal scales of fire activity is crucial in order to understand how future global climate changes will affect fire regimes (Hessl 2011; Girardin *et al.* 2013b). Empirical studies of natural fire regimes at millennial-scales form our understanding of how the current landscape evolved, how major fire regime drivers and environmental changes interacted, and how boreal forest ecosystems responded to recurrent natural disturbances. In the North American boreal forest, where observational records of historical fire and vegetation are short (< 100 years), fossils preserved in lacustrine sediments potentially contain the most complete post-glacial histories of naturally occurring wildfire and vegetation dynamics. Quantitative studies that seek to improve our understanding of large-scale controls of fire regimes are highly relevant

to creating fire policy and sustainable forest management strategies in the context of anticipated future changes in climate and fuels (Gavin *et al.* 2007; Cyr *et al.* 2009; de Groot *et al.* 2013b).

Individual fire events rely upon four variables: an ignition source, available fuels, oxygen and a chemical chain reaction to sustain the burn (Johnson and Gutsell 1994; Halsey *et al.* 2000). Fossil charcoal indicates that wildfires began soon after the appearance of terrestrial plants in the Silurian Period (420 million years ago (Ma)), but was not widespread until the Early Carboniferous Period (350 – 300 Ma) (McAndrews *et al.* 1973; Bowman *et al.* 2009). Fire has continued to play a central role in structuring the natural vegetation of many terrestrial ecosystems not only leading to convergent evolutionary adaptations in widely separated species (Kerby *et al.* 2007), but influencing vegetation community structure, nutrient cycling, slope stability, soil formation and atmospheric composition. Globally, the frequencies of fire ignitions, fuel abundance and distribution, local geographic conditions and atmospheric oxygen have varied throughout geologic time and have altered fire regimes. Additionally, the relative importance of various fire regime controls have not remained constant through time (Marlon *et al.* 2008; Power *et al.* 2008; Krawchuk *et al.* 2009; Oris *et al.* 2013) necessitating the construction and interpretation of multiple paleoenvironmental records to assess the natural variability and understand the spatial controls of fire regimes (Heyerdahl *et al.* 2008; Blarquez *et al.* 2013).

Complex interactions between the controls of fire operate at multiple temporal and spatial scales (Kashian *et al.* 2006). Broadly, these controls can be characterized as top-down and bottom-up controls. Top-down controls typically refers to climate or biome transformations that can homogenize fire regimes over large regions by overriding the importance of local factors. Climatic variability over short (annual) to long (millennial) time scales drives fire regimes

directly by modifying fuel moisture and indirectly through vegetation assemblages, abundance and density (Flannigan and Van Wagner 1991; Turner and Romme 1994). Bottom-up controls of the fire regime include vegetation types and density, fuel connectivity, surficial deposit drainage, local physiographic features (aspect, slope, relief) and other local site factors (Cyr *et al.* 2007; Mansuy *et al.* 2010; Senici *et al.* 2010; Barrett *et al.* 2013). The relative importance of these controls varies depending on the spatial scale examined and through time in response to climatic and natural ecosystem changes (Gavin *et al.* 2003; Gedalof 2011; Barrett *et al.* 2013).

In the boreal forest of North America there exists temporal limitations on dendrochronological approaches to fire history reconstructions primarily due to the short life span of many boreal tree species and limited historical records of fire activity. In contrast, paleoecological techniques can be used to examine fire regime temporal and spatial variability throughout the Holocene (*c.* 11,700 cal. yrs BP to present) (Whitlock and Larsen 2001; Blarquez *et al.* 2013). When compared to eastern and western North American boreal forests, the central boreal region is only beginning to become explored palynologically to describe fire-climate-vegetation dynamics. Due in part to its intermediate geographical position, the central boreal forest region is potentially different from eastern and western boreal regions because of variability among several factors linked to initiating changes in fire activity including climate (Girardin *et al.* 2006; Ali *et al.* 2012) and physical site characteristics (Cyr *et al.* 2007; Genries *et al.* 2012).

Research objectives

The objective of this dissertation is to improve our understanding of long-term fire-climate-vegetation dynamics in the central boreal forest and determine how fire and vegetation

dynamics may have been influenced by climate and local environmental characteristics. To further this goal, this study aims to:

1) Develop multiple robust Holocene-scale proxy records of wildfire (charcoal) and vegetation (plant macroremains and pollen) preserved in lake sediments in the central boreal forest.

2) Analyse multiple sites across environmental gradients to examine the relative importance and spatiotemporal variability of multiple environmental influences on long-term fire regime by making use of the reconstructed paleoecological records.

General philosophy

<u>Fire regime</u>

Fire has been the dominant natural disturbance regime in the North American boreal forest since the last Ice Age, and is process important for several boreal species and is responsible for shaping landscape diversity and influencing biogeochemical cycles (Stocks *et al.* 2002). The basic theoretical concepts of fire history were laid out by Johnson and Van Wagner (1985) and subsequently refined by Johnson and Gutsell (1994). Fire regimes are a critical foundation for understanding and describing effects of climate on fire patterns and characterizing their combined effects on vegetation and the carbon cycle (Bond-Lamberty *et al.* 2007; Burton *et al.* 2008; Pechony and Shindell 2010).

In general, a fire regime characterizes the spatial and temporal patterns and ecosystem impacts of fire on a landscape. Fire frequency, size, seasonality, intensity, severity, and type are among the most common descriptors of a fire regime (Malanson 1987; Whelan 1995; Weber and Flannigan 1997; Stocks *et al.* 2002). Fire frequency refers to the number of fires of a given size occurring per unit time in a given area. Size, or total area burned, largely determines the forest

mosaic and sizes of different aged patches within a given landscape. Size also influences the dispersal of propagules from the edges of a fire's boundaries thereby indirectly influencing post-fire regeneration. The season (timing) of a fire not only influences successional trajectory by moderating vegetative or seed reproductive responses based on the phonological state of the pre-fire vegetation composition (Weber and Flannigan 1997), but affects fire intensity through seasonal climate effects on fuel moisture. Fire intensity measures the energy output from a fire and is strongly correlated with factors like pre-fire species composition, stand age, topography, substrate, fuel loading, weather, and regional climate. Fire severity describes how fire intensity has affected an ecosystem and is a measure of the magnitude of impact including combined above and below ground biomass losses and mortality (Keeley 2009). Lastly, type describes fire class, whether ground, surface, or crown, based on the fuel layer(s) consumed in the combustion process.

The boreal fire regime is characterized by infrequently occurring, high intensity stand-replacing crown fires that occur throughout the principal fire season (April to mid-October) that can incinerate well over a million of hectares of standing vegetation (Rowe and Scotter 1973; Bonan and Shugart 1989; Stocks *et al.* 2001). The large wildfires that account for the majority of area burned are usually caused by lightning (Nash and Johnson 1996; Wotton and Martell 2005; Krawchuk *et al.* 2006), and occur during persistent high-pressure systems that dry forest fuels (Skinner *et al.* 1999; Skinner *et al.* 2002). Smaller fires usually occur under marginal burning conditions, and while numerous, only account for a small percentage of area burned (Stocks *et al.* 2002).

<u>Vegetation succession</u>

In the field of ecology, the study of succession has a long history, being discussed unofficially as early as the nineteenth century. Succession remains a core tenet within ecology, although it is sometimes incorporated into the broader discussion of vegetation dynamics. In this dissertation ecological succession refers to the observed directional non-seasonal cumulative change in the types of plant species that occupy a given area through time.

Two major views of this process were taught by Clements (1916) and Gleason (1926). In Clement's model, vegetation changes from pioneer species through a series of predictable communities which replace each other until a final stable or climax community dominates. This model is said to be linear (always follows the same order) and deterministic (predictable), where the present pattern is governed by the past pattern. Gleason's model suggests that vegetation change following disturbance is a function of the kinds of plants involved and their characteristics relative to the disturbance. Gleason's individualistic concept sees the relationship between coexisting species as the result of similarities in their requirements and tolerances, and partly due to chance. In the modern era, ecological research has focused on understanding and predicting forest succession using more rigorous and data-driven testing of the underlying mechanisms driving community changes (Connell and Slatyer 1977; Heinselman 1981; Tilman 1982; Pickett *et al.* 1987; Taylor and Chen 2011). Debates continue as to the general predictability of successional dynamics and the relative importance of various mechanisms, consequently understanding plant succession is a on-going key challenge for ecologists and resource managers (Taylor *et al.* 2009).

Methodological approach

<u>Paleolimnology</u>

Paleolimnology can be broadly defined as the study of the physical, chemical and biological information stored in lake and river sediments (Last and Smol 2001). The overall paleolimnological approach is relatively straightforward. The raw materials used are lake sediments which, under ideal conditions, accumulate at the bottom of a basin in an continuous and undisturbed manner. In a typical study, sediment cores are extracted from the bottom of a lake, after which the sediment profiles are sectioned into appropriate time slices, and the age-depth profile can be established using geochronological techniques (Last and Smol 2001). In this study we collected complete lacustrine sediment sequences at eight different lakes from atop the frozen surface early spring 2010. Within these sediments are various indicators and other proxy data that can be interpreted in a statistically rigorous manner that can useful to other scientists and the general public. Chronologies for six of the eight sampled lakes were established; all six final sites were analysed for macroscopic charcoal and two lakes were analysed for plant macroremains and pollen.

<u>Age-depth modeling</u>

An accurate and precise chronology is an essential pre-requisite for any paleoecological investigation. Chronologies give time scales for events, and hence rates of patterns and processes, and make it possible to compare and correlate events across space in different stratigraphical sequences. The chronologies in this dissertation are based on radiocarbon dating by ^{14}C accelerated mass spectrometry (AMS) from two laboratories: Poznan Radiocarbon Laboratory, Poznan, Poland (Poz-) and Beta Analytic Inc., Miami, Florida (Beta-). Chronologies of deposits are obtained by drawing a curve through a number of dated depths. Raw radiocarbon

ages are expressed as "^{14}C BP" or "years BP", where "before present" is defined as 1950 CE

(Willard Libby obtained first ^{14}C dates 1949). Calibrated ^{14}C ages are given in "cal yr. BP" or

"cal a BP" (or variations thereof) dependant on specific journal author guidelines.

General methods for reconstructing forest fire history

Burning, or combustion, of biomass is a complex process that rapidly oxidizes fuel, releasing

energy in the form of heat and greenhouse gases. During a fire, organic matter may not be

equally exposed to the combustion process, resulting in the production of charred particles that

can be quantified and analysed to produce a fire history record. Through a variety of transport

mechanisms and taphonomic processes including convective dispersal as well as postfire wind

transport, overland flow, and sediment focusing (Clark 1988; Higuera et al. 2007), charcoal

particles may enter nearby depositional environments such as lakes or wetlands where they are

preserved. Over time, charcoal from subsequent fires accumulates within these environments,

eventually forming a long-term record of local disturbance. Sedimentary charcoal records have

proven useful for identifying long-term trends in fire activity at local to global scales, studying

interactions with vegetation (Blarquez and Carcaillet 2010; Girardin et al. 2013a), and

understanding the linkages with climatic changes (Marlon et al. 2008; Ali et al. 2012).

Interpreting fire history from sediment charcoal records depends upon understanding the

processes controlling charcoal accumulation and the use of analytical methods that appropriately

reflect these processes (Higuera et al. 2007; Peters and Higuera 2007). Macroscopic charcoal,

usually fragments > 150 μm in diameter are predominantly derived from local (~ 3 km) fire

events (Lynch et al. 2004a; Higuera et al. 2007). Once charcoal has been tallied, the record is

typically decomposed into separate time series that describe different aspects of fire history

(Clark et al. 1996; Long et al. 1998). Most time series of charcoal accumulation rates (CHAR)

contain a slowly varying component, or background CHAR, and a rapidly changing component called peak CHAR. Where the background component may represents changes in fuel accumulation (Millspaugh *et al.* 2000), burning rates, and local erosion within the basin catchment (Higuera *et al.* 2007), the peak component represents past fire 'episodes' or 'events' (the term 'fire event' is used exclusively throughout the dissertation). This approach to decomposing fire records is facilitated by the CharAnalysis software (Higuera 2009); detailed accounts of the statistical parameters selected and how this software was used to reconstruct fire histories are presented in each chapter.

General methods for reconstructing vegetation history

Past vegetation assemblages can be inferred through the analysis of subfossil plant remains preserved in lake sediments. In this dissertation we used two different proxies, macroremains (Birks and Birks 2000) and pollen (Faegri and Iversen 1989) to reconstruct vegetation history at the local and regional scale respectively. Although each proxy has particular strengths and weaknesses, there are several reasons why macroremains and pollen are valuable as indicators of past conditions. First, they are more easily preserved in sediments due in part to their structural chemistry; under conditions of low oxygen and microbial activity i.e. the bottom of a lake, they are decomposed very slowly. Second, due to their small size they can be carried some distance from their source. While macroremains e.g. fruits, seeds, cones, twigs, etc. are mainly derived from the local flora, pollen grains can be carried some distance from their source, suspended in turbulent air masses, and therefore represent a flora from a wider area of surrounding landscape (Moore *et al.* 1991). Third, pollen grains and spores have unique structure and sculpturing that make them highly recognizable. Often pollen identification can be taken to the species level, though sometimes it is possible to only deduce the genus or the family (McAndrews *et al.* 1973;

Moore *et al.* 1991). Some types of macroremains can be identified with greater taxonomic precision and can often be frequent of taxa that produce very little pollen and are therefore valuable as a fossil material (Birks and Birks 2000). The fourth and final reason is the abundance with which these fossils occur in sediment. Macroremains are produced in small numbers when compared to pollen, and large samples are needed for fossil analysis; in contrast, pollen production is much greater and smaller subsamples can be used in analysis. Complimentary macroremains and pollen analysis of the same sediments can provide local species compositional patterns (macroremains) and regional species abundances and regional vegetation patterns (pollen)

Dissertation organization

The format of this dissertation is as follows: Chapter 1 describes the overall approach and methodological context for the use of lake sediment stratigraphies to examine and interpret fire and vegetation changes throughout the Holocene. Due to differences in acquisition dates of ^{14}C AMS ages and pollen data related to laboratory access, combined with the impetus to publish original research, original research chapters 2 and 3 reflect the data available when they were written and submitted for publication, and have not been altered to reflect data (pollen vegetation records) obtained at later dates. Chapter 2, examines how local tree abundance responded to fire frequency throughout the Holocene. Chapter 3, examines the influence of local non-climatic factors on local-to-regional fire frequency. Chapter 4, examines regional vegetation compositions and species specific responses to fire. Chapter 5 describes potential future work, some limitations related to this work and the general conclusions.

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

Abstract/Summary

1. Macroscopic sedimentary charcoal and plant macroremains from two lakes (Ben and Small), 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 individual FRIs 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, Neoglaciation, palaeoecology, 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 *et al.* 2008; Fauria and Johnson 2008; Chen and 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 and Martell 2005; Krawchuk *et al.* 2006); under natural

settings these factors are primarily controlled by large-scale climatic patterns (Fauria and

Johnson 2006; Girardin and 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 *et al.* 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 *et al.* 2009a). 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. yr BP), a documented climatic trend

during the Holocene affecting the onset of cooler and wetter conditions, decreased fire frequency

in coniferous boreal forests (Ali *et al.* 2009a) 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 *et al.* 2004b; Briles *et al.* 2008; Higuera *et al.* 2009; Blarquez *et al.* 2010). Differences in fire regimes among landscapes may also be correlated with relative proportion of area under different fire hazards, i.e. relative amount of xeric and mesic sites (Heinselman 1981; Romme 1982), or forest type (Hely *et al.* 2000; Cumming 2001), with the interaction between fuel characteristics and topography generating different fire frequencies (Hellberg *et al.* 2004; Wallenius *et al.* 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 *et al.* 2004b; 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 *et al.* 2006). Although fire frequencies in the current climate determine the relative abundance of trees (Bergeron 2000; Bouchard *et al.* 2008; Chen and 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: (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 regimes (Bessie and Johnson 1995; Fauria and Johnson 2008). We also expected increasing FRIs after the onset of Neoglaciation (*c.* 4500 cal. yr BP) (Viau *et al.* 2006b) 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

<u>Study area</u>

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 northwestern Ontario, Canada (Fig. 2.1). The lakes (Table 2.1) are located approximately 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 700-800 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 dystric 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 approximately 10% and 27% of the terrestrial area within a 2 km radius from Lake Ben and Lake Small, respectively.
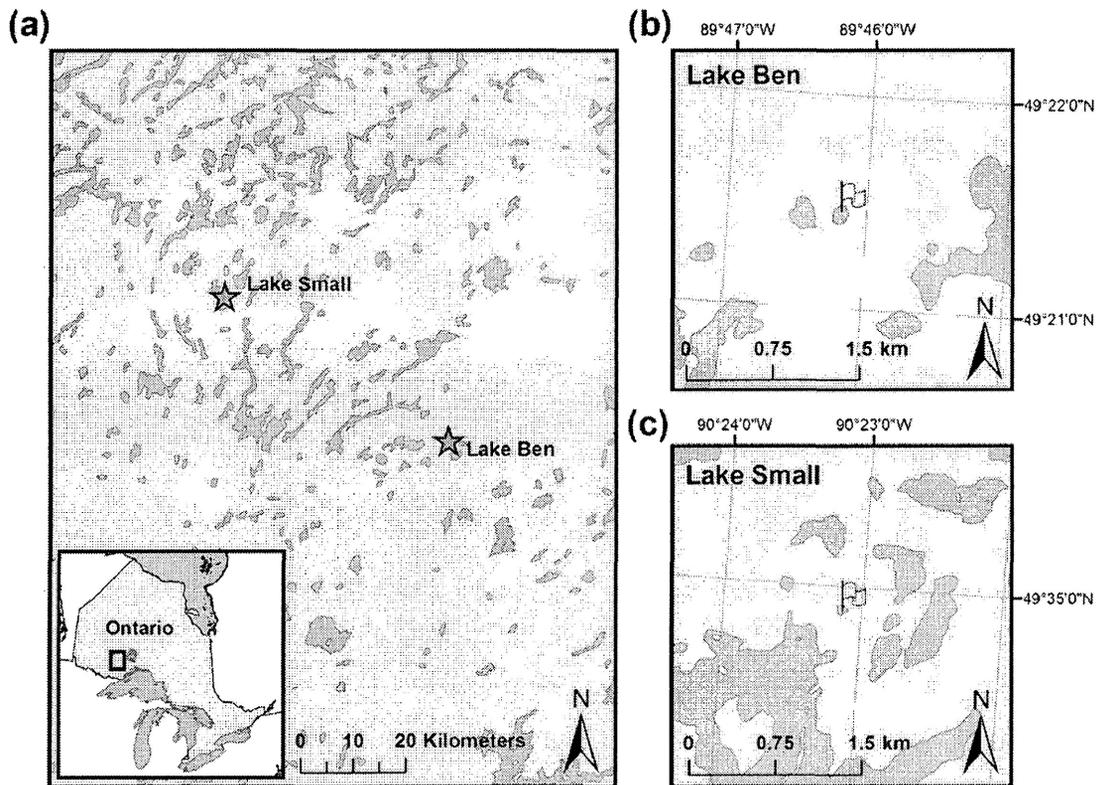
Figure 2.1 Location of the study sites in the boreal mixedwood forest.

Table 2.1 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	*Pinus banksiana, Picea mariana, Larix laricina, Betula papyrifera, Abies balsamea,*	*Picea mariana, Abies balsamea, Pinus banksiana*
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 yr^{-1})	0.0866	0.0626
Median time-resolution (yr per sample^{-1})	16	26

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 and 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.

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 *et al.* 1984). Sediment was wrapped in

polyurethane and aluminum foil for preservation and transported to the laboratory. Cores were

sliced into disks at contiguous 1-cm intervals.

Charcoal analysis

Subsamples of 1 cm^3 were taken from each disk 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 was 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 *et al.* 2004a; 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). Charcoal measurements (cumulative area per cm^3) are multiplied by the

estimated sedimentation rate based on the numerical age-depth model to obtain the charcoal

accumulation rate (CHAR, $mm^2.cm^2.yr^{-1}$).

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 *et al.*

(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 ^{14}C Accelerated Mass Spectrometry (AMS) measurements. Samples were processed by AMS in ^{14}C laboratories in Poznan, Poland (Poz-) and Miami, Florida (Beta-). The CALIB program (Reimer *et al.* 2004) was used to calibrate the ^{14}C ages to dendrochronological years using the IntCal09 (Reimer 2009) calibration curve. Ten and seven ages were obtained for Lake Ben and Lake Small respectively (Table 2.2), based on terrestrial plant macroremains and charcoal fragments. Bulk sediment was used in a single case (Beta-293636; Table 2.2) 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 *et al.* 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.

Table 2.2 Accelerator mass spectrometry ^{14}C dating of Lake Ben and Lake Small (mean ± 1 SEM)

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

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

Reconstruction of fire history

CHAR series (Supplementary Information 1 hereafter SI1) were decomposed into background ($C_{background}$), and peak (C_{peak}) 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.* (2008; 2009) and summarized below. Prior to decomposition, charcoal data were interpolated to

constant 20-yr time steps, corresponding approximately to the average of median resolution-time per sample of the 2 lakes.

Low-frequency variations in a charcoal record ($C_{background}$) which represent changes in charcoal production, sedimentation, mixing and sampling, were subtracted to obtain a residual series, C_{peak} (i.e., $C_{peak} = C_{interpolated} - C_{background}$). Consistent with theoretical evidence (Higuera et al., 2007) and previous work (e.g., Gavin et al., 2006; Higuera et al. 2008, 2009), we assume that C_{peak} is composed of two subpopulations, C_{noise}, representing variability in sediment mixing, sampling and analytical and naturally occurring noise, and C_{fire}, representing charcoal input from local fires. For each sample, we used a Gaussian mixture model to identify the C_{noise} distribution. We considered the 99th percentile of the C_{noise} distribution as a threshold to separate samples into "fire" and "non-fire" events. We estimated $C_{background}$ with a locally-weighted regression using a 900-yr window at Lake Ben and a 700-yr window at Lake Small. 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 C_{noise} 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. (2008; 2009), because this procedure is specific to charcoal count data only (Ali et al2009b). All statistical treatments for charcoal analysis were performed using the program CharAnalysis, written by Philip E. Higuera and freely available at http://charanalysis.googlepages.com.

Reconstruction of vegetation history

The plant macroremains counts (Supplementary Information 2; SI2) were transformed into influx values (#. cm^2. yr^{-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: *Betula papyrifera, Pinus banksiana, Pinus*

strobus, Picea mariana, Larix 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 if fire histories differ between the sites we examined the median fire return intervals

(mFRI) using the nonparametric two-sample Mann-Whitney test (MW-test) and the overall FRI

distributions using the nonparametric two-sample Kolmogorov-Smirnov test (KS-test) (Clark

1989; Ali *et al.* 2009a). The complete series, 10,000 – 0 cal. yr BP (BP = 1950 CE), and defined

temporal periods of 10,000 – 4500 cal. yr BP and 4500 – 0 cal. yr BP were examined and

analysed. These divisions were defined in regard to the Neoglacial climate cooling trend in

central Canada (*c.* 4500 – 1500 cal. yr BP) (Viau *et al.* 2006b) and allowed us to examine if 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. yr BP), early

Holocene (10,000 – 4500 cal. yr BP) and late Holocene (4500 cal. yr 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, *i.e.* 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.

<u>Fire and vegetation analysis</u>

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. yr 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

<u>Age-depth model</u>

The age-depth models represent 10,374 and 9975 years of sedimentation at the Lake Ben and Lake Small sites, respectively. The two age-depth models (Fig. 2.2a,b) are comparable in sedimentation rate with Lake Ben having a higher mean sedimentation rate at 0.0866 ± 0.0534 cm yr^{-1} to Lake Small's 0.0626 ± 0.0495 cm yr^{-1} (Table 2.1). Both models exhibit acceleration in the sedimentation rate between *c.* 5000 - 3500 cal. yr BP, with the maximum deposition occurring at 4310 cal. yr BP (0.0291 cm yr^{-1}) in Lake Ben and 3785 cal. yr BP (0.0333 cm yr^{-1}) in Lake Small.
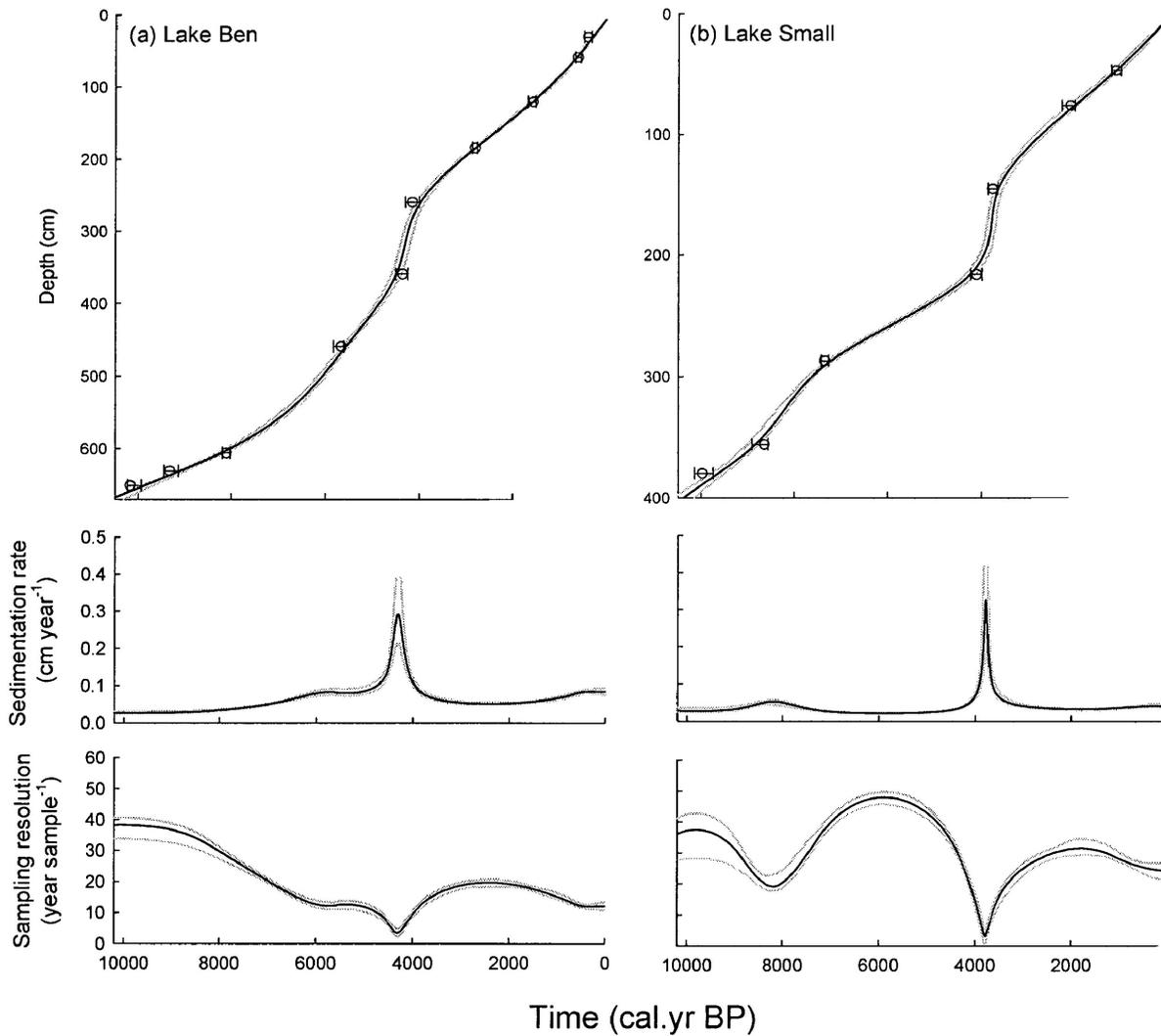
Figure 2.2 Age-depth models, sedimentation rate, and sampling resolution for Lake Ben and Lake Small. Heavy grey lines correspond to 95% CI.

Fire history reconstruction

In total, fifty two (52) fire events were identified at Lake Ben between 10,174 cal. yr BP and the present, with the first fire recorded c. 9660 cal. yr 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 ± SE) and a median FRI (mFRI) of 140 years. FRIs were shortest

between 5000 and 4000 cal. yr BP (Fig. 2.3a). FRI length was relatively stable throughout the Holocene with no major changes recorded between time periods (Fig. 2.3a and Table 2.3).

Forty three (43) fire events were identified at Lake Small between 9972 cal. yr 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 an mFRI of 170 years. FRIs at the Lake Small site are longer than those at the Lake Ben site throughout the early Holocene (Fig. 2.3a,b). FRIs decrease markedly *c.* 4500 – 4000 cal. yr BP (Fig. 2.3b); the shortest FRIs at the Lake Small site occurred between 4000 – 2000 cal. yr BP. FRIs increased between 2000 – 1000 cal. yr BP but have been decreasing from 1000 cal. yr BP to the present.

Table 2.3 Two-sample MW-test comparisons of median fire-return intervals (mFRI, mean ± 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. yr BP time period (in bold)

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

Lake Ben Lake Small

Fire return interval
(yr fire^{-1})

600
400
200
0

Macroremains influx
(re-scaled unitless)

0.4 Betula papyrifera
0.2
0.0

0.4 Pinus banksiana
0.2
0.0

0.4 Pinus strobus
0.2
0.0

0.4 Larix laricina
0.2
0.0

0.4 Picea mariana
0.2
0.0

0.4 Herbaceous
0.2
0.0

10000 8000 6000 4000 2000 0 10000 8000 6000 4000 2000 0

Time (cal.yr BP)
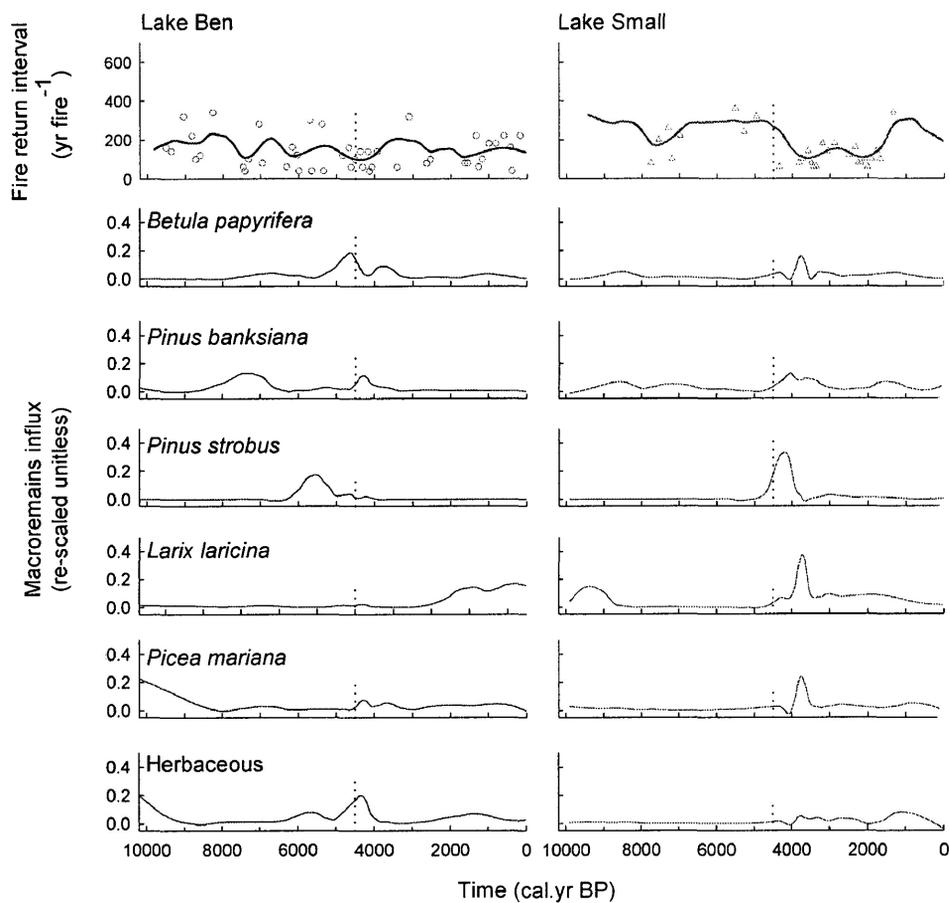
Figure 2.3 Fire events and Fire Return Intervals (FRIs) at (a) Lake Ben and (b) Lake Small. Macroremains influxes smoothed by LOESS (sampling proportion of 0.2) of dominant woody plant and herbaceous species at Lake Ben and Lake Small respectively in the time period 10,000 – 0 cal. yr BP. The vertical dotted lines indicate the onset of Neoglacial climate cooling in Central Canada (c. 4500 cal. yr BP).

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 2.3). 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. 2.4a). 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).

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 2.3). The analysis of the bivariate Ripley's K-function (Fig. 2.4b) 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 2.3), with fires events occurring independently (Fig. 2.4c). The data indicates that local factors likely overrode climatic controls of the fire regime at one (or both) of the sites in these time periods (*Scenario 2*).
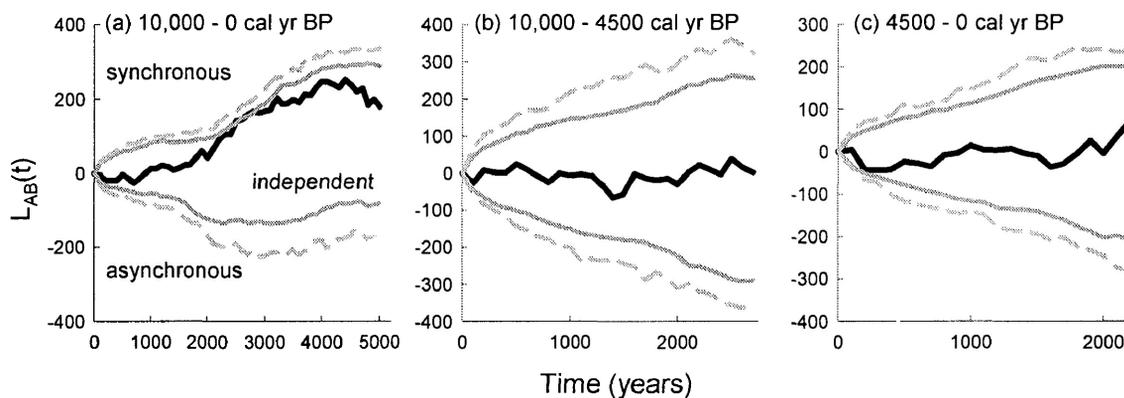
Figure 2.4 Bivariate L-function analyses performed on the fire events detected at Lake Ben and Lake Small. Analysis was performed for 3 time periods (10,000 – 0, 10,000 - 4500, and 4500 - 0). Heavy grey lines correspond to 95% CI and dashed grey lines correspond to 99% CI based on 1000 randomizations of shifting records relative to one another.

Local vegetation history

In total, 18 taxa were identified in the plant macroremains assemblages at each lake (SI2). 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. yr BP was dominated by *P. mariana* transitioning to dominance of *P. banksiana* approx. 8000 – 6500 cal. yr BP (Fig. 2.3a, SI2). The period 6000 – 4000 cal. yr 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. yr 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. 2.3b). *L. laricina* dominates the record between 10,000 – 9000. Influx of woody species increased considerably at *c.* 4000 cal. yr 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. yr 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 ($p < \pm 0.4$) strength (Fig. 2.5). At Lake Ben, *P. mariana* (Fig. 2.5g) 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. 2.5h) 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. 2.5i). At Lake Small, a strong negative correlation (ρ = - 0.4) was found for *L. laricina*

(Fig. 2.5j), 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. 2.5k) but not at Lake Small (Fig. 2.5l). 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. 2.5a,b) and *P. banksiana* (Fig. 2.5c,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).
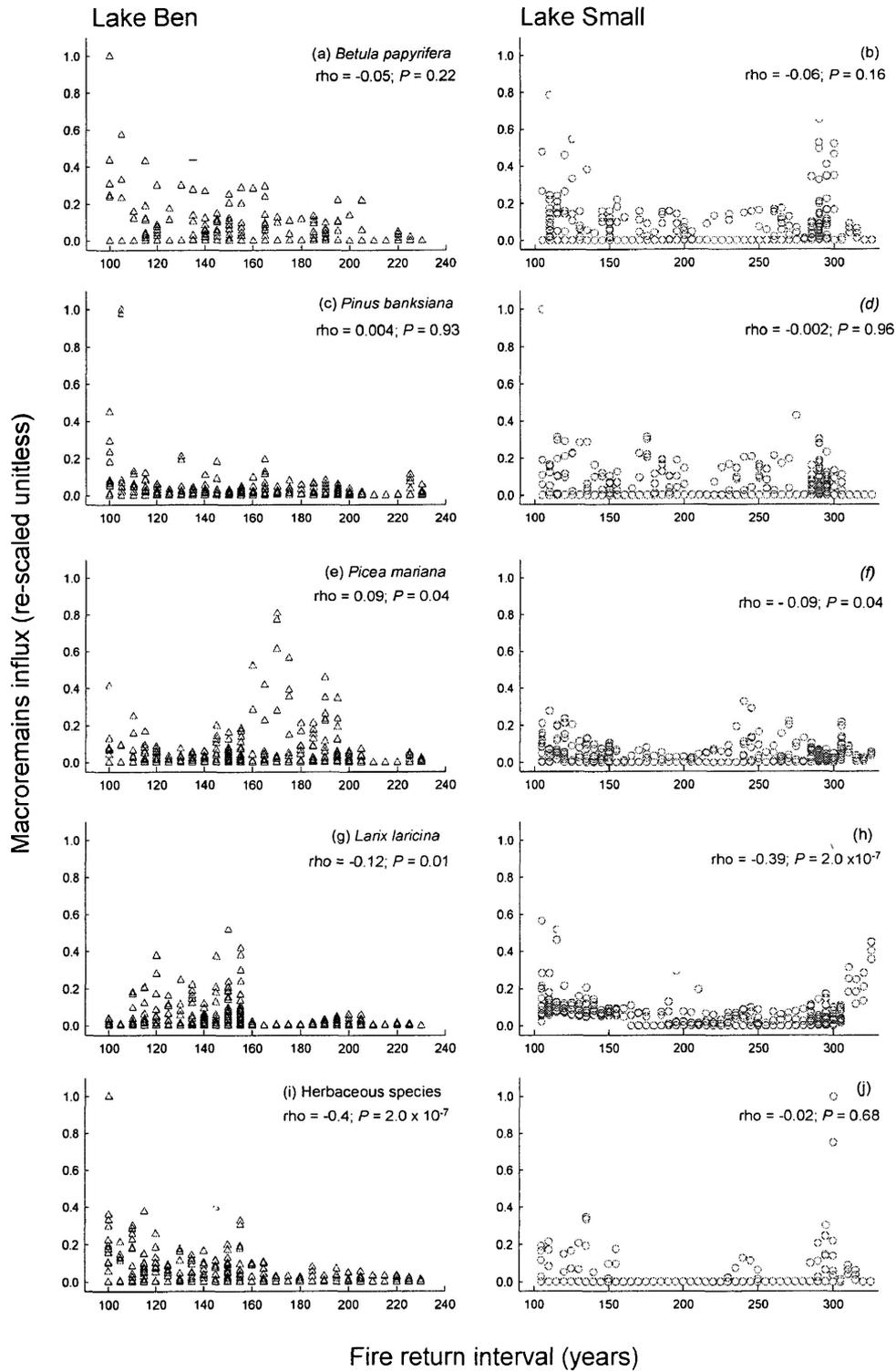
Figure 2.5 The relationship between macroremains influx and fire return interval (FRI) for Lake Ben and Lake Small. Spearman's ρ and *P*-values were calculated for dominant woody species and a grouping of herbaceous plants.

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 – 3000 cal. yr BP with conditions becoming cooler and wetter in comparison to the early Holocene (Kerwin *et al.* 2004; Viau *et al.* 2006b; Viau and Gajewski 2009). The establishment of cooler and moister environmental conditions in the late Holocene should not have been favourable for fire ignition, yet the expression of this climactic shift on fire frequency varies between sites, with FRIs at Lake Ben (Fig. 2.3a) remaining similar to those of the early Holocene and FRIs at Lake Small (Fig. 2.3b) decreasing significantly. Data from both sites are different from the increased FRIs observed in coniferous boreal forests during the late Holocene (Ali *et al.* 2009a), 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 *et al.* 1999) prior to the growth deciduous foliage (mainly *B. papyrifera*, and *P.tremuloides*). Since 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. yr 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. 2.1c); 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 paleo-record. At the Lake Ben site, surrounding waterbodies are few (Fig. 2.1b) allowing local fires to spread relatively unhindered.

The similar FRIs among sites in the late Holocene could due to be increased water-logging at the Lake Small site (Lynch *et al.* 2004b), 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* have been shown to increase boreal landscape flammability (Hallett and 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. 2.2), 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 were

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

Since 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 and

Scotter 1973; Johnston 1990). The early development of *L. laricina* at Lake Small at the

beginning of the Holocene, i.e. *c.* 10,000 cal. yr 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. 2.3, SI2) 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. Since *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 - 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 and 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.

B. 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 and 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 and Chen 2011). Similarly, *B. papyrifera* is well-adapted to post-fire regeneration (Brassard and 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 and 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 and 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 and 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 (SI2).

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 *Pinus banksiana*, *Pinus strobus* and *Betula papyrifera* can maintain their presence on xeric and mesic sites irrespective of local fire frequency. The abundance of pioneer *Larix laricina* generally increases with fire frequency, but the effect of fire frequency on the abundance of slow-growing shade-tolerant *Picea mariana* is landscape-dependent. These results underline the complexity of fire-climate-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 fire-climate-vegetation interactions in the boreal forest.

Acknowledgements

CHAPTER THREE The effects of forest fuel connectivity and drainage on spatiotemporal dynamics of Holocene fire regimes in the central boreal forest of North America.

Abstract

Understanding fire regime dynamics is central to predicting forest structure and compositional dynamics of fire driven boreal forests. Spatial and temporal variations in fire frequency in central Canadian boreal forest over the last 10k years were examined to evaluate the influence of bottom-up controls on the regional fire regime. We performed macroscopic-charcoal analysis of sediment cores from six lakes and a GIS analysis of landscape features to investigate the effects of regional non-climatic factors relevant to fire frequency. Our results revealed longer fire intervals (FI) were associated with increasing time before present and near sites with high non-fuel cover. Also there were significant interactions between time and regional environmental factors like drainage and organic terrain. Poorly connected regional landscapes had significantly higher FIs than highly connected landscapes, particularly between 10k – 4k cal a BP, suggesting that natural fuel break coverage may have limited fire spread. Increased fire activity over time among poorly connected sites may be related to climatic changes facilitating increased forest connectivity via the expansion of organic terrain and associated *Picea mariana*. Results clarify some fire regime controls and imply that climate changes will interact with environmental factors to affect future boreal fire regimes.

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 changes. The influence of fire intervals (FI) and 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 frequency for ecosystems and resource management (Littell *et al.* 2009; Westerling *et al.* 2011; Girardin *et al.* 2013b).

Variations in natural fire regimes are generated by both the stochastic nature of fire and complex interactions among environmental factors such as weather, fuels, ignition pattern and topography (Van Wagner 1987; Bowman *et al.* 2009; Parisien *et al.* 2011; Ali *et al.* 2012). In the North American boreal forest, fire-environment relationships differ among regions, indicating that factors controlling fire regimes vary throughout the biome (Flannigan *et al.* 2005; Fauria and Johnson 2008; Parisien *et al.* 2011); moreover, the relative influence of these factors varies, because top-down (e.g., climate) and bottom-up (e.g., connectivity) controls on fire ignition and spread change, depending on the temporal and spatial scales examined (Gavin *et al.* 2003; Parisien *et al.* 2011).

Climate is the principal control of fire (Johnson 1992; Payette 1992) and influences fire at a broad scale (Fauria and Johnson 2008) by creating a latitudinal gradient in the severity of fire weather conditions, influencing 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 of time known as the Holocene, the warmest portion of which in boreal North America,

the Holocene Climatic Optimum (HCO), prevailed from about 9k to 5k a BP. Afterward, climate

cooled and precipitation increased as the region experienced a Neoglacial period (*c.* 4.5k – 2.5k a

BP). Several paleofire studies (Ali *et al.* 2009a; Kelly *et al.* 2013; Senici *et al.* 2013) from the

North American boreal forest indicate significant fire frequency changes concurrent to

Neoglacial cooling, the direction and magnitude of such changes are variable between boreal

regions. Fire frequency decreased in some eastern coniferous boreal forests (Ali *et al.* 2009a;

Hely *et al.* 2010) due to a 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). The

variable fire frequency responses across the boreal region suggest interactions with bottom-up

controls that may influence future fire regime variation to climatic changes.

Environmental factors operating at regional-to-local scales like forest connectivity,

surficial deposits and drainage (Cyr *et al.* 2007; Mansuy *et al.* 2010) are increasingly recognized

in paleofire research as important drivers of temporal and spatial variation in millennial-scale

wildfire activity (Ali *et al.* 2009a; Genries *et al.* 2012; Barrett *et al.* 2013; Senici *et al.* 2013).

However, local environmental factors are numerous and variable and interact with climate

making their effects on fire regimes difficult to partition. For instance, fire size is influenced by

forest connectivity through a function of fuel loads, fuel-bed bulk density and fuel moisture

(Miller and Urban 1999, 2000). Dendrochronological approaches to understanding modern fire

regime spatial variation confirm that lakes, watercourses and wetlands can disrupt fuel continuity

and thereby inhibit fire spread and final size (Larsen 1997; Hellberg *et al.* 2004; Cyr *et al.* 2005;

Senici *et al.* 2010). 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. The relative influences of local environmental controls on North American boreal fire regimes may change over timescales longer than existing observational records ($20^{th} - 21^{st}$ centuries), thereby obfuscating the long-term relationships between drivers and fire regimes. In the North American boreal forest where detailed fire records prior to the early 1970s are incomplete, a paleoecological approach to fire history reconstruction can reveal changes in fire activity occurring at centennial-millennial timescales (Gavin *et al.* 2003) and clarify some long-term fire-environment relationships. We intend to use paleofire reconstructions to explore the influence of environmental factors specifically landscape connectivity, organic terrain and drainage type on regional fire regimes. Understanding the roles of climatic and non-climatic factors in influencing fire frequency is a basic issue for forecasting how fire regimes might change in response to global warming.

We examined spatial and temporal variations in fire interval for a mixedwood boreal forest in central Canada (Northwestern Ontario) over the last 10,000 years. This region is well suited for exploring the effects of connectivity and surficial geology because of the highly variable distribution of water bodies, surficial deposits and drainage at the landscape scale and relatively homogenous elevation, slope and aspect. Fire histories were reconstructed using high-resolution macroscopic charcoal records obtained from six lakes separated by distances of less than 80 km. Spatial analysis of landscape features was performed to examine local environmental controls on regional FIs. Given the relative proximity among sites, we hypothesize that if climate is the main factor controlling regional fire frequency comparable fire histories should exist among all sites. Because forest fuel connectivity is a strong predictor of regional fire frequency (Miller and Urban 2000; Peters *et al.* 2004), our main hypothesis predicts

that poorly connected landscapes as inferred through high modern non-forest cover in the form

of open-water and wetlands will have longer FIs throughout the Holocene. We expect that dry

surficial deposit drainage (SDD) could promote conditions favourable to drying of soils, fuels

and vegetation, thereby resulting in shorter FIs where dry SDD comprise large portions of the

regional landscapes. Finally, we expect the influence of local environmental controls on FIs to

decrease in response to shifting landscape cover following deglaciation and ongoing climatic

changes.

Materials and methods

<u>Study area</u>

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; 478), in the boreal forest of Northwestern Ontario, Canada (Fig. 3.1). The regional

climate is humid continental, with short and warm summers and long and cold winters. The lakes

(Table 3.1) 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 700-800 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 broadleaf 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. Broad-leaved trees

include *Betula papyrifera* Marsh. and *Populus tremuloides* Michx. These trees tend to be

successional, forming pure stands of variable extent following disturbance contingent on pre-

disturbance forest cover and substrate ecophysiological characteristics (Brassard and Chen 2006;

Taylor and Chen 2011).
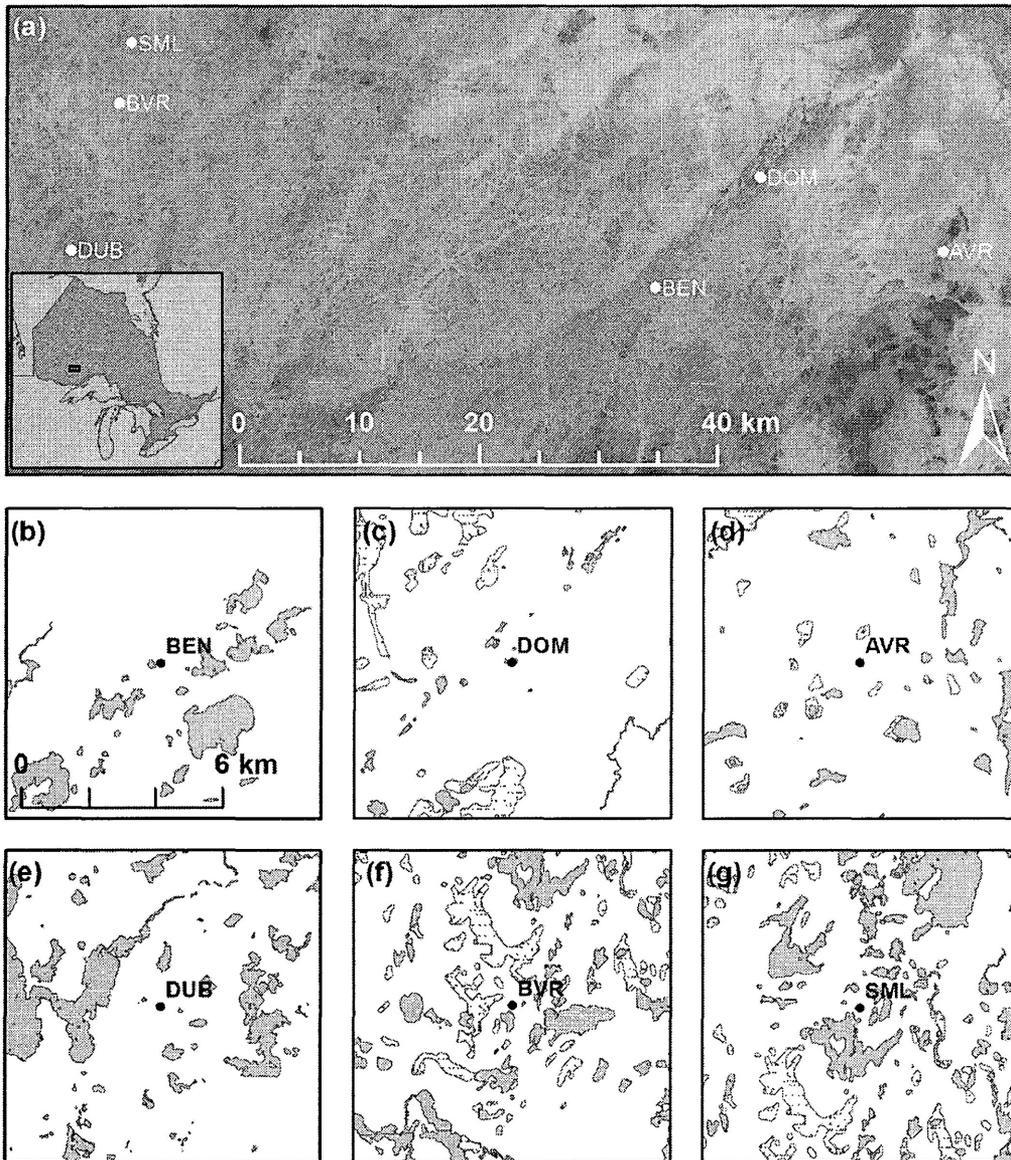
Figure 3.1 Study region. (a) The six study sites (white dots) in the central boreal forest of Northwestern Ontario, Canada. Inset is a map of Ontario highlighting the location of the sites. Blue polygons are open water and symbol polygons are wetlands surrounding the sites, (b) Lake Ben (BEN), (c) Lake Dom (DOM), (d) Lake Avril (AVR), (e) Lake DuBerger (DUB), (f) Lake Beaver (BVR), and (g) Lake Small (SML).

Table 3.1 Characteristics of the study lakes, surrounding landscapes within a 5 km radius, and charcoal records in the central boreal forest of Northwestern Ontario, Canada

Characteristics	Study site					
	Avril (AVR)	Ben (BEN)	Dom (DOM)	Beaver (BVR)	DuBerger (DUB)	Small (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 (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 (%)	85.6	60.8	62.1	71.1	76.1	72.2
Wet (%)	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 (degrees)	142 ± 120	114 ± 124	150 ± 112	118 ± 121	84 ± 110	110 ± 119
Sediment records						
Core length (cm)	480	660	460	375	415	390
Sedimentation rate (cm/yr, 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 (yr/sample, mean ± SD)	21 ± 7	16 ± 9	23 ± 9	31 ± 14	25 ± 10	26 ± 12
Median signal-to-noise index	5.1	8.7	7.5	4.9	4.9	5.9

Sites were chosen on two criteria. First, to evaluate the potential effects of various geophysical characteristics on fire activity, preliminary regional topographic mapping and onsite evaluation was required to provide qualitative evidence that an equal number of sites would be located in two distinct regional landscapes. Second, lakes needed to have small surface area (< 5

ha), deep water depths (> 3 m) and lack inflowing or outflowing streams to optimize local fire

reconstruction with undisturbed sediment deposits.

Sampling

Sediment sequences were extracted from the deepest point in each lake in the form of 1 m

overlapping cores using a modified Livingstone piston corer (Wright *et al.* 1984). A Kajak-

Brinkhurst (KB) 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 Accelerated Mass Spectrometry (AMS)

measurements performed on plant macroremains and bulk organic sediment when macroremains

were not abundant enough for AMS measurements (Supporting Information (SI): 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 2009) calibration curve. Age-

depth models were created with a weighted cubic smoothing spline 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 stereo microscope using an attached digital camera connected to WinSeedle (Regent Instruments Incorporated, Quebec). Charcoal concentrations (cumulative area/cm^3) were multiplied by the estimated sedimentation rates (cm/yr) estimated from our age-depth models to obtain charcoal accumulation rates (CHAR, mm^2.cm^{-2}.yr^{-1}).

Fire events at each lake were identified through peak analysis of its sedimentary charcoal record using CharAnalysis 1.1(Higuera 2009), available online at http://charanalysis.googlepages.com. To account for uneven sampling intervals resulting from variable sediment accumulation rates among sites, prior to decomposition, all charcoal data were interpolated to a temporal resolution of 25 years/sample, corresponding to the approximate median sample resolution (23.5) of the six records (Table 3.1). 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 C_{back} with a locally-weighted regression using a 1000-year moving median applied to the raw charcoal series. C_{back} were subtracted to obtain a residual series, C_{peak}. We assume that C_{peak} is composed of two subpopulations, C_{noise}, representing variability in sediment mixing, sampling and analytical and naturally occurring noise, and C_{fire}, representing charcoal input from local fire events (Higuera *et al.* 2010). C_{fire} and C_{noise} 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 C_{noise} 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 C_{noise} distributions (KS-test, P-value > 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).

Fire intervals (FIs) were calculated as the number of years between two consecutive fire events. Median FIs occurring during the HCO (9k – 5k cal a BP, hereafter referred to as early-Holocene) and during the Neoglacial and modern period (5k – 0 cal a BP, late-Holocene) between highly and poorly connected sites were calculated. To test whether fires occurred synchronously (± 100 years) between highly and poorly connected sites in these time periods, we used the L function, a modified version of Ripley's K-function in the program K1D (Gavin 2010).

Landscape analysis

We analysed landscapes at spatial scales larger than local fire event detection inferred from charcoal peaks (~1-3 km radius) to evaluate the potential importance of regional-to-local non-climatic environmental factors on fire spread and occurrence. We characterized the local environment at 3 – 5 km radiuses around each lake using ESRI's ArcMap version 10.1 (ESRI 2012). We present the 5 km results (Table 3.1). Surficial deposit, open-water and wetland cover were calculated using data from Digital Northern Ontario Engineering Geology Terrain Study (Ontario Geological Survey 2005) and CanVec (Natural Resources Canada 2013). Surficial deposits were classified as glaciofluvial, encompassing outwash, delta and esker, morainal, which included ground moraine and mixed terrain, and organic terrain. In this paper we make a distinction between wetlands and peatlands; wetlands include riparian fen or bog dominated by graminoid non-woody vegetation, marshes and shallow water wetlands (< 2 m deep); peatlands

encompass terrain where organic substrate > 40 cm, drainage is poor, and dominant vegetation is *Picea mariana* and *Larix laricina*. Wetland and peatland type and extent were verified on site using the Canadian Wetland Classification System (National Wetlands Working Group 1997). Regional SDD was classified into wet and dry. Total modern non-fuel cover (open water + wetlands) representing a minimum value for regional landscape connectivity was calculated and used to categorize each site as highly or poorly connected. Additionally, total organic terrain (wetlands + peatlands) was calculated, representing maximum landscape cover by organic material and associated coniferous vegetation. Area calculations were converted to percent cover. Elevation, slope and aspect were calculated using a 8 – 23-m resolution digital elevation model (Natural Resources Canada 2007).

Statistical analysis

We used generalized linear mixed effect models (GLMM) in the package *arm* (Gelman *et al.* 2013) in the statistics program R (R Development Core Team2013) to model both fixed-effects and random effects. Since some time is measured on a very different scale than our geophysical predictors, all independent variables were standardized prior to analysis. All models used lake (site) as a random variable to account for variance derived from the hierarchical levels in the data. To examine temporal and connectivity controls on fire frequency we examined three scenarios. In Scenario 1, modern wetland cover is considered an impediment to fire spread, similar to open-water; correspondingly in Model 1, we considered the effects of time and modern non-fuel cover on FIs.

(3-1)

$$FI_{ijk} = \mu + T_i + NF_j + T \times NF_{ij} + \pi_k$$

Where FI_{ijkl} is FI (years); T_i is time (cal a BP), NF_j is non-fuel cover in percentage; π_k is random

effect of sampling lake.

Given that wetland abundance and composition likely changed through time and may not

have been an impediment to burning we developed additional scenarios. In Model 2 – we

examine the effects of modern open-water and wetlands separately, where open-water is a more

conservative estimate of landscape connectivity and wetlands are treated as potential fuel. In

Model 3 – we examine the effects of modern open-water and total organic terrain, total organic

terrain represents a maximum value for regional peat and associated vegetation.

(3-2)

$$FI_{ijkl} = \mu + T_i + OW_j + W_k + T \times OW_{ij} + T \times W_{ik} + \pi_l$$

Where FI_{ijkl} is FI (years); T_i is time (cal a BP), OW_j is modern open-water cover in percentage;

W_k is modern wetland cover (%) in Model 2 and total organic terrain (%) in Model 3; π_l is

random effect of sampling lake.

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. To avoid multicollinearity among predictors (Graham 2003), we investigated the

correlation matrix of environmental factors (SI; Table S2). Variables were omitted from full

models in favour of our initial model variables when bivariate correlations exceeded $|r_{spearman}| > \pm$

0.50. In Model 1, we added main effects and interaction terms of peatlands and dry SDD. In

Model 2, we added dry SDD and the interaction term with time. No additional variables were

added to Model 3. Model goodness of fit was assessed by R^2, calculated using the methodology

presented in Nakagawa & 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.

Fire reconstructions from lake sediments are strongly influenced by user choices during statistical treatment (Blarquez *et al.* 2013; Brossier *et al.* 2014), consequently CHAR records were analysed using 20 and 30 year sample resolutions and Models 1 – 3 were analysed to assess GLMM robustness using FIs from the median (25 year) sample resolution reconstruction.

Results

<u>Dating and age-depth models</u>

The age-depth models represent 10,004 at AVR, 11,700 at BVR, 10,212 at BEN, 10,299 at DOM, 10,108 at DUB and 10,007 at SML years of sedimentation. The models (Fig. 3.2) are comparable in sedimentation rate, with BEN having the highest mean sedimentation rate at 0.0866 ± 0.0534 cm yr^{-1} and BVR having the lowest at 0.0468 ± 0.0495 cm yr^{-1} (Table 3.1). Models for BEN, BVR and SML exhibit acceleration in the sedimentation rate between *c.* 5k – 3.5k cal a BP.
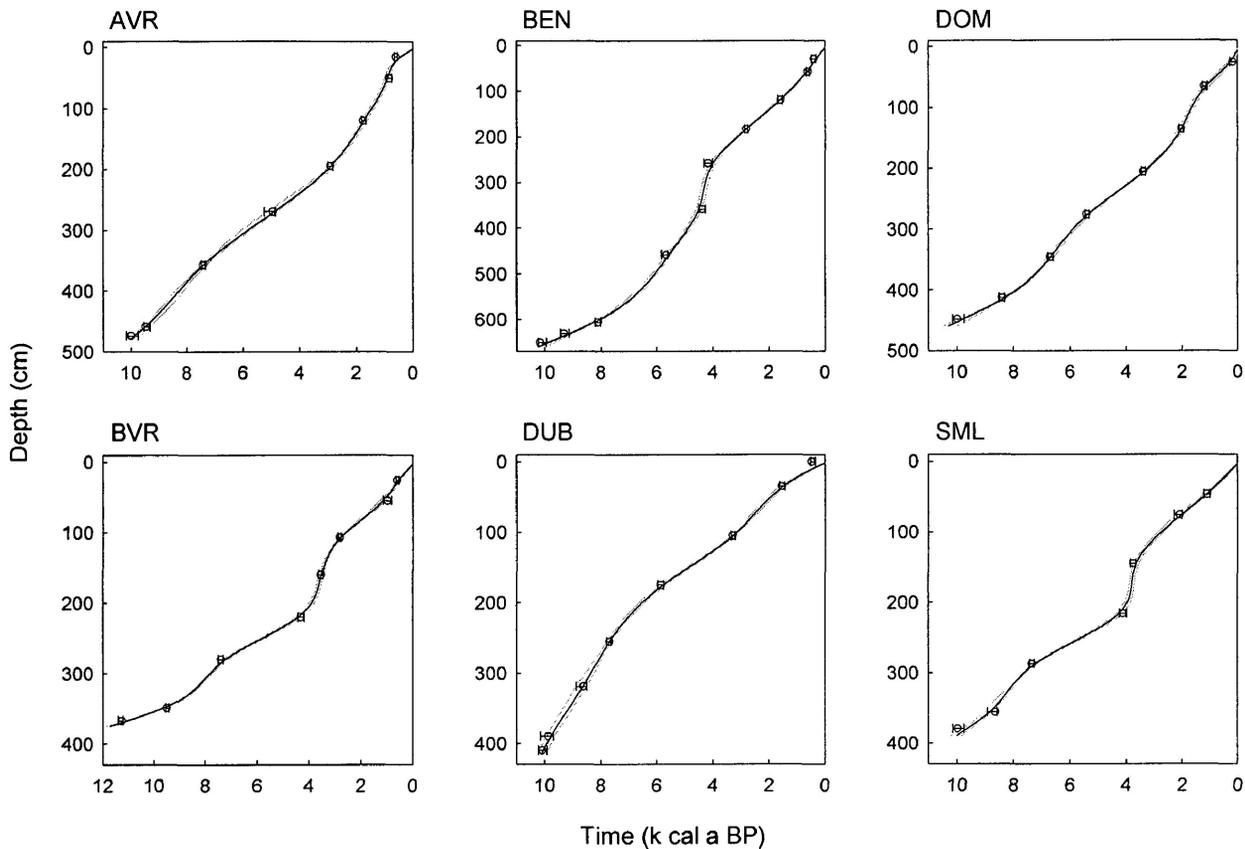
Figure 3.2 Age-depth models for sediment cores from the six lakes calculated using a cubic spline. Hollow circles are ^{14}C ages, and error bars represent estimated 95% confidence intervals based on 1000 bootstrapped samples of the calibrated dates. Ages are expressed in 1k years BP.

Charcoal analysis and fire history reconstruction

Global SNI values for all charcoal records are high (median SNI > 3.0) (Fig. 3.3d,e,f,m,n,o) and show a clear separation between background charcoal and fire event signals indicating that these records are suitable for fire history reconstructions using peak analysis (Kelly *et al.* 2011). There are two instances where SNI < 3.0 exist at BVR between *c.* 10.5k and 10k cal a BP (Fig 3m) and DUB between *c.* 8.4k – 8.2k cal a BP, however, overall median SNIs are high (BVR = 4.7 and DUB = 4.3), and the period of low SNI is short (< 300 years), consequently we felt safe to include these sites in subsequent analyses.

In total, 50 fires were detected at AVR, 46 at BEN, 47 at DOM, 39 at BVR, 39 at DUB and 36 at SML, (Figs. 3g,h,i,p,q,r). FI reconstructions (raw FIs interpolated to annual values and smoothed with LOESS) indicate that fires were most frequent late-Holocene among all sites save DOM. Among highly connected sites, fires recur at relatively consistent intervals throughout the reconstruction; fires occur most frequently between *c.* 10k and 9k cal a BP at AVR, between *c.* 6k and 4k cal a BP at BEN and between *c.* 8k – 6k cal a BP at DOM. Among poorly connected sites, fire occurrence was somewhat irregular following deglaciation but increased with time; fires were most frequent *c.* 4k cal a BP at BVR and DUB, and between *c.* 4k and 2k cal a BP at SML.
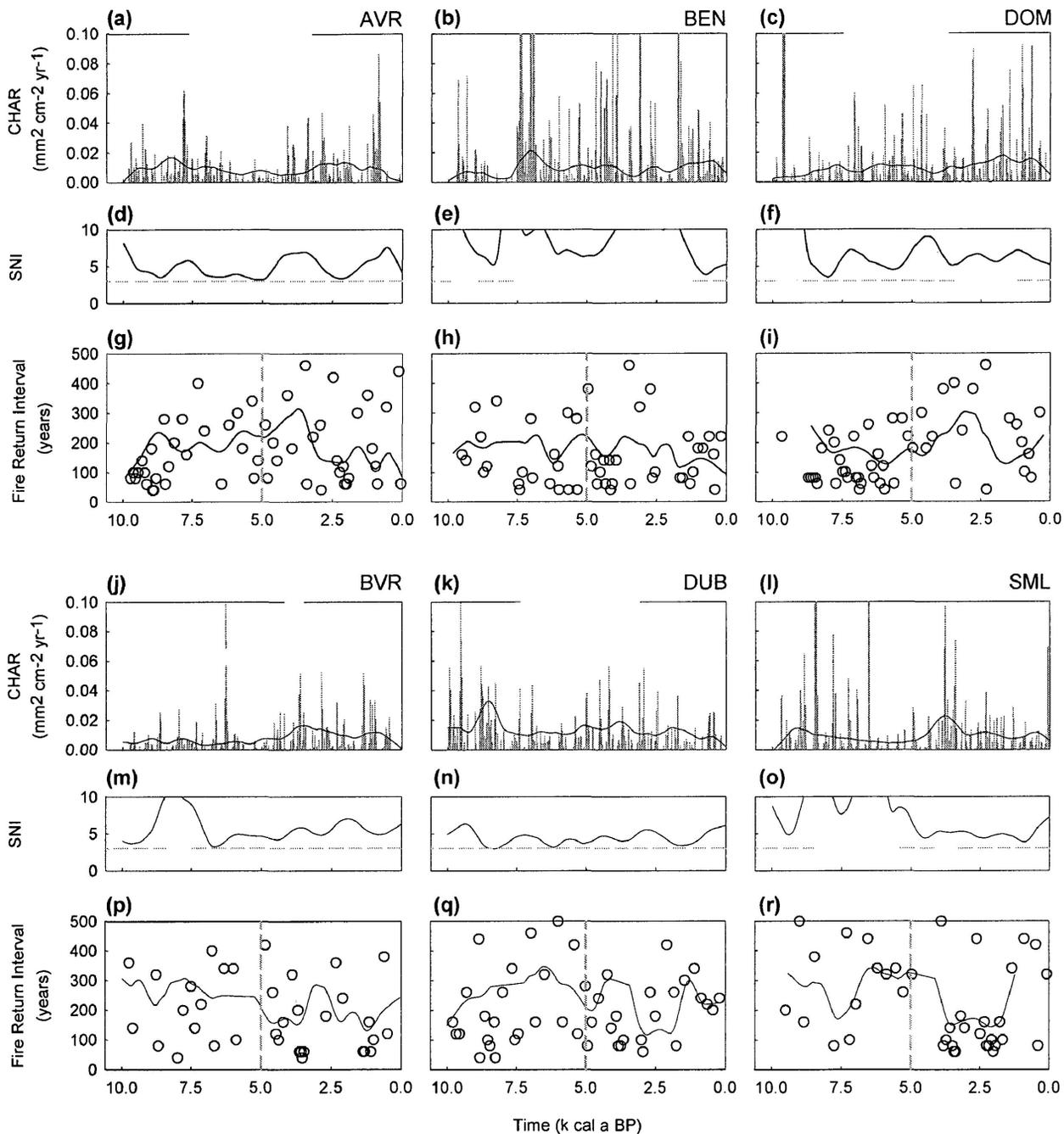
Figure 3.3 Sediment-charcoal records over time for AVR (a, d, g), BEN (b, e, h), DOM (c, f, i), BVR (j, m, p), DUB (k, n, q), and SML (l, o, r). (a-c, j-l) Charcoal accumulation rates plotted against time. Vertical gray lines are the interpolated CHAR peaks, the heavy black line represents background values and the light gray dashed line indicates the threshold used to identify potential fires. (d-f, m-o) Signal-to-noise index plotted against time. The dashed gray line indicates the threshold (SNI = 3) used to evaluate the suitability of the charcoal record for peak detection. (g-i, p-r) Smoothed fire return intervals (FRIs) plotted against time. Circles represent fire events and the corresponding fire interval.

Median FIs (mFI) were longer among poorly connected sites throughout the Holocene (Table 3.2); differences were especially pronounced in the early-Holocene where mFI variations between highly and poorly connected sites was > 100 years. Fire occurrence was predominantly independent among highly connected sites (Fig.3.4c, d), with limited temporal synchrony between 1000 – 1100 year window widths in the early-Holocene and 800 – 1000 year window widths in the late-Holocene. Among poorly connected sites fires occurred independently throughout the early-Holocene (Fig.3.4a), but were mostly synchronous throughout multiple window widths during the late-Holocene (Fig.3.4b).

Table 3.2 Median fire intervals (years) in the early (10k – 5k cal a BP), late (5k – 0 cal a BP) and complete (10k – 0 cal a BP) Holocene time periods among highly and poorly connected sites using three fire history reconstructions at different temporal sample resolutions.

	Poorly connected		Highly connected		Complete sequence	
	Early	Late	Early	Late	Poorly	Highly
FI (years)	300 ± 52	175 ± 45	200 ± 39	150 ± 38	225 ± 32	175 ± 29
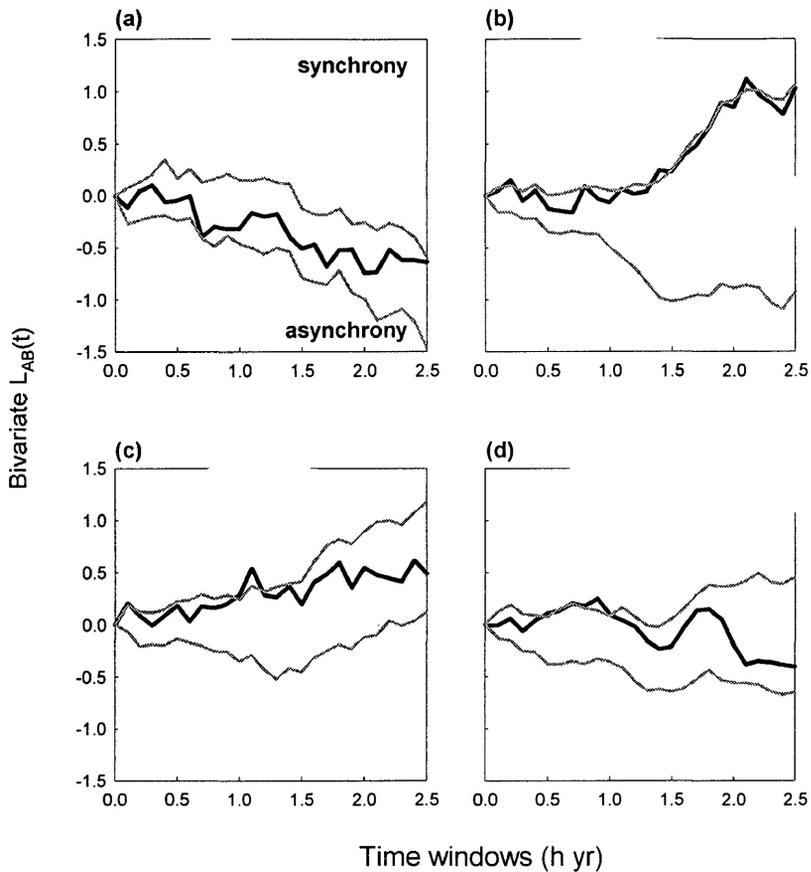
Figure 3.4 Synchrony analysis of fire occurrence between poorly connected (a, b) and highly connected (c, d) sites in the early (a, c) or late (b, d) Holocene time periods. In each plot, fire event synchrony is assessed by comparing the bivariate L function (black line) to a bootstrapped 95% confidence envelope (gray lines). Fire occurrence within a specified time window is considered significantly synchronous if the L function exceeds the upper CI, asynchronous if the L function exceeds the lower CI, or occurring independently if no CIs are exceeded.

Landscape analysis

The spatial distributions of land cover surrounding the six lakes are dissimilar between highly

and poorly connected sites (Table 3.1). 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 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 3.1), however this area is a heterogeneous

mixture of peat, sand and gravel in glaciofluvial outwash with a subordinate landforms of till and sand in ground moraine with overall dry SDD; accordingly this area was not considered a peatland nor was it pooled in total organic terrain at this site. Elevation, slope and aspect were relatively homogenous among all sites.

<u>Temporal and spatial effects on fire interval</u>

We present results from the median resolution fire reconstruction as there were no significant differences among different temporal resolutions (SI: Table S3). In all three GLMMs longer FIs are associated with increasing time into the past, indicating an overall increase in fire frequency following deglaciation to present (Table 3.3; Fig.3.5a). In Model 1, FIs were longer near sites with higher modern non-fuel cover (Fig.3.5b, c), and FIs were longer near sites with high non-fuel cover and increasing time BP (Fig.3.5b). The main effect of peatlands and dry drainage were not significantly related to FIs, however their interactive terms with time were significant; FIs were longer near sites with high peatland cover and increasing time BP, and FIs were shorter near sites with high dry drainage and increasing time BP. For Model 1 the marginal R^2 was 0.82 and the conditional R^2 was 0.86. In Model 2, longer FIs were found near sites with higher coverages of both open-water and wetlands (Fig.3.5c). The interactive terms between time and these variables were both significant but differ in magnitude, with longer FIs near sites with high open-water and wetlands and increasing time BP. The effect of dry drainage was not significant; the interactive term with time was significant with lower FIs associated with increasing landscape dryness and time BP. For Model 2 the marginal R^2 was 0.84 and the conditional R^2 was 0.86. In Model 3, longer FIs are associated with high open-water coverage; the open-water effect also increased with time BP. Total organic material was not found to significantly influence FIs; the interactive term with time was significant, indicating that longer FIs occurred

in the early-Holocene near sites with high organic landscape cover. For Model 3 the marginal R^2 was 0.70 and the conditional R^2 was 0.85.
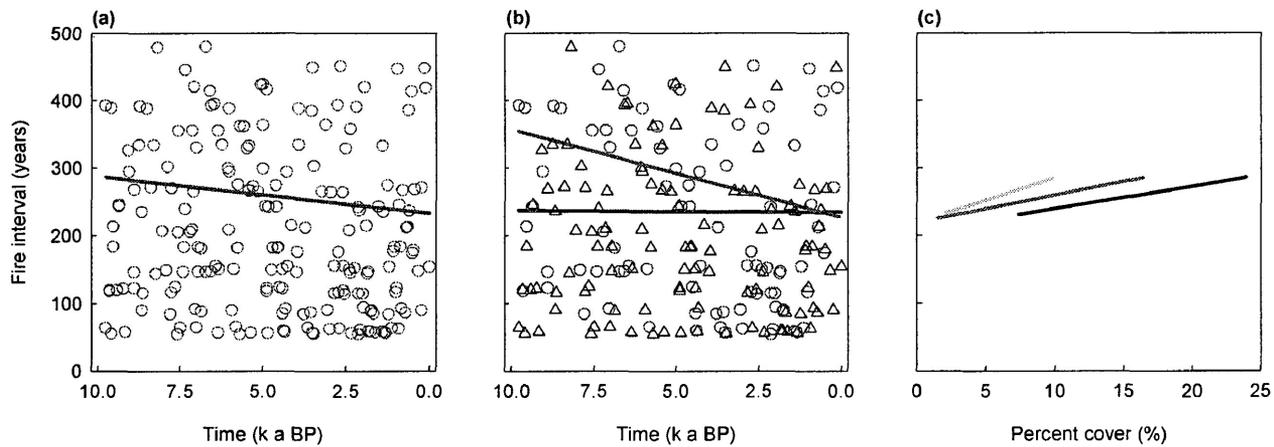
Figure 3.5 Scatterplots and fitted fire intervals (FI) of significant fixed effects from generalized linear mixed models. (a) Time, (b) interactive effect of modern connectivity and time, and (c) modern non-fuel cover, open-water cover and wetland cover. For illustrative purposes we present simple linear regression lines. In (b) blue triangles and regression line represents highly connected sites (AVR, BEN and DOM) while red circles and regression line represents poorly connected sites (BVR, DUB and SML).In (c) the black regression line represents modern non-fuel cover, the medium grey line represents open-water cover and the light grey represents wetland cover.

Table 3.3 Parameter estimates and standard error of the fixed effects from generalized linear mixed models with fire intervals as dependent variable (Poisson distribution; log-link).

Model	Term	Estimate	SE	*p-value*
Model 1	(Intercept)	5.450	0.015	< 0.001
	Time	0.075	0.004	< 0.001
	Non-fuel	0.119	0.015	< 0.001
	Peatlands	-0.012	0.015	0.407
	Dry SDD	-0.007	0.016	0.673
	Time × Non-fuel	0.013	0.004	0.001
	Time × Peatlands	0.016	0.004	< 0.001
	Time × Dry SDD	-0.057	0.004	< 0.001
Model 2	(Intercept)	5.450	0.010	< 0.001
	Time	0.075	0.004	< 0.001
	Open-water	0.069	0.012	< 0.001
	Wetlands	0.075	0.012	< 0.001
	Dry SDD	0.008	0.012	0.471
	Time × Open-water	0.014	0.005	0.006
	Time × Wetlands	0.036	0.005	< 0.001
	Time × Dry SDD	-0.051	0.005	< 0.001
Model 3	(Intercept)	5.453	0.028	< 0.001
	Time	0.076	0.004	< 0.001
	Open-water	0.113	0.036	0.002
	Total organic	0.014	0.037	0.705
	Time × Open-water	0.041	0.005	< 0.001
	Time × Total organic	0.074	0.005	< 0.001

Discussion

Our results suggest regional patterns of fire frequency observed throughout the Holocene in the central boreal forest were controlled by a complex combination of local environmental factors and regional climate. Overall, FIs have decreased over time, indicating that regional fire activity has increased from deglaciation to the present. Fire intervals were significantly shorter in the early-Holocene near sites with high percent cover of dry SDD and longer FIs tend to occur near sites where landscapes have abundant non-fuel cover in the form of open-water lakes and treeless

wetlands, indicating that the long-term influence of climatic changes on central boreal forest fire regimes may differ by drainage and connectivity. Additionally, organic terrain cover in the modern form of treed peatlands with wet drainage was significantly associated with longer FIs with increasing time BP. The temporal changes in FIs associated with these environmental factors support the idea that top-down controls, like climate, strongly influenced regional centennial-millennial scale fire frequency dynamics with bottom-up controls affecting fire ignition and spread thereby generating variable FI distributions.

The observed differences in FIs between poorly and highly connected landscapes may be a consequence of forest fuel continuity on fire behavior, since heat transfer is reduced by fuel discontinuity, fire spread was diminished amongst landscapes with large fuel gaps. Among sites considered poorly connected where regional landscapes are fragmented by large areas of open-water and wetland cover, FIs decrease from deglaciation to present. During the HCO of the early-Holocene when it was significantly warmer than it is today, mFIs were approximately 42% longer (Table 3.2) than those of the last 5k years; even though the regional climate was favorable for burning, fires ignition and spread may have been limited by a lack of burnable materials. Similar mFIs and synchronous fire occurrence among poorly connected landscapes in the Neoglacial and modern period of the late-Holocene indicate that large-scale processes, likely climate and biome transformations were the main factors determining fire frequency, and the effect of natural fuel breaks were diminished. These results contrast those of highly connected forests where mFIs did not change significantly with time nor were fire events significantly synchronous over multiple temporal windows. These observations complicate our expectation of generally increasing fire activity because the increase was driven primarily by poorly connected

sites. The non-uniform fire frequency response suggest that in addition to non-fuel cover other ecological mechanisms and climatic interactions contributed to the observed FI variations.

Similar mFIs in the late-Holocene amongst all sites may be explained by Neoglacial climate cooling; cooler temperatures and increased precipitation directly influence soil hydrology, creating environmental conditions unfavorable for fire ignition and spread, but also conditions favorable for the growth and development of highly flammable coniferous vegetation. Throughout the Neoglacial period *Picea mariana* expanded in eastern mixedwood boreal forests (Carcaillet *et al.* 2001; Carcaillet *et al.* 2010; Genries *et al.* 2012), and in boreal forest of Alaska (Lynch *et al.* 2002; Higuera *et al.* 2009; Kelly *et al.* 2013). In central boreal forest where the fire regime is characterized by few very large fires occurring under specific weather conditions, regional landscapes could have become highly flammable during intermittent dry periods resulting in very large and severe fires able to overcome natural fuel breaks which may account for the significantly decreased FIs and synchronous fire event occurrence among poorly connected sites in this time period. One plausible explanation for why FIs did not significantly change in the early-Holocene among highly connected sites, is that the high-severity fires also promoted increased broadleaved growth (Chen *et al.* 2009; Kelly *et al.* 2013). Deciduous pioneers like *Betula papyrifera* and *Populus tremuloides*, may have increased post-fire recruitment in the late-Holocene on dry SDD where increased soil moistures may have be unfavorable for *Pinus banksiana* (Rudolph and Laidly 1990), thereby producing a negative feedback to increased regional burning (Beck *et al.* 2011; Johnstone *et al.* 2011; Girardin *et al.* 2013a). These interpretations are partially supported by local plant macrofossil data (Senici *et al.* 2013), where decreasing local *Pinus banksiana* and increasing local *Betula papyrifera* and *Picea*

mariana abundance were found after *c.* 4.5k cal a-BP at BEN (highly connected), and *Picea*

mariana abundance was continuous c.4.5k cal a BP at SML.

Shorter FIs in the early-Holocene tended to occur where dry surficial deposit drainage

was high. Regional dry SDD highlights the effects of moisture on fuels and as a result, the

potential to ignite and propagate fire. Although, it is likely dry SDD was responsible for shorter

FIs due to ecological effects on soil moisture because of the length of time these trends persist, it

is possible that dry SDD cover may indicate differences in the time required for regional

landscapes to become suitable for forest vegetation and subsequent fire occurrence due to

different temporal and spatial patterns of the retreating Laurentide Ice Sheet among sites. The

earliest recorded post-glacial fires and shortest first fire intervals occur at DUB and AVR where

dry SDD is the highest and Latitude are among the lowest indicating these sites may have had a

head start in regional vegetation development. Alternately, shorter FIs in the early-Holocene

associated with high dry SDD may be a reflection of the post-glacial landscape, where a greater

proportion of terrestrial area influenced the biomass available for burning and subsequently fire

event detection as inferred through charcoal peaks. Although surficial deposit and drainage

compositions can be a main controlling factor of fire regimes when climate seems less conducive

to fire (i.e. the Neoglacial period) (Mansuy *et al.* 2010), we found no such changes in fire

activity amongst our sites in the late-Holocene. This may be because differences in SDD only

become significant under certain climatic conditions, like when the level of moisture is limiting

to plant growth on specific substrates (Brubaker 1975). It is also possible that SDD combinations

captured in our landscape analysis of our study area were not diverse enough to generate regional

fire frequency variations.

In comparison with lakes, wetlands are highly dynamic fuel breaks since hydrology and vegetation varies over time scales much shorter than that of a paleoecological reconstruction, thus complicating our understanding of their potential for stopping fires (Hellberg *et al.* 2004). We sought to mitigate this uncertainty by categorizing organic terrain into wetlands; comprised of non-woody, riparian, marsh and shallow water, and peatlands encompassing other wooded types (i.e. swamp, bogs and fens). While it is clear that wetland cover contributed in reducing fire spread, peatlands as a whole may not have acted as absolute fuel breaks throughout the Holocene as only with increasing time BP are regional peatlands associated with longer FIs. This is in agreement with studies that indicate organic deposits with poor drainage tend to burn less (Mansuy *et al.* 2010), however that this trend was observed only with increasing time BP indicates several possible scenarios involving interactions with climate and the post-glacial landscape conditions in the early-Holocene. In the first scenario, the pattern and timing of peatland succession and development may explain the observed FI variation among sites where wetlands and organic terrain comprise large portions of the regional landscape. Many peatland successional pathways in northwestern Ontario originate from lakeshores, shallow water depressions and ponds (Harris *et al.* 1996; Rydin and Jeglum 2006); there is an average 4,000 year (Gorham *et al.* 2007) lag time between deglaciation and peak peat development due to the time it takes for land to become amenable to peat formation (Halsey *et al.* 2000). Consequently, modern terrestrial cover considered peatland may have acted as non-fuel following deglaciation, thereby decreasing regional forest connectivity resulting in longer FIs in the past but not the present when regional peatlands are a viable source of forest fuels. Alternatively, in scenario two, rising temperatures following the end of the Neoglacial climate cooling period (*c.* 2.5k cal a. BP) (Kerwin *et al.* 2004; Viau *et al.* 2006a; Viau and Gajewski 2009), may have increased fire

activity in peatlands as they have large organic matter stocks in vegetation and surface soil layers that may have become more susceptible to burning during dry weather periods (Turetsky *et al.* 2004). Decreased FIs at these sites may be ecologically significant as over the past 10k years boreal peatlands have functioned as net sinks for carbon (Thornley and Cannell 2004; Kashian *et al.* 2006; Lecomte *et al.* 2006), and increased fire activity could release large amounts of atmospheric CO_2.

Conclusion

This study demonstrates complex spatial and temporal variability in fire regimes over the past 10k years. Our results clearly show the extent of the variability of the fire intervals between two distinct landscapes and emphasize that the influence of long-term climate on boreal fire regimes at regional-to-local scales differs with forest connectivity. These results also highlight the importance of considering the effects of local landscape features when interpreting Holocene-scale paleofire records in the boreal forest. These results clarify some patterns and controls of central boreal fire regime spatial variation, and imply that climate changes will interact with land cover to affect boreal fire dynamics in the future with far-reaching implications for forest ecology, carbon sequestration and wildfire management

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CHAPTER FOUR Fire-vegetation interactions in mixedwood central boreal shield forests of Northwestern Ontario, Canada

Abstract

Vegetation assemblages and associated disturbance regimes are spatially heterogeneous throughout the boreal forest due to the complex terrain, varying climate, and strong environmental gradients. Given this complexity, multiple sites describing postglacial vegetation and fire histories are needed to adequately understand forest development and ecosystem responses to varying climate and disturbance regimes. We analysed charcoal and pollen from sediments obtained from two kettle lakes in the central Canadian boreal forest in order to reconstruct fire return intervals and vegetation dynamics over the last 10,000 years. Overall, fire frequency has increased following deglaciation to present. The pollen-inferred vegetation exhibits different trajectories of boreal forest dynamics after afforestation. At both sites, *Picea* populations were most extensive shortly after deglaciation, with vegetation later shifting towards mixed woodlands with more extensive *Betula papyrifera* and *Pinus banksiana* populations. Mean fire intervals appeared to have no significant impacts on pollen communities, in terms of diversity or trajectories. Species-specific responses to median fire interval (mFI) were more varied, likely due to species specific fire adaptations, site specific local environmental conditions, climatic changes and competition. Although wildfire is the dominant natural disturbance in boreal ecosystems, this study does not support the hypothesis that changes in fire frequency is the main controlling factor of the long-term dynamics of boreal forest vegetation at regional spatial scale.

Introduction

In boreal forest ecosystems naturally occurring wildfire is a prominent disturbance factor driving

vegetation dynamics over decadal to centennial scales (Burton *et al.* 2008; Bowman *et al.* 2009;

de Groot *et al.* 2013a). Fire regimes, which describe long-term patterns of fire activity, vary

significantly throughout the North American boreal forest and these variations play a central role

in determining patterns of ecosystem response and landscape legacies left by fire (Turner 2010).

Frequent forest fires have pronounced impacts on species composition, tree age, size structures

and nutrient cycling; nonlinear responses to changes in fire frequency may cause rapid changes

in plant community diversity and forest structure consequently providing different fuel

compositions that will feed new fire regimes (Paine *et al.* 1998; Johnstone and Chapin 2006;

Girardin *et al.* 2013a). In recent decades, boreal ecosystems have experienced marked changes in

response to ongoing climatic changes, including increased burning (Gillett *et al.* 2004; Kasischke

and Turetsky 2006; Kelly *et al.* 2013). Continued climate warming will increase the incidence of

severe fire weather conditions (hot and dry) that favour larger and more severe fires (de Groot *et*

al. 2013b; Flannigan *et al.* 2013). Furthermore, fire occurrence is also likely to increase as

average temperatures rise and summer precipitation declines with far-reaching ecological and

socioeconomic consequences (Marlon *et al.* 2009; Wotton *et al.* 2010).

The boreal forest of North America has low diversity and is comprised mainly of *Abies,*

Betula, Larix, Picea, Pinus and *Populus*. Many boreal species have strategies to cope with fire

and recolonize burns, either by seed or vegetative means. *Pinus banksiana* and *Picea mariana*

use serotinous or semi-serotinous cones to protect and disperse seeds post-fire (Greene *et al.*

1999). *Populus tremuloides*, and *Betula papyrifera* regenerate vegetatively through root suckers

or stump sprouts (Perala 1990; Greene *et al.* 1999), or seed in from outside the burn (Greene and

Johnson 1999). Fire sensitive species like *Abies balsamea* and *Larix laricina* can only seed into a burn from edges or unburned residual patches within the burn perimeter (Greene and Johnson 1999). Because fire is one of the most important abiotic disturbances in boreal forest ecosystems, it is critical to examine historical rates of change and the mechanisms interacting at various spatial and temporal scales to understand how future climate and vegetation changes could affect fire regimes and vice versa (Turner 2010; Hessl 2011). Retrospective studies using lake-sediment charcoal as a proxy for past fire regimes provide valuable long-term records, but are scarce in the central boreal shield region of Canada. When paired with high temporal-resolution and contiguous paleobotanical reconstructions, charcoal records can be used to infer the ecological impacts of changing fire regimes over millennia (Whitlock and Anderson 2003; Power *et al.* 2008; Power *et al.* 2010). Long-term records of vegetation and fire regime variability are necessary to inform land management policy and decision making (Gavin *et al.* 2007)

This chapter uses a Holocene macroscopic charcoal record from the central Canadian shield ecoregion in Canada that has been previously published (Senici *et al.* 2013), with a new pollen record. We present a 10,000-year record of vegetation and fire activity in the central boreal shield forest of North America. We examine the local area fire history through high resolution macroscopic charcoal analysis, and the regional vegetation history through pollen records established from lacustrine sediment cores from two separate lakes. We then integrate vegetation data with the charcoal record to investigate Holocene fire-vegetation interactions. Having previously identified differences in fire activity among the study sites (Senici *et al.* 2013), we expect significant changes in regional vegetation dynamics temporally concurrent to changes in local median fire interval (mFI).

Methods

Study Area

Lake surface area and morphometry strongly influence the relevant source-area shape for the

collection of pollen (Sugita 1993) and macroscopic charcoal (Higuera *et al.* 2007). To provide

the best historical records, small lakes with simple bathymetries, narrow littoral zones, and no

inflow or outflowing streams were targeted for sampling (Fig. 4.1, Table 4.1) (Whitlock and

Millspaugh 1996). The two lakes, Ben (BEN, 49°21'25" N; 89°46'10" W; 480 m above sea level

[a.s.l]) and Small (SML, 49°34'52" N; 90°23'08" W; 478 m a.s.l) are located within the Central

Canadian Shield boreal forests of northwestern Ontario, Canada. Climate is typically moist and

cold with a mean summer temperature of 14°C and mean winter temperature of -13°C

(Ecoregions Working Group 1989); annual precipitation ranging from 654 to 879 mm, and mean

summer rainfall from 231 to 298 mm (Crins *et al.* 2009). Recent climate models indicate that this

area is cooler than immediately adjacent areas of similar latitude and hence, exhibits a stronger

boreal nature with lower mean annual temperatures (-1.7 to 2.1°C) and a shorter mean growing

season length (161 to 182 days) (Mackey *et al.* 1996; Colombo *et al.* 2007).
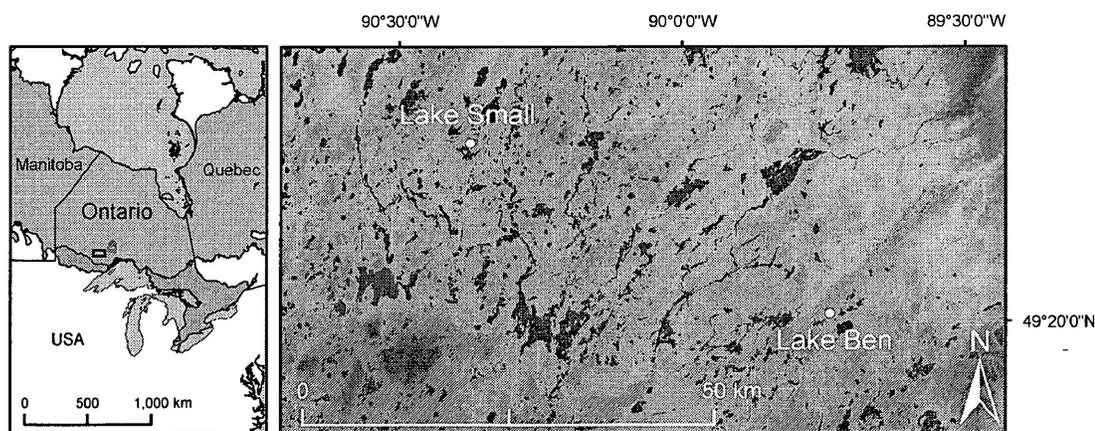
Figure 4.1 Map of the study area.

Table 4.1 Study lake characteristics. Local vegetation belongs to the three most dominant species listed in descending order of abundance at each site.

	Ben	Small
Latitude (N)	49°21'25.02"	49°34'52.19"
Longitude (W)	89°46'10.36"	90°23'08.34"
Local woody vegetation	*Pinus banksiana,* Picea mariana, Betula papyrifera,	*Picea mariana,* Abies balsamea, Pinus banksiana
Lake surface (ha)	1.6	0.5
Water depth (m)	5	4

Regional modern vegetation

Dominant vegetation includes coniferous species like *Picea mariana* (Mill.) B.S.P. (black spruce), *Picea glauca* (Moench) Voss. (white spruce), *Abies balsamea* (L.) Mill. (balsam fir), *Larix laricina* (Du Roi) K. Koch. (tamarack) and *Pinus banksiana* Lamb. (jack pine), and deciduous species like *Populus tremuloides* Michx. (trembling aspen) and *Betula papyrifera* Marsh. (white bitch). Other extant species with small contributions to regional vegetation include *Pinus resinosa* Ait. (red pine), *Pinus strobus* L. (white pine), and *Thuja occidentalis* L. (Eastern white cedar). The most frequent landcover type in the region is mixed forest (23.5%), followed by coniferous forest (23%), water (17.1%), sparse forest (15.1%), deciduous forest (9.0%), and cutovers (5.7%) (Crins *et al.* 2009). Vegetation in the mixedwood portion is typically mixed closed-canopy forest, characterised by coniferous *P. mariana, P. glauca* and *A. balsamea* with deciduous *P. tremuloides* and *B. papyrifera*. In the coniferous portions, *P. mariana* and *L. laricina* predominate in swamps and peatlands in low-lying areas, while large areas of pure *P. banksiana* and mixed *P. banksiana – P. mariana* stands dominate on sandy materials throughout the region. Other trees such as *P. strobus* and *P. resinosa* occur in pockets near warm microclimates or sites protected from lethal fires (Bergeron *et al.* 2004)as the study region is at the modern northern range limit of these species.

Lake sediments

Sediment cores were taken atop frozen lake surfaces from the centre of each lake using a

modified Livingstone-type square-rod piston corer (100×5 cm) (Wright *et al.* 1984) in the

spring of 2010. Sediment cores were preserved in polyurethane and aluminum foil and

transported to the laboratory. Cores were sliced into disks at contiguous 1 cm intervals. The most

recently accumulated materials (soft, fine grained sediments) at the water-sediment interface

were collected using a Kajak-Brinkhurst (KB) gravity corer (Glew 1989). These materials were

extruded on site at 1 cm intervals.

Chronologies

Datings were obtained from terrestrial plant macroremains and charcoal or bulk organic

sediments when macroremains were not abundant enough for ^{14}C Accelerated Mass

Spectrometry (AMS) measurements. Radiocarbon ages were calibrated with CALIB 6.1.1

(Stuiver and Reimer 2011) using the Intcal09 calibration curve (Reimer 2009). We used a

weighted cubic smoothing spline derived from 1000 bootstrapped samples from the calibrated

age distributions using the program MCAgeDepth 0.1 (Higuera *et al.* 2009).

Charcoal analysis and fire reconstructions

To reconstruct fire history, we performed charcoal peak analysis on each of our records.

Contiguous subsamples of 1 cm^3 were obtained from each sediment core at 1 cm intervals for

charcoal analysis. Samples were deflocculated in a 10% KOH or 6% NaClO (bleach) to increase

the visibility of charcoal particles and wet-sieved through a 160 μm mesh. Macroscopic charcoal

fragments were identified, counted and measured for surface area under a $\times 20$ stereo microscope

using an attached digital camera connected to WinSeedle (Regent Instruments Inc.2007).

Empirical and modelling studies indicate that peaks of charcoal particles > 160 μm are indicative

of fire occurrence within a distance of ~1.2 – 3.0 km from lakeshore (Higuera *et al.* 2007;

Higuera *et al.* 2010).

Prior to decomposition into Charcoal Accumulation Rates (CHAR) each record was

interpolated to equivalent time steps and volumes along the sedimentary sequences. We used a

temporal resolution of 20 years/sample, the approximate median sample resolution of the two

records (Table 4.1). Sedimentary macro-charcoal records (C_{raw}) were broken down into low

frequency variation ($C_{background}$) and peak components (C_{peak}) using a locally defined threshold to

reconstruct and identify local fire events. We estimate $C_{background}$ with a locally weighted

regression (lowess) using a 1000 year window width. We then subtracted $C_{background}$ from C_{raw} to

obtain the residual high-frequency C_{peak}; C_{peak} is composed of two subpopulations C_{noise},

representing variability in sediment mixing, sampling and analytical and natural noise, and C_{fire}

representing the occurrence of one or more local fire events (Gavin *et al.* 2006; Higuera *et al.*

2010). The C_{fire} and C_{noise} distributions were estimated in a 1000-year moving window using a

Gaussian mixture model with a threshold defined as the 99th percentile of the modeled noise

distribution. Residual CHAR values greater than the threshold was considered a C_{peak} and a

potential fire event. We use the term fire event to describe events from C_{fire} that could represent

one or more local fires occurring near our sites. The signal-to-noise index (SNI) was used to

evaluate the effectiveness of the discrimination (Kelly *et al.* 2011). The goodness-of-fit (GOF)

metric is used to assess the degree of contrast between C_{noise} and C_{fire} by comparing C_{noise} with

the one derived from the Gaussian mixture model. C_{fire} was used to reconstruct local fire-return

intervals (FRI) and fire frequency (FF) trends.

Pollen analysis and vegetation reconstruction

Subsamples of 1 cm^3 were taken at 4 cm intervals from BEN and SML sediment sequences to be chemically treated following the standard procedures described by Faegri and Anderson (1989) in preparation for pollen identification. A small amount (0.5 mm) of Eucalyptus pollen solution (222, 367 ± 6403) was added at the beginning of each treatment as an exotic marker to estimate pollen concentrations (grains cm^{-3}). Samples were soaked with hot 10% KOH and sieved through 700 μm mesh to deflocculate the sediments and remove humic acids and particles (plant macroremains) larger than known pollen or spores. Carbonate, silicate, and a fraction of the organic materials (cellulose) were eliminated with hot 10% HCl, 40% HF, acetic acid (CH3COOH), and acetolysis using acetic anhydride (CH3CO)2O and 97% sulphuric acid H2SO4. Samples were rinsed with water and 30% glycerine solution. Contrast dye was added to each sample to facilitate identification. Samples were mixed with glycerine and mounted on glass slides. Pollen was identified under 4000-1000x magnification to a minimum terrestrial pollen count of 300 pollen grains. Pollen treatment and identification was performed at Université Laval (UL) from September 2012 to January 2013. For identification we used the reference collection housed at UL and several dichotomous keys (Richard 1970; McAndrews *et al.* 1973; Moore *et al.* 1991).

Pollen data are expressed as a percentage of total pollen grains from terrestrial plants excluding pollen from obligate aquatics and spores. The genus *Picea* includes pollen from *P. mariana* and *P. glauca*. *Populus* pollen was identified as the *P.* cf. *tremuloides* type, which may include several species (mainly *Populus balsamifera* L. and *Populus grandidentata* Michx). *P. strobus* pollen grains can be differentiated from other pines; as a haploxylon subgenera its pollen grains characteristically possess distal verrucae whereas *P. banksiana* and *P. resinosa* are

diploxylon and lack distal verrucae. Pollen grains from *P. banksiana* and *P. resinosa* cannot be reliably distinguished and were grouped together as *P.* cf. *banksiana*. To avoid the influence of an ecologically non-relevant pollen taxon, in subsequent statistical analyses the counts of non-identified *Pinus* pollen (e.g. single sacci, broken pollen grains) were redistributed into the two identified *Pinus* classes (*P.* cf. *banksiana* and *P. strobus*) based on their relative abundance in each sample. Pollen zones were established through constrained incremental sums of squares cluster analysis (CONISS) of the relative abundance of pollen taxa (Grimm 1987) with the number of statistically significant zones obtained by comparison with the broken-stick model (Bennett 1996) implemented in the statistical computing program R 3.1.0 (R Development Core Team 2013) using the 'rioja' package (Juggins 2014).

Rate of change and diversity and richness

The rate of change (ROC) is a dissimilarity measurement, defined here as the amount of ecological change per unit time, determined from our pollen records. In these analyses, ROC was the dissimilarity based on a Euclidian distance between pollen assemblages from two adjacent pollen spectra divided by the time interval between them. ROC was used to detect any rapid vegetation changes like those associated with changes in fire frequency (Shuman *et al.* 2005; Urrego *et al.* 2009). Two estimations of ROC were calculated, the first with the complete terrestrial pollen dataset from each site and the second with only terrestrial taxa with a mean frequency greater than 1%.

Two biodiversity indices were used to estimate variations in the pollen-inferred vegetation composition: Shannon index (*H'*) and Simpson index (*D*). These indices help compare the structure of those pollen assemblages in which the record of each species is comparable through time, and are calculated here using the complete terrestrial taxa dataset from each site.

H' is calculated by determining the proportional contribution of each taxon to the total number of pollen in the complete spectrum.

(4-1)

$$H' = -\sum_{i=1}^{S} p_i \ln p_i$$

Where p_i is the pollen frequency for the ith taxon. Simpson's diversity index (D) is calculated as:

(4-2)

$$D = \frac{1}{\sum_{i=1}^{S} p_i^2}$$

While Simpson's index squares the relative abundance, the weight of rare species is reduced relatively more than that of more abundant species, the Shannon's index includes the log-normal transformation of species, thus the importance of abundant species is reduced slightly relative to rare species. Both indices were used together to assess the potential roles of both abundant and rare taxa in the diversity scores at each lake. Temporal variability in pollen diversity was assessed by the Kruskal-Wallis test (KW-test) on mean pollen diversity scores per millennia.

To assess changes in pollen richness we performed a rarefaction analysis.

(4-3)

$$E(T_n) = \sum_{i=1}^{T} 1 - \left[\frac{\binom{N - N_i}{n}}{\binom{N}{n}}\right]$$

Where $E(T_n)$ is the expected number of taxa in a random sample of n individuals from a larger population of N individuals containing T taxa (Heck et $al.$ 1975). We performed rarefaction

analysis on the complete set of terrestrial pollen. Shannon's and Simpsons's diversity indices and the rarefaction analysis were calculated using the 'vegan' package (Oksanen *et al.* 2010) in R (R Core Development Team 2013).

Fire and vegetation interactions

To describe the relationships among the pollen assemblages the pollen data from Lake Ben and Small were ordinated by Principal Component Analysis (PCA) using the 'vegan' package (Oksanen *et al.* 2010). In ordination, pollen percentages were calculated using only pollen types from each site. Taxa < 1% in at least one sample were excluded (Flakne 2003). To decipher the changes in the main plant populations, pollen percentages were standardised to allow a comparison of the magnitude of changes independent of the pollen productivity differences among taxa and the taphonomical properties of each taxon (Fuller 1998). Each taxon is displayed individually at a scale that is the same for all, allowing an estimate to be made of the magnitude of pollen population changes within and among pollen taxa (Carcaillet *et al.* 2010). The rescaled pollen percentages were based on a min-max transformation:

$$(4\text{-}4)$$

$$P_i' = \frac{P_i - P_{min}}{P_{max} - P_{min}}$$

Where P_i' is the standardised value of the *i*th sample P_i, and P_{min} and P_{max} are the minimum and maximum of the P_i'.

To assess the relationship between individual pollen taxa and fire, Spearman's rank correlation coefficient (Spearman's ρ) was calculated for mFI and pollen percentages of the dominant tree and shrub taxa at Lake Ben and Lake Small throughout the complete reconstruction. Charcoal data were interpolated to the age/depths per sample used in pollen

analysis using the package 'rioja' (Juggins 2014). mFIs were also calculated for each statistically significant pollen zone as determined by CONISS for each site.

Results

Chronologies

The age-depth models (Fig. 4.2a, b) represent approximately 10,375 and 9975 years of sedimentation at the Lake Ben and Lake Small sites, respectively. Sites are comparable in sedimentation rate with Lake Ben having a higher mean sedimentation rate at 0.086 ± 0.06 cm yr^{-1} to Lake Small's 0.063 ± 0.05 cm yr^{-1}. Each sequence exhibits acceleration in sedimentation rate between $c.$ 5000 - 3500 cal. yr BP, with the maximum deposition occurring at 4,310 cal. yr BP (0.029 cm yr^{-1}) in Lake Ben and 3785 cal. yr BP (0.033 cm yr^{-1}) in Lake Small. Due to the increased sedimentation rate, our fire and vegetation records for the time period $c.$ 5,000 – 3,500 cal. yr BP have high temporal resolutions.
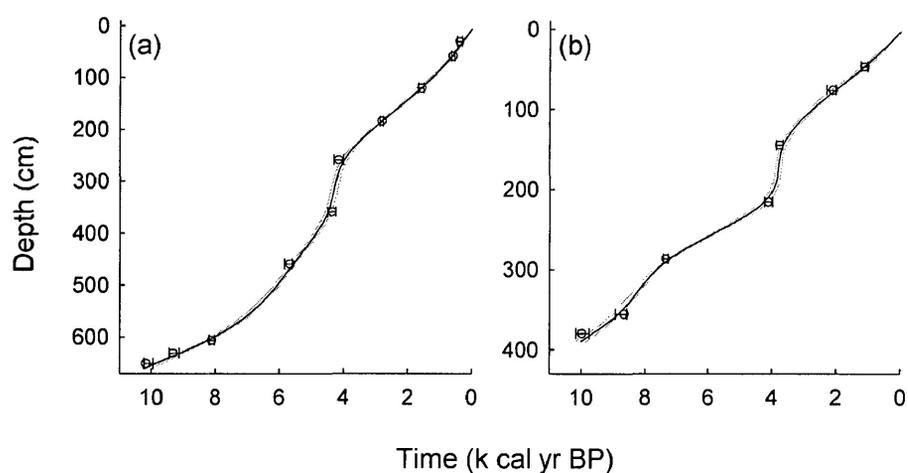
Figure 4.2 Age-depth models for (a) Lake Ben and (b) Lake Small

Fire reconstruction

The trends in the new reconstructions of median fire intervals (Fig. 4.3c, d) are not significantly different from previous reconstructions using a shorter temporal resolution and smoothing window (Chapter 2) (Senici *et al.* 2013). Forty-six fires were detected at Lake Ben throughout the Holocene, with fire intervals ranging from 50 to 750 years (Fig. 4.3c). The highest fire frequencies occurred between 2,000 cal. yr BP and the present and the lowest fire frequencies occurred 6,000 – 5,000 cal. yr BP. Global mFI for the reconstruction was 150 ± 24 years (mean ± SE). Thirty-six fires were identified at Lake Small between 9,800 cal. yr BP and the present, with fire intervals ranging from 50 to 850 years (Fig. 4.3d). The highest fire frequencies occurred between 3,000 and 1,500 cal. yr BP and the lowest fire frequencies occurred 6,500 – 4,500 cal. yr BP. Overall mFI at this site was approximately 213 ± 24 years.
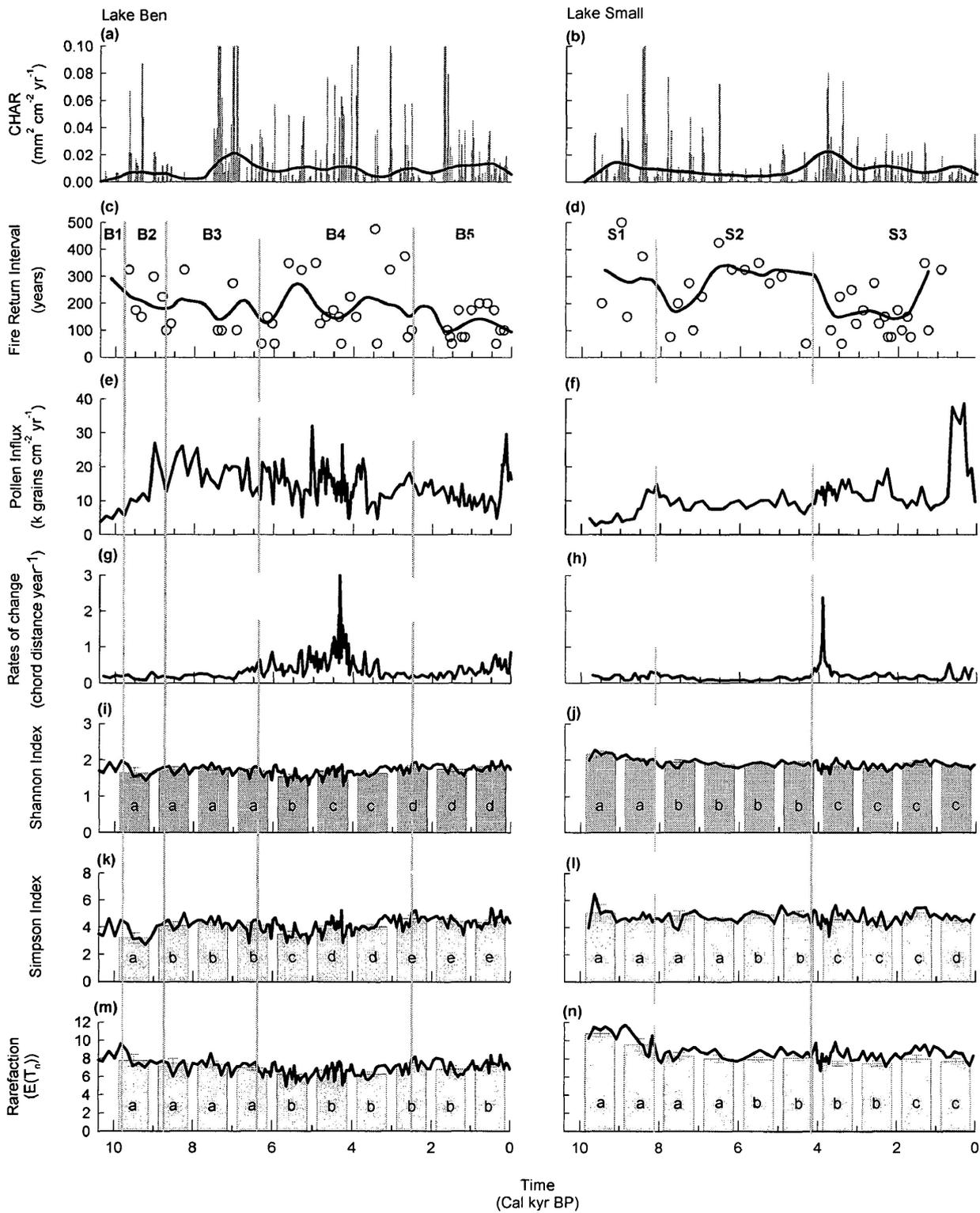
Figure 4.3 Sedimentary charcoal and pollen records at Lake Ben and Lake Small plotted against time. (a, b) Charcoal accumulation rates; vertical gray bars are CHAR peaks, the heavy black line represents CHAR background. (c, d) Smoothed fire return intervals (FRIs); circles are identified fire events and corresponding fire interval. (e, f) Pollen influx. (g, h) Rate of change

(ROC). Three indices of vegetation change: (i, j) Shannon's index (*H*); (k, l) Simpson's index (*D*); and (m, n) rarefaction analysis (*E*(*T_n*)); the histograms show the mean values of *D, H* and (*E*(*T_n*)) calculated per millennia; the letters refer to differences based on the Kruskal-Wallis test (different letters mean significant differences). The solid grey vertical lines indicate statistically significant pollen zones derived from CONISS at Lake Ben and at Lake Small.

Pollen influx and diversity

Total pollen influx was low at both sites following deglaciation to *c.* 9,000 cal. yr BP at Lake Ben (Fig. 4.3e) and *c.* 8,500 cal. yr BP at Lake Small (Fig. 4.3f). Overall pollen influx was higher at Lake Ben throughout the complete sequence. The ROC is based on pollen count data for all identified terrestrial pollen taxa. The first elevated ROC at Lake Ben and Small corresponds to the post-glacial afforestation phase and can be dated at 9,750 and 8,220 years BP respectively (Fig. 4.3g, h). Lake Ben exhibits fluctuations between 7,000 and 4,000 cal. yr BP likely resulting from vegetation transformations following afforestation; after 4,000 cal. yr BP ROC remains low. At Lake Small, the ROC is very low throughout most of the sequence save two peaks, the first *c.* 8,250 cal. yr BP and the second *c.* 4,000 cal. yr BP. This suggests that while very little vegetation transformations have occurred there were short time periods where vegetation transformed rapidly into a new state after which vegetation remained stable. However the periods of high ROC are at least partially due to the shorter intervals (high sample resolution) between pollen samples, which in turn reflects the high sediment accumulation rates in both chronologies. The diversity indices (Fig. 4.3i-l) and the rarefaction analysis (Fig. 4.3m, n) for both sites have remained relatively stable following the afforestation phase at each site.

Vegetation dynamics

Tree pollen abundance among our sites was greater than 60% throughout the entire profile (Fig. 4.4a, b), indicating that trees were a ubiquitous presence in the surrounding landscape following deglaciation. The pollen record of BEN was divided into five zones using

CONISS (Fig. 4.4a). In zone B1 (*c.* 10,390 – 9,750 cal. yr BP), woodland cover values were high

(80%) following deglaciation with pollen assemblages dominated by coniferous *Picea.* Other

tree species like *L. laricina* and *T. occidentalis* are at their peak values (2 – 5%) in this zone.

Quercus spp. and *Ulmus* spp. pollen are also at peak abundances (5%). Pollen from deciduous

trees and shrub taxa was scarce, but herbaceous pollen was high, particularly among the

Asteraceae (artemisia and ambrosia).
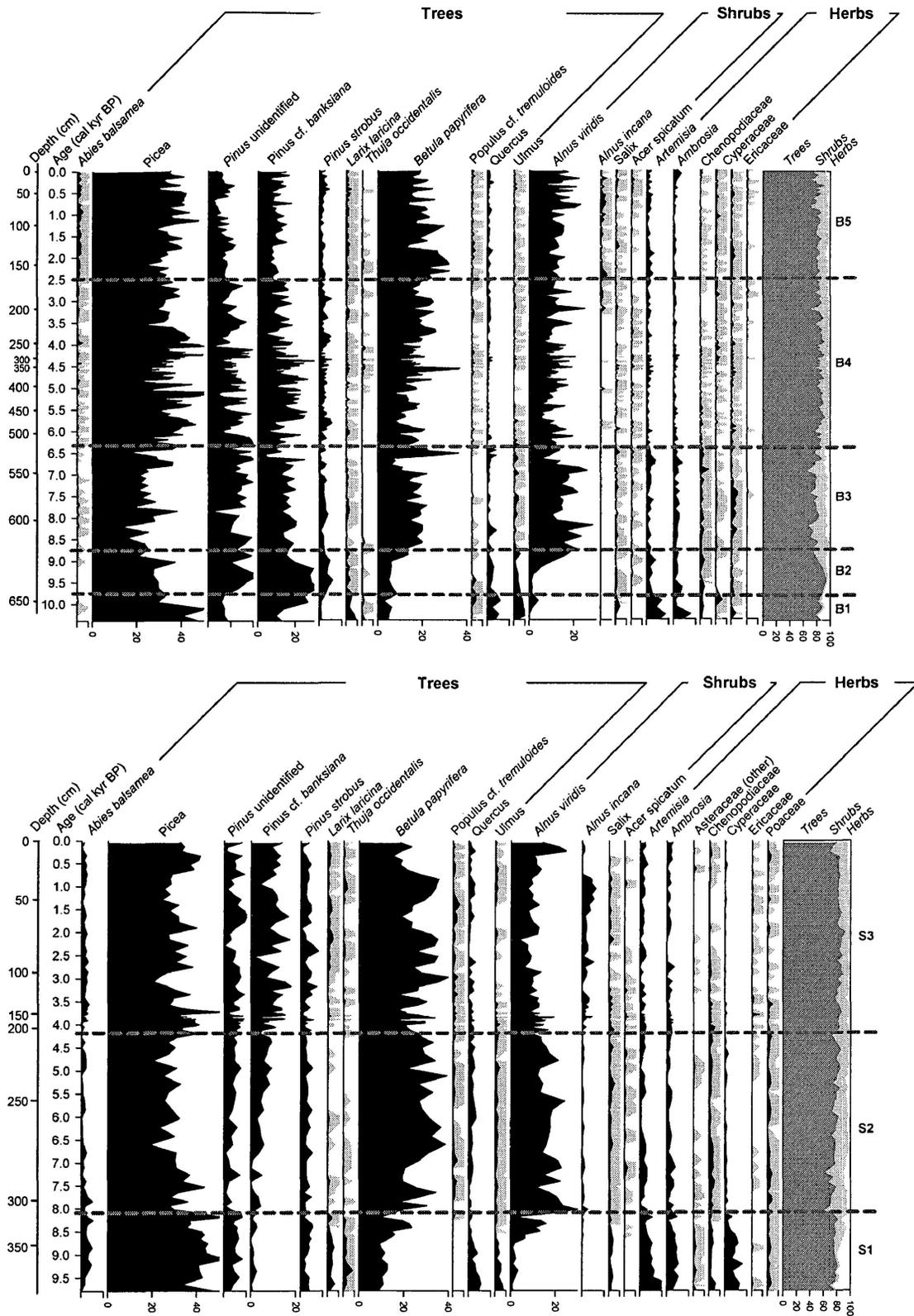
Figure 4.4 Simplified diagrams of pollen percentages at (a) Lake Ben and (b) Lake Small. The taxa include only those reaching mean pollen percentages ≥ 1% in at least one sample. Dashed red lines separate the pollen zones.

The onset of zone B2 (*c*. 9,750 – 8,750 cal. yr BP) was marked by a rapid rise in *P. banksiana* accompanied with a concomitant decline in *Picea* and herbaceous taxa. The highest abundance of *P. tremuloides* (> 2%) and *P. strobus* (> 5%) occurs midway in this zone. *Abies* remained mostly low or absent throughout. *Quercus* spp. and *Ulmus* spp. pollen abundance remain relatively high (2 – 5%) but decline towards zone B3. Herbaceous Asteraceae and Chenopodiceae remained abundant (> 1%) throughout, however Cyperaceae was mostly absent as was Ericaceae. Except for a sharp increase in *A. viridis* near the zone's endpoint, shrub taxa was largely absent.

In zone B3 (*c*. 8,750 – 6,350 cal. yr BP), *B. papyrifera* pollen increases sharply from 5% to > 20% as does *A. viridis*. *P. banksiana* abundance remains high (18 – 20%) and is generally stable in this zone. While *Picea* pollen is abundant, it is least abundant (25%) in this zone. The continuous presence of *P. strobus* pollen indicates its apparent persistence in the regional landscape. The presence of *A. balsamea* is intermittent and scarce (< 1%). Abundance of *P. tremuloides* decreases and is mainly absent throughout this zone. Abundance of *L. laricina* decreases in this zone while *T. occidentalis* is mostly absent. *Quercus* spp. and *Ulmus* spp. pollen continue to decline in this zone but remain a relatively continuous presence. Asteraceae, Chenopodiaceae and Ericaceae are abundant throughout (>2%), however overall herbaceous pollen declines with a concomitant increase in shrub pollen.

Zone B4 (*c*. 6,350 – 2,500 cal. yr BP), is marked by increased *Picea* (30 – 40%) and decreased herbaceous taxa. *Pinus* cf. *banksiana* pollen abundance steadily declines, while *P. strobus* remains stable (2 – 5%). *T. occidentalis* reappears *c*. 5,000 cal. yr BP after a 3,500 year absence. *L. laricina* persists with discontinuous low (< 1%) abundances. Mainly discontinuous *P. tremuloides* abundances are recorded after 6,350 cal. yr BP. This zone marks the first

appearance of shrub *A. incana* (subsp. *rugosa*) *c.* 5,500 cal. yr BP. The increased abundance of

A. balsamea and *L. laricina* pollen, indicate more diverse mixed forests. *Quercus* spp. and *Ulmus*

spp. pollen continues to decline and become discontinuous. *A. viridis* remains the dominant

shrub (10 – 20%), however abundance is lower compared to prior zone B3. Salix and *A.*

spicatum are intermittently present (<2%). Herbaceous plant taxa are least abundant and

predominantly discontinuous in this zone, with Chenopodiaceae becoming rare after 4,000 cal. yr

BP.

In zone B5 (2,500 – 0 cal. yr BP), *A. balsamea* and *B. papyrifera* pollen increase to their

highest levels of abundance (2% and 20% respectively) in the BEN record. *Picea* abundance

remains similar to zone B4. *P. banksiana* and *P. strobus* decline to levels similar to the

immediate post-glacial zone B1. *L. laricina* remains a constant low-level presence. Overall shrub

pollen abundance increases, due mainly to an increase in *A. incana.* Overall understory

herbaceous taxa remain low.

At SML between 9,800 and 8,100 cal. yr BP (zone S1, Fig. 4.4b), woodland were

dominated by coniferous vegetation including *Picea* (40%), *P. strobus* (7%) *A. balsamea* (5%),

T. occidentalis (2 – 5%) and *L. laricina* (2 – 5%). *Pinus* cf. *banksiana* percentages were at their

lowest levels (< 3%). Deciduous species abundance is low, with *B. papyrifera* abundance at the

lowest recorded values at this site (10 – 20%) and *Populus* cf. *tremuloides* absent until the onset

of zone S2. *Quercus* spp. and *Ulmus* spp. pollen are abundant (5%) at the start of zone S1 but

decline over time (< 1%). Overall, shrub pollen is scarce; *A. viridis* abundance increases sharply

midway through the zone (*c.* 8,750 cal. yr BP), and *Salix* reaches maximum recorded abundance

(3%). This zone is characterized by high herbaceous pollen frequencies, in particular

Cyperaceae, Artemisia and Ambrosia were abundant (> 5%). There was overall low pollen accumulation rates for all species.

Around 8,100 cal. yr BP (onset of Zone S2), a sharp rise in *B. papyrifera* and *A. viridis* abundance is associated with lower relative abundances of coniferous *Picea, A. balsamea,* and *L. laricina*. While abundant, *Picea* percentages were at their lowest values (30%) in this zone. *P.* cf. *banksiana* pollen progressively increases while *P. strobus* abundance remains relatively constant (5%). *L. laricina* and *T. occidentalis* abundances were low throughout, never exceeding 1% and disappearing from the fossil record entirely for > 1,000 years towards the end of the zone. The presence of *P. tremuloides, Quercus* spp., and *Ulmus* spp. pollen indicates a more diverse and mixed forest composition with higher abundances of deciduous vegetation and shrubs. Cyperaceae, Artemisia and Ambrosia decline from their high zone S1 levels with a concomitant increase in shrub pollen.

In Zone S3 *(c.* 4,250 cal. yr BP to present), *P.* cf. *banksiana* percentages are at their highest values, the increase being primarily at the expense of *A. viridis* and herbaceous plants. *Picea* abundance remains similar to Zone S2. Abundance of *L. laricina* increases. Pollen abundance of *A. incana* increased along with an accompanying decrease in herb pollen (mainly Chenopodiaceae and Ericaceae). *A. viridis* pollen is at lower levels throughout the zone but increased sharply in the last 300 years. *A. incana* increases to peak abundances for this species in this zone. All herbaceous taxa, save Artemisia and Ambrosia display low abundance with discontinuous appearances.

Fire and vegetation interactions

The first two axes of each PCA explain a significant amount of variation, accounting for 38%

and 50% of the total variance of the Lake Ben and Small datasets (Fig. 4.5a-d, Table 4.2),

respectively. Only the first axes of each PCA account for large amounts of variation for Lake

Ben (22.4%) and Lake Small (36.2%) (Fig. 4.5a, b, Table 4.2). The first axis, shows a strong

contrast between the initial vegetation assemblages following the retreat of the Laurentide Ice

Sheet and proglacial waters in the late Holocene between sites (Fig. 4.5a, b). The gradual

transition observed at Lake Ben (Fig. 4.5a), suggests a long-term and gradual process dominated

the vegetation dynamics at this site; while the abrupt change at Lake Small followed by relative

stability suggest rapid afforestation in a short time span that occurred later than afforestation at

Lake Ben, which was followed by relatively stable states to present. The second PCA axis

accounts for ~ 14 – 15% (Table 4.2) of the variation at both sites; at Lake Ben following

afforestation phase, the axis is relatively stable to present. At Lake Small this axis is more

variable with change points roughly corresponding to CONISS identified pollen zone change

points (c. 8,100 and 4,250 cal. yr BP). The eigenvalues for the third and greater PCA axes are

less than the mean eigenvalues for each PCA (Table 4.2), suggesting these axes do not account

for a significant amount of variability (Legendre and Legendre 1998).

Table 4.2 Variance (%) explained and eigenvalues of the two PCAs.

	Lake Ben		Lake Small	
Axes	%	Eigenvalue	%	Eigenvalue
1	22.4	0.11	36.2	0.24
2	15.3	0.07	13.8	0.09
3	10.9	0.05	10.7	0.07
4	9.2	0.04	7.7	0.05
5	7.4	0.04	6.2	0.04
6	6.9	0.03	5.3	0.03
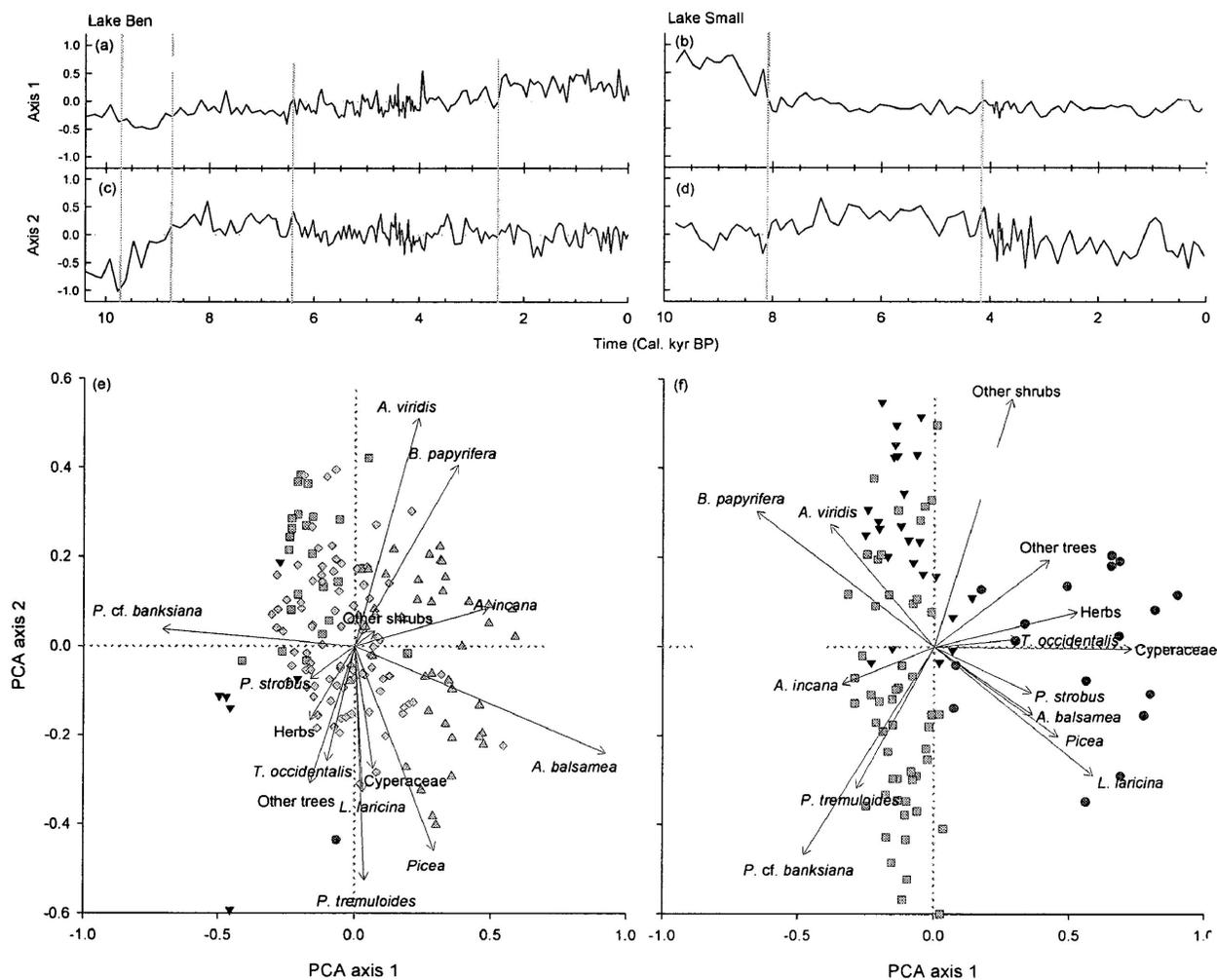
Figure 4.5 Axis scores of the principal component analyses (PCA) based on pollen data plotted against time for Lake Ben (a, c) and Lake Small (b, d). Ordination biplot of pollen taxa on PCA axes 1 and 2 at (e) Lake Ben, and (f) Lake Small. Red circles represent site scores for pollen zone 1, blue inverse triangles for zone 2, and orange squares for zone 3. In (a) yellow diamonds represent zone B4 and upright grey triangles zone B5.

The main long-term vegetation trajectories in relation to fire interval at Lake Ben (Fig. 4.5e) are characterized by *Picea*, *Quercus* spp., *Ulmus* spp, and *T. occidentalis* (zone B1) in the afforestation phase and are most dominant in the absence of fire (Table 4.3). As fire begins to recur regularly (mFI 190 years; Table 4.3) we find increasing *P. strobus* and *P. banksiana* in zone B2. Following the afforestation phase, mixed forest assemblages dominate in zone B3 where fire frequency is at a record low; in this zone increased *B. papyrifera* and shrubs *A. viridis*

and *A. incana* are significant contributors to local pollen assemblages. Zone 4 has the most

diverse mixed forest while mFIs decrease from zone B3. Zone B5 has the highest fire frequency

(mFI 119 years) and is predominantly mixed forest with dominated by *Picea,* and *B. papyrifera,*

A. balsamea, and shrubby vegetation. The main long-term vegetation trajectories at Lake Small,

as summarized by the first axis (Fig 4.5f), are characterized by a shift in coniferous dominated

assemblages of *Picea, L. laricina,* and *A. balsamea* (zone S1) where fire frequency is low, to

mixed assemblages with increasing abundances of *B. papyrifera, A. viridis,* and other deciduous

shrub cover (zone S2), to mixed assemblages dominated by *P.* cf. *banksiana, P. tremuloides,* and

A. incana in zone S3 where fire frequency is at the highest recorded levels. The second PCA axis

at Lake Small is mainly related to changes in *P.* cf. *banksiana, P. tremuloides,* and other shrub

vegetation. Kruskal-Wallis tests were used to assess differences in mFIs between adjacent pollen

zones; there were no significant differences in mFIs at each site as indicated by the overlapping

confidence intervals.

Table 4.3 Median fire return intervals (mFIs) and number of identified fire events (N_{fe}) for each site for pollen zones identified by CONISS.

	Lake Ben		Lake Small	
Pollen Zone	mFI	N_{fe}	mFI	N_{fe}
1	-	1	290 (221 - 359)	4
2	190 (135 - 255)	5	269 (200 - 342)	13
3	318 (150 - 489)	7	197 (137 - 284)	19
4	199 (142 - 256)	19		
5	119 (90 - 148)	13		

Spearman's correlations between species and mFI reveal different patterns at Lake Ben

and Lake Small. At Ben, among woody taxa, *A. balsamea, B. papyrifera,* and *P. tremuloides*

abundances are significantly negatively correlated with mFI as is shrub *A. incana* (Table 4.4).

Significant positive correlations were found among *P* cf. *banksiana* and *P. strobus.* Other species

were insensitive to changes in mFI ($P \leq 0.05$). At Lake Small, *P* cf. *banksiana*, *L. laricina*, *P.*

tremuloides, and *A. incana* are negatively correlated with mFI. Tree taxa, *Quercus* spp. and

Ulmus spp. are positively correlated with mFI as were shrub *A. viridis* and *Salix* spp.

Table 4.4 Correlation analyses (Spearman's rho) between the mFI and pollen percentages for
Lake Ben and Lake Small.

Taxon	Lake Ben		Lake Small	
	rho	p-value	rho	p-value
Abies balsamea	-0.36	< 0.001	-0.21	0.060
Picea sp.	-0.15	0.059	0.02	0.889
Pinus cf. *banksiana*	0.38	< 0.001	-0.42	< 0.001
Pinus strobus	0.23	0.003	0.21	0.063
Larix larixina	-0.13	0.083	-0.12	< 0.001
Thuja occidentalis/Juniperus	-0.04	0.619	0.11	0.313
Betula papyrifera	-0.17	0.029	-0.06	0.624
Populus cf. *tremuloides*	-0.27	< 0.001	-0.28	0.013
Quercus spp.	-0.08	0.296	0.50	< 0.001
Ulmus spp.	0.02	0.803	0.53	< 0.001
Alnus viridis	-0.15	0.056	0.24	0.032
Alnus incana	-0.33	< 0.001	-0.57	< 0.001
Salix spp.	-0.03	0.730	0.41	0.000
Acer spicatum	-0.05	0.537	-0.15	0.180

Discussion

Holocene fire dynamics

Reconstructed local fire events show that the trend in local fire frequency changed over time

(Fig. 4.3c, d) with an overall increase from deglaciation to the present. Our results suggest that

while individual species were affected by fires, overall regional compositions were only

somewhat affected. The following discussion examines the long-term consequences of these

processes on central boreal vegetation, i.e., species-specific reactions to mFI and the community assemblages through time

Early post-glacial vegetation history

Based on the estimated ages and sedimentation rates of the lower most ^{14}C at both sites, it appears that gyttja formation started rapidly following the retreat of the Laurentide Ice Sheet. At Lake Ben, the forested landscape potentially burned as early as c. 10,265 cal. yr BP and at Lake Small the first fire event occurred c. 9,690 cal. yr BP. The rapid afforestation by *Picea* at Lake Ben agrees with other studies in central North American boreal forest (Ritchie and Yarranton 1978; Genries *et al.* 2012) showing that moisture-tolerant trees were present near the front edge of the retreating ice sheet. However, the low pollen influx ($< 10,000$ grains cm^{-2} yr^{-1}) and low $C_{background}$ suggest that the *Picea* and Herb dominated forests of the early Holocene was not as dense as the mid- and late-Holocene forests (Fig. 3a, b, e, f; Fig 4a, b). $C_{background}$, an indicator of biomass burning in the local terrestrial landscape (Marlon *et al.* 2006) was lowest during this afforestation period, and the relatively high abundance of herbaceous species indicates a more open environment and thus biomass was probably too low to support large fires that would be preserved in sedimentary charcoal records (Tinner *et al.* 1996). Following deglaciation, local fire activity was negligible in zone B1 with the onset of zone B2 marking significant increases in fire activity (Fig. 3c). At Lake Small low pollen influx ($< 10,000$ grains cm^{-2} yr^{-1}) persists until c. 8,500 cal. yr BP, coinciding with the first peak in ROC (c. 8,220) which roughly corresponds to the end of pollen zone S1. This seems to indicate that the forest landscape at Lake Small was sparse for much longer when compared to Lake Ben. Low average pollen influx at Lake Small may also be a reflection of lower terrestrial cover and thus vegetation in the surrounding

landscape, as Lake Small is encircled by abundant open-water lakes and wetlands. This delayed afforestation may account for the longer regional mFIs in the early Holocene.

Transition and long-term vegetation dynamics

The beginning of zone B2 corresponds to a densification of the forest cover, as indicated by a sharp increase in overall pollen influx (Fig. 4.3e) and pollen percentages of *P.* cf. *banksiana* specifically (Fig. 4.4b). Vegetation dynamics at both lakes have followed similar trajectories after *c.* 8,750 cal yr BP, which is consistent with vegetation dynamics in nearby northeastern Ontario (Genries *et al.* 2012) and other sites farther east (Liu 1990; Carcaillet *et al.* 2010). However there was one notable difference between sites, where at Lake Ben, *P.* cf. *banksiana* abundance gradually declines following afforestation, the opposite is true at Lake Small where abundance gradually increases to the present. Overall, the main long-term vegetation trajectories identify transitions from *Picea* dominated forests to mixed forests, where *P. banksiana*, *B. papyrifera*, *P. tremuloides*, and *A. viridis* became predominant. Although overall fire frequency fluctuated throughout the Holocene (Fig 4.3c, d) and between pollen zones (Table 4.3), vegetation has changed slightly, much less than might be expected on the basis of observed local fire history, which may indicate that regional compositions are resilient to changes in fire interval (Carcaillet *et al.* 2010).

Fire-climate-vegetation interactions

Because *Abies balsamea* is a late successional tree and the least fire-resistant conifer in the North American boreal forest (Frank 1990), it is counterintuitive that *A. balsamea* pollen abundance was highest when fire was most frequent at Lake Ben (Fig. 4a, zone B5) and marginally significant ($P= 0.06$) at Lake Small. Despite its relatively low pollen abundance (Fig. 4a, b), *A. balsamea* was likely locally present because it has low pollen productivity rates and short

dispersal distances (1 – 2 km) (Richard 1976; MacInnis 2012); as a result, the elevated

abundances were likely inputs from communities near lakeshores or on lake islands where the

species could avoid lethal regional fires and continue to contribute to the fossil pollen record

(Bergeron *et al.* 2004).

The *Picea* taxon was not found to be significantly correlated with mFI at either site.

While *P. mariana* is often a postfire pioneer on both uplands and peatlands and fire typically

results in the immediate regeneration of the species provided an extant local seed source, both *P.*

glauca and *P. mariana* are shade-tolerant and can be abundant in late-successional stands

(Taylor and Chen 2011). The immediate post-glacial afforestation by this species and ubiquitous

presence thereafter (20 - 40%, Fig. 4a, b), attests to the resilience of the taxon to fire frequency

variations. The regional successional role of this taxon is somewhat ambiguous, as its life-history

characteristics can make it suited as both a pioneer and late successional species (Payette 1993;

Taylor and Chen 2011); this also highlights a limitation in using a single taxon to represent

multiple species (Birks and Line 1992; Blarquez *et al.* 2014). Several studies show that increased

regional burning in the Holocene, particularly during the Neoglacial period (*c.* 4,500 – 2,500 cal.

yr BP) can be linked to an increase in the growth of flammable conifer species like *Picea*

(Carcaillet *et al.* 2001; Lynch *et al.* 2002; Higuera *et al.* 2009); no significant increases in *Picea*

abundance were detected at our sites. However, shorter mFIs in the Neoglacial period were

associated with increased abundance of *P.* cf. *banksiana* at Lake Small in zone S3 (4,250 – 0 cal.

yr BP). It is possible that increased fire frequency favored the growth and development of mixed

P. banksiana stands (Fig. 5f) with likely positive feedbacks to the local fire regime.

At Lake Ben, high abundance of *P.* cf. *banksiana* is associated with longer mFIs, this is

noteworthy particularly in zones B4 and B5 where mFIs are shortest and *P.* cf. *banksiana* is least

abundant (6,350 to 0 cal. yr BP). This time period corresponds to the end of the Holocene Climatic Optimum (HCO; *c.* 6,000 yr BP) and continues through the Neoglacial period; since the PCA (Fig. 5e) indicates that the decline in *P.* cf. *banksiana* abundance is associated mainly with increased *B. papyrifera* and *Picea* abundances. Where *B. papyrifera* and *Picea* can grow on a wide variety of soil moistures, optimal growth of *P. banksiana* is limited to very or moderately dry soil moisture regimes (Rudolph and Laidly 1990); as a result the decline in *P. banksiana* may be due to increased regeneration competition post-fire from moisture-tolerant pioneers under cooler and moister regional climatic conditions.

At Lake Ben, *P. strobus* pollen abundance was found to be higher when mFIs were longer; at Lake Small this correlation was only marginally significant (P= 0.06). However, because *P. strobus* pollen is abundantly produced and aerially transported over long distances, there is some doubt as to its true local abundance, particularly due the species continuous low level abundance in both vegetation records, relative insensitivity to changes in local fire frequency at Lake Small, and that the study area is at the northern limit of the modern natural range of the species.

At Lake Small, *L. laricina* is most abundant when mFIs are short (zone S3, Fig. 4b). These results are consistent with local macroremains presented in Senici *et al* (2013), and may indicate that increased fire frequency favoured *L. laricina* in the regional mesic landscape. At both sites, *P. tremuloides* was most abundant when mFIs were short. While *P.* cf. *tremuloides* is the most abundant deciduous species in the central boreal forest, *Populus* pollen is typically underrepresented in palynological reconstructions because it is more susceptible to corrosion than are most other pollen types (Campbell 1999). Abundant *Populus* pollen in our reconstructions may indicate that either the *Populus* pollen preserved very well in our

sedimentary deposits, or that the taxon may have been more abundant in the regional landscape than our pollen stratigraphies suggest.

Prolific growth of clonal shrubs can be a major obstacle in conifer regeneration, due to the speed in which they regenerate by sprouting from basal or underground stems following fire (Mallik *et al.* 1997; Titus and Bishop 2014). In the PCA from Lake Small (Fig. 4.5f), *A. viridis* is in direct opposition to multiple conifers including *Picea, P. strobus, A. balsamea,* and *L. laricina* while at Lake Ben the shrub is most frequent at the expense to *P. strobus, Quercus* spp., *Ulmus* spp. and Herbaceous plants. The correlation analysis indicates higher abundances at Lake Small when mFIs are long which occurs primarily in the mid-Holocene within zone S2 (Fig. 4.4b); no significant correlations were found at Lake Ben. However, *A. viridis* remains one of the most dominant taxa at both sites following afforestation indicating the species is very adaptable and successful regardless of length of mFIs. *A. incana* is significantly negatively correlated to mFI at both site, indicating high local abundance when mFIs are short.

Conclusions

Delayed afforestation at Lake Small may account for the longer mFIs detected at this site in the early Holocene. Overall vegetation composition trajectories move from *Picea* dominated coniferous stands to mixed compositions including *Pinus banksiana, Betula papyrifera,* and *Alnus viridis*. While overall communities appeared insensitive to mFI variations, individual taxons exhibit varied responses between sites indicating potential interactions with local environmental factors, interspecific competition and climate. Additional high-resolution analyses of vegetation variability may reveal more information regarding fire-climate-vegetation interactions and would be beneficial to land management and conservation planning in the region.

Acknowledgements

CHAPTER FIVE Future Work and Conclusion

Future work in the region should focus the development of additional long-term paleoecological records, and the incorporation of the data into broad-scale syntheses. The development of additional charcoal and pollen records in the central boreal shield region would contribute to a more complete understanding of the variability of climate-vegetation-fire interactions across North America. When compared to eastern and western boreal forests there is a relative dearth of paleofire and vegetation records in the vast central region. New records should be developed to provide greater coverage across the various topographic and vegetation gradients in the region. To this end, increased paleoecological reconstructions in the region should focus towards northern and north-western latitudes, where the projected impacts of climate warming are likely to be the greatest (Field *et al.* 2007). Additionally, new sedimentary records could be analysed for multiple proxies using various paleoecological techniques not considered in this dissertation, including but not limited to physical sedimentology, isotope geochemistry, carbon-nitrogen ratios, planktonic assemblages, insects (chironomids, coleopterans) and diatoms, all of which could provide insight into past environmental states and terrestrial-aquatic interactions allowing examinations of how the local ecosystems respond to a wide array of environmental changes. This research could generate useful data and knowledge about the variability of disturbance regimes and interactions between various types of disturbance.

Future work on the unpublished chapters presented in this dissertation should also focus on 2 main areas: 1) the incorporation of pollen data into chapter 3; and 2) the use of long-term paleoclimate data and improved rigor of the main statistical analyses in chapter 4. The third chapter could be significantly improved by the addition of pollen data from chapter four, as it would help to clarify the discussion section and some of the proposed climate-vegetation

interactions that may have influenced the fire regimes at poorly and highly connected sites. Currently, the fourth chapter is largely an exploratory data analysis approach to analyzing the multiple pollen data sets and represents the author's first attempt at understanding pollen records and performing various pollen analyses. The work could be improved by using more rigorous statistical analyses such as a permutational Multivariate Analysis of Variance (formerly 'nonparametric' MANOVA) on the pollen data sets using paleoclimatic (temperature and precipitation) and fire regime (CHAR, $C_{background}$, and FRI) variables to examine fire-climate-vegetation interactions more explicitly and partition the variance throughout the Holocene.

General Conclusion

The development of multiple Holocene records of forest fire has allowed for the analysis of the relative importance of various spatial controls of fire as well as how some of those controls have varied over time. The results from this study highlight the importance of considering local-environmental factors when interpreting paleoecological records of fire and vegetation. By quantifying how fire regimes have responded to past environmental change, the information in this dissertation can be used to better construct models of how forest vegetation and fire regimes may respond to ongoing global climate change. The most important ecological insights provided by this dissertation is also one of the most obvious, that change is typical, fluctuations and variability in fire activity and ecosystem response are normal and expected. Only by understanding the natural variability of wildfire, how and where it originates and its consequences to communities and ecosystems can we truly begin to develop research programs necessary to understand and protect the boreal forest in the future.

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Appendices

SI 2.1: Figure S1

Lake Ben – CHAR raw series
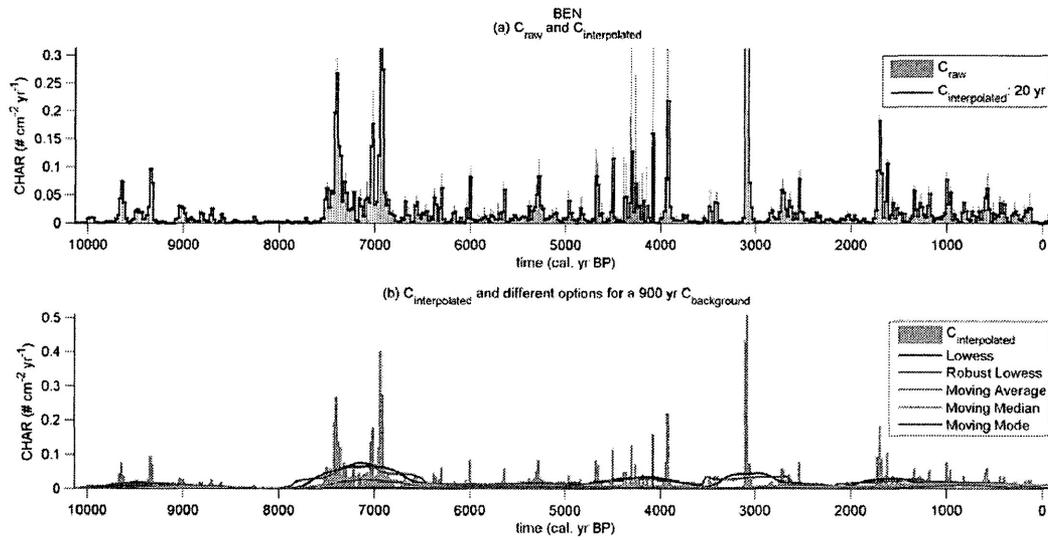
Lake Small – CHAR raw series
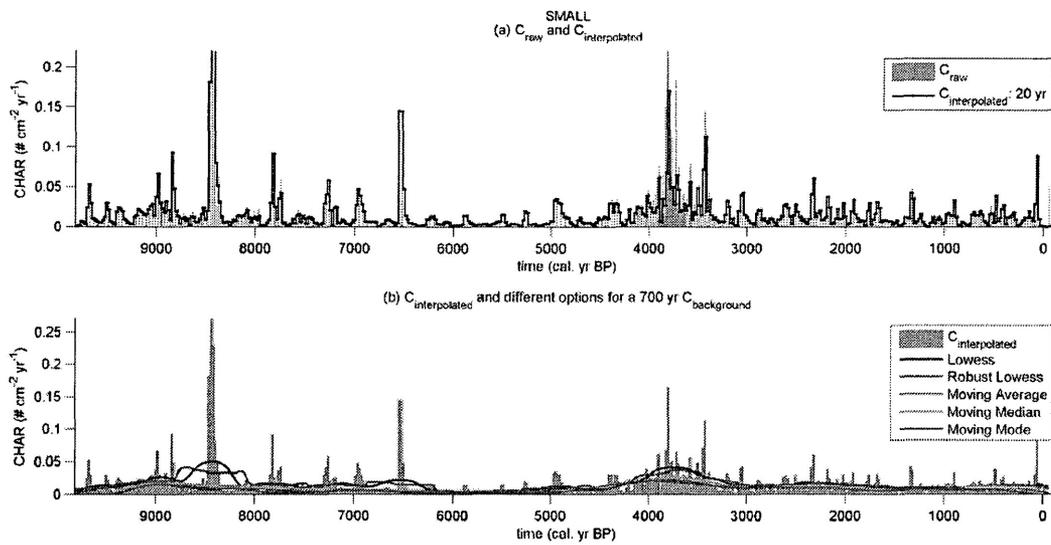
SI 2.2: Figure S2

Lake Ben – Macroremains raw counts
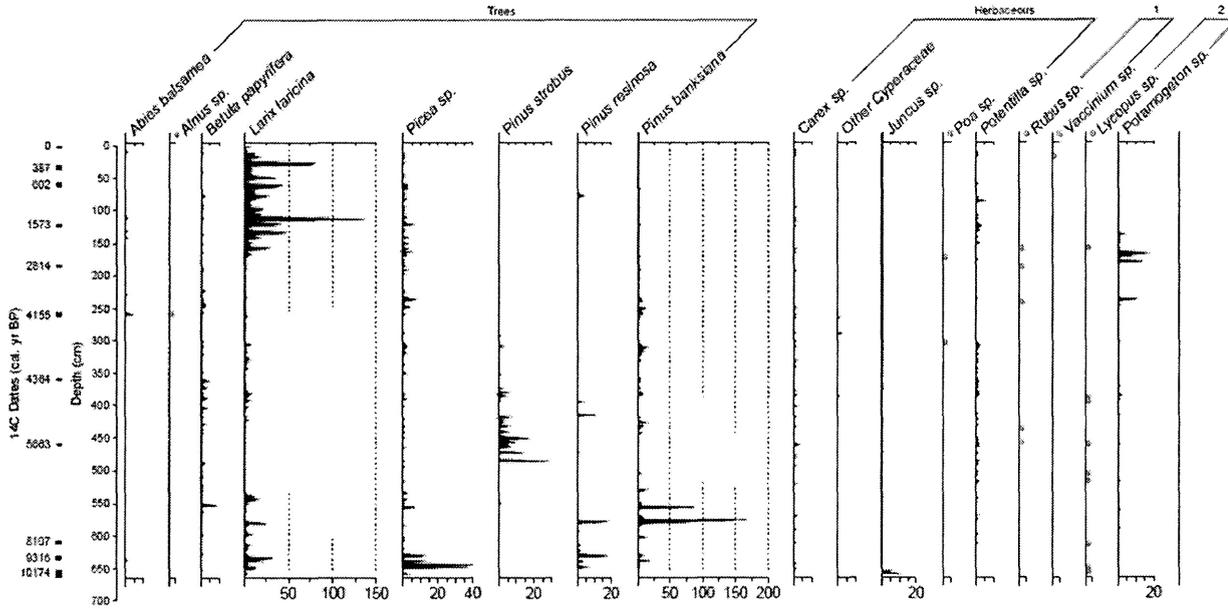
Lake Small – Macroremains raw counts
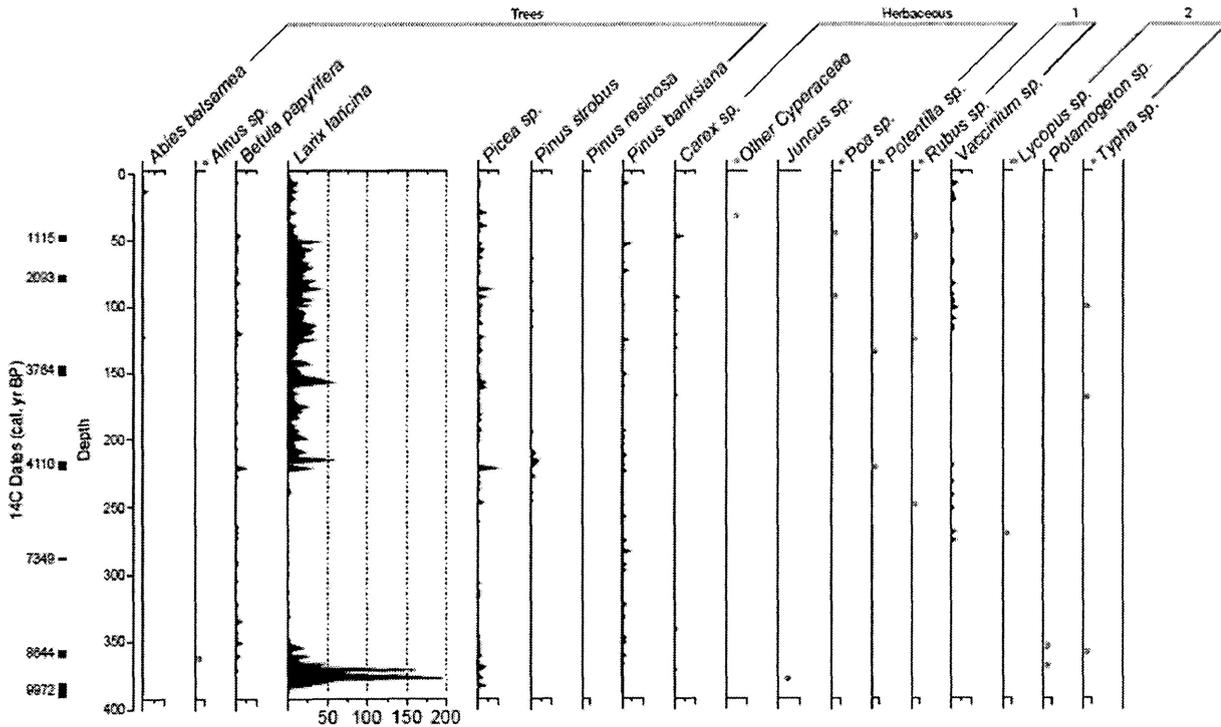
SI 3.1: Table S1

Table S1: Accelerator mass spectrometry 14C dating of the study lakes (mean ± 1 SEM)

Site and depth (cm)	^{14}C year BP	Calibration range (cal. years BP; 2σ)	Materials dated	Lab. Code
AVR				
415-420	615 ± 30	601 (549-656)	Plant macroremains	Poz-48149
450-455	905 ± 30	833 (744-911)	Plant macroremains	Poz-48150
520-525	1815 ± 30	1757 (1640-1825)	Plant macroremains	Poz-48151
595-600	2800 ± 35	2902 (2803-2994)	Plant macroremains	Poz-48152
670-675	4400 ± 35	4953 (4851 - 5253)	Plant macroremains	Poz-48169
757-758	6500 ± 40	7418 (7323-7486)	Bulk sediment	Poz-48147
859-860	8430 ± 50	9461 (9317-9524)	Bulk sediment	Poz-48148
874-880	8860 ± 50	9989 (9734-10161)	Plant macroremains	Poz-48155
BEN				
30-35	320 ± 30	387 (309-473)	Plant macroremains	Poz-39543
58-60	605 ± 30	602 (545-653)	Plant macroremains	Poz-39542
120-122	1670 ± 30	1573 (1512-1685)	Plant macroremains	Beta-293602
184-185	2720 ± 30	2814 (2764-2874)	Plant macroremains	Beta-293601
259-260	3780 ± 40	4155 (4008-4302)	Plant macroremains	Beta-293600
359-360	3930 ± 40	4364 (4247-4504)	Plant macroremains	Beta-293599
459-460	4940 ± 40	5663 (5603-5831)	Plant macroremains	Beta-293598
606-610	7310 ± 40	8107 (8025-8190)	Plant macroremains and charcoal	Poz-39541
631-635	8300 ± 50	9316 (9134-9440)	Plant macroremains and charcoal	Beta-293597
651-661	8990 ± 50	10174 (9934-10232)	Plant macroremains	Poz-39891
DOM				
576-581	180 ± 30	179 (2-287)	Plant macroremains	Poz-48166
616-621	1255 ± 30	1210 (1088-1271)	Plant macroremains	Poz-48167
686-691	2065 ± 30	2033 (1950-2118)	Plant macroremains	Poz-48168
756-761	3155 ± 30	3382 (3305-3443)	Plant macroremains	Poz-48169
826-831	4630 ± 35	5407 (5302-5462)	Plant macroremains	Poz-48170
896-899	5880 ± 40	6702 (6585-6788)	Plant macroremains	Poz-48171
963-971	7590 ± 50	8396 (8314-8508)	Plant macroremains	Poz-48172
998-1007	8860 ± 50	9989 (9734-10161)	Plant macroremains	Poz-48173
BVR				
306-307	575 ± 30	602 (534-644)	Bulk sediment	Poz-48156
335-336	1090 ± 35	977 (821-1131)	Bulk sediment	Poz-48300
387-388	2710 ± 35	2809 (2759-2876)	Bulk sediment	Poz-48158
440-441	3300 ± 35	3524 (3451-3623)	Bulk sediment	Poz-48159
500-501	3870 ± 35	4306 (4166-4409)	Bulk sediment	Poz-48161

560-561	6490 ± 50	7391 (7295-7493)	Bulk sediment	Poz-48162
629-630	8480 ± 50	9495 (9416-9536)	Bulk sediment	Poz-48163
647-648	9850 ± 50	11251 (11200-11384)	Bulk sediment	Poz-48165
DUB				
410-420	395 ± 30	467 (331-506)	Plant macroremains	Poz-48175
455-460	1640 ± 30	1538 (1424-1618)	Plant macroremains	Poz-48176
525-530	3085 ± 35	3306 (3217-3375)	Plant macroremains	Poz-48177
595-600	5120 ± 40	5843 (5753-5947)	Plant macroremains	Poz-48178
675-674	6860 ± 40	7689 (7617-7786)	Bulk sediment	Poz-48179
739-740	7830 ± 50	8613 (8485-8865)	Bulk sediment	Poz-48180
810-820	8820 ± 50	9874 (9681-10141)	Plant macroremains	Poz-48181
830-840	8960 ± 50	10085 (9919-10221)	Plant macroremains	Poz-48182
SML				
47-50	1190 ± 30	1115 (1014-1221)	Plant macroremains and charcoal	Beta-293608
76-80	2120 ± 30	2093 (2006-2285)	Plant macroremains and charcoal	Beta-293607
145-150	3490 ± 40	3764 (3652-3865)	Bulk sediment	Beta-293606
216-220	3750 ± 40	4110 (3989-4233)	Plant macroremains and charcoal	Beta-293605
287-288	6410 ± 40	7349 (7349-7419)	Plant macroremains	Beta-293609
356-360	7860 ± 40	8644 (8563-8917)	Plant macroremains	Beta-293604
380-390	8850 ± 40	9972 (9972-10150)	Plant macroremains	Beta-293603

SI 3.2: Table S2

Table S2: Spearman correlation matrix of environmental variables.

	Non-fuel	Glaciofluvial	Morainal	Peatlands	Open-water	Wetlands	Dry drainage	Total organic
Non-fuel	1	-0.01	-0.38	0.01	0.94	0.71	0.07	-0.50
Glaciofluvial	-0.01	1	-0.79	-0.13	-0.01	0.00	-0.82	0.68
Morainal	-0.38	-0.79	1	-0.37	-0.31	-0.36	0.84	-0.53
Peatlands	0.01	-0.13	-0.37	1	-0.10	0.24	-0.34	0.28
Open-water	0.94	-0.01	-0.31	-0.10	1	0.44	0.19	-0.61
Wetlands	0.71	0.00	-0.36	0.24	0.44	1	-0.22	-0.06
Dry drainage	0.07	-0.82	0.84	-0.34	0.19	-0.22	1	-0.89
Total organic	-0.50	0.68	-0.53	0.28	-0.61	-0.06	-0.89	1

SI 3.3: Table S3

Table S3: Final model results using 20 and 30 year temporal resolution fire reconstructions.

Model	Term	20-year resolution			30-year resolution		
		Estimate	SE	*p-value*	Estimate	SE	*p-value*
Model 1	(Intercept)	5.334	0.012	< 0.001	5.555	0.008	< 0.001
	Time	0.060	0.004	< 0.001	0.068	0.004	< 0.001
	Non-fuel	0.091	0.012	< 0.001	0.087	0.008	< 0.001
	Peatlands	-0.017	0.012	0.162	-0.055	0.008	< 0.001
	Dry drainage	0.016	0.013	0.227	0.017	0.008	0.042
	Time × Non-fuel	0.040	0.004	< 0.001	0.073	0.004	< 0.001
	Time × Peatlands	-0.052	0.004	< 0.001	0.011	0.004	0.015
	Time × Dry drainage	-0.065	0.004	< 0.001	-0.076	0.004	< 0.001
Model 2	(Intercept)	5.332	0.011	< 0.001	5.557	0.022	< 0.001
	Time	0.058	0.004	< 0.001	0.067	0.004	< 0.001
	Open-water	0.049	0.013	< 0.001	0.061	0.027	0.023
	Wetlands	0.058	0.013	< 0.001	0.039	0.027	0.142
	Dry drainage	0.029	0.012	0.018	0.037	0.025	0.142
	Time × Open-water	0.011	0.005	0.032	0.047	0.005	< 0.001
	Time × Wetlands	0.033	0.005	< 0.001	0.038	0.005	< 0.001
	Time × Dry drainage	-0.040	0.005	< 0.001	-0.075	0.004	< 0.001
Model 3	(Intercept)	5.335	0.023	< 0.001	5.558	0.027	< 0.001
	Time	0.060	0.004	< 0.001	0.066	0.004	< 0.001
	Open-water	0.072	0.030	0.016	0.068	0.034	0.047
	Total organic	-0.017	0.030	0.577	-0.030	0.035	0.381
	Time × Open-water	0.059	0.005	< 0.001	0.119	0.005	< 0.001
	Time × Total organic	0.063	0.005	< 0.001	0.105	0.005	< 0.001