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Holocene fire regimes and treeline migration rates in sub-arctic Canada

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ABSTRACT

Holocene climate change resulted in major vegetation reorganization in sub-arctic Canada near modern treeline. However, little is known of the effects of long-term climate change on boreal forest composition and fire regimes below treeline in this region. We present a high-resolution vegetation and fire history from two sites within the modern boreal forest in the central Northwest Territories, Canada, to provide new insight on sub-arctic vegetation response to Holocene climate dynamics and the role of fire in boreal ecosystems. Palynological analysis of sediments retrieved from Waite and Danny's lakes (informal) is used to reconstruct regional vegetation dynamics and boreal fire regimes. The longer Danny's Lake record documents treeline expansion beginning at ca. 7430–7220 cal yr BP. Integration of our new data with previous work shows that treeline expanded between ca. 4050 cal. yr BP and ca. 3840 cal yr BP at a rate of ca. 50 m/yr in response to the 1–2 °C increase in temperature estimated for the Holocene Thermal Maximum. Forest fires were relatively frequent during the early Holocene, before declining in frequency in response to development of cooler and wetter climate conditions associated with the Neoglacial (beginning after ca. 2200–2320 cal yr BP). We document a trend of increasing fire frequency in the 20th century that is correlated with warming at this time. These dynamics south of modern treeline provide insight into factors creating heterogeneity in plant community responses to large-scale climate events in high northern latitudes and suggest that large scale reorganization of boreal vegetation and fire regimes can be expected over the coming decades.

1. Introduction

The large areal extent of the northern boreal forest affects the radiative balance of Earth by acting as a sink in the global carbon cycle (Ahlgren and Ahlgren, 1960; Bonan et al., 1992; Juday et al., 2005). The northern treeline is linked to the summer position of the Arctic Front, which is the southern boundary of the cold, dry arctic air. Through this connection with the Arctic Front, the northern treeline is linked to ocean-atmospheric phenomena and teleconnections (Bryson, 1966; Moser and MacDonald, 1990; Allan et al., 1996). Due to connections between latitudinal treeline and climate, factors influencing boreal forest composition and treeline position are important for climate research. To better understand and forecast climate-terrestrial feedback effects, we look to past climate events and their specific effects on the boreal forest.

Our new data and integration with previous work provides insight into rates of boreal terrestrial ecosystem change in response to climate variability in an ecologically sensitive sub-arctic region. Rates of ecosystem change are critical for understanding how systems will respond in coming decades to current and forecasted climate change. We also document changes in regional forest fire history in sub-arctic Canada. This is important because forest fires shape forest communities through elimination and because lightning produced during summer storms is the primary ignition source for boreal forest fires (Kochtubajda et al., 2006). Due to the link between summer storms and forest fires, fire history is likely to reflect climate changes. For instance, longer, warmer and drier summer months are linked to an increase in lightning-initiated forest fire occurrences (Kochtubajda et al., 2006).

Previous studies across the sub-arctic, including Canada, Sweden, Finland, Norway, and Russia document mid-Holocene northern treeline expansion and subsequent late Holocene contraction. In Russia, postglacial forests covered the landscape by ca. 9000 to 8000 cal yr BP at relatively high latitudes (60° N) but began to retreat by ca. 4000 to 3000 cal yr BP (MacDonald et al., 2000). In Sweden, Finland, and

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Norway, treeline expansion occurred at ca. 6300 cal yr BP, and was followed by retreat at ca. 4500 cal yr BP (Barnekow, 1999; Barnett et al., 2001; Barnekow and Sandgren, 2001; Bergman et al., 2005).

Increased solar insolation centred at ca. 10,000 cal yr BP left much of northwestern North America ice free and covered by birch-shrub tundra, while eastern North America remained covered by the Laurentide Ice Sheet (Berger and Loutre, 1991; Overpeck et al., 1987; Dyke, 2005). By ca. 7000 cal yr BP, boreal forest or forest tundra stretched across most of western and central North America and by ca. 5000 cal yr BP, boreal forests had expanded at least 150 km north of current position in North America. Modern day North American latitudinal treeline limit was reached between ca. 4000 to 3000 cal. yr BP, with regional variation (Dyke, 2005).

Circumpolar forest expansion occurred in response to elevated temperatures regionally associated with the Holocene Thermal Maximum summer insolation anomaly peaked 12–10 ka, but the effects were expressed in a time-transgressive manner following the final melting of the Laurentide Ice Sheet. These temperature effects began to manifest at ca. 11,000 cal yr BP in Alaska and the northwestern Northwest Territories (NWT) and later in central and eastern Canada between ca. 7000 to ca. 5000 cal yr BP (Kaufman et al., 2004). The Holocene Thermal Maximum was expressed at Carleton Lake (central NWT) between ca. 4000 to 6000 cal yr BP (Upiter et al., 2014).

Estimates of Holocene Thermal Maximum warming from Alaska, central northern Canada, Baffin Island, Labrador, Sweden, Finland, Norway, and Russia suggest a temperature increase of 1–2 °C during its expression (MacDonald et al., 1993; Edwards et al., 1996; Pienitz et al., 1999; Barnett et al., 2001; Barnekow and Sandgren, 2001; Seppa and Birks, 2002; MacDonald et al., 2000; Kerwin et al., 2004; Kaufman et al., 2004; Clegg et al., 2010; Upiter et al., 2014).

To better understand the response of boreal forest ecosystems to climate change, we focus on the central NWT of sub-arctic Canada to reconstruct regional vegetation and forest fire regime over the last ca. 9000 years. We know based on previous work that this region experienced treeline expansion and contraction during the mid-Holocene (Moser and MacDonald, 1990; MacDonald et al., 1993; Pienitz et al., 1999; Huang et al., 2004; Dyke, 2005; Upiter et al., 2014). However, little is known of vegetation dynamics below treeline and the role of forest fires remains poorly understood in boreal systems in general and not known at all for the central NWT in particular. Study of sites below modern treeline can provide information on vegetation reorganization within forest communities during episodes of treeline movement and must be used to study the role of fire in boreal landscape change (Larsen and MacDonald, 1998).

High resolution study of lake sediments can provide insight into rates of vegetation change in response to climate variability. Understanding rates of change are particularly important for accurate prediction of terrestrial ecosystem response to current and forecasted change. We present a decadal-to-centennial scale resolution analysis of pollen, spores, and microscopic charcoal preserved in well-dated sediment cores retrieved from Danny's Lake (informal name) located 30 km south of modern treeline and Waite Lake (informal name) located 80 km south of modern treeline in the central Northwest Territories, Canada (Fig. 1b). These lakes are located along the Tibbitt to Contwoyto Winter Road, a 600 km long winter ice road that is critical to the continued success of the Canadian natural resource industry (Galloway et al., 2010a; Macumber et al., 2011). These areas are of particular interest from a socio-economic perspective because use of the winter road has been affected by recent climate change. **We aim to reconstruct regional vegetation dynamics, including the rate of treeline migration and changes in boreal forest fires in sub-arctic Canada in response to Holocene climate change**. Results from our high-resolution paleoecological study of two new lakes are integrated with previously published paleoecological work on nearby Toronto, Waterloo, Queen's, McMaster, UCLA and Carleton lakes (Moser and MacDonald, 1990; MacDonald et al., 1993; Pienitz et al., 1999; Huang et al., 2004; Upiter et al., 2014) as well as carbon and nitrogen isotope analyses (Griffith, 2014) and grain-size data (Macumber, 2015) from Danny's Lake.

2. Regional setting

Danny's Lake (63° 28′32″N, 112°32′15″ W) is located ~30 km south of latitudinal treeline within the boreal forest of the central Canadian sub-arctic (Fig. 1b; Dyke, 2005). Danny's Lake has a maximum depth of 9 m, a surface area of ~20 ha, and a catchment size of ~400 ha (Macumber et al., 2011). Danny's Lake is not connected to other lakes by any major river or streams. Waite Lake (62°50′59″ N, 113°19′39″W) is located within the boreal forest approximately 80 km south of treeline (Fig. 1b; Dyke, 2005). Waite Lake has a maximum depth of 11 m and a surface area of 685 ha (Macumber et al., 2011). Both lakes lie within the Slave Geological Province of the Precambrian Shield and are underlain by amphibolite-grade paragneiss to quartz biotite schists (Davis et al., 1996). Topography of both sites is characterized by gentle hills covered with forest composed of black spruce (*Picea mariana*), jack pine (*Pinus banksiana*), and dwarf birch (*Betula nana*). Climate is continental, characterized by long, cold winters and brief, warm summers. Data from the nearest weather station in Yellowknife document mean January temperatures of −26.8 °C and mean July temperatures of 16.8 °C and a mean annual precipitation of 302.8 mm (based on records from 1971 to 2000; National Climate Data and Information Archive). Both sites are located within the discontinuous permafrost zone (Brown, 1967).

3. Materials and Methods

3.1. Core Collection

A 118-cm long freeze core was collected from a 4.4 m deep sub-basin of Danny's Lake in March 2010 (Fig. 1c; Macumber et al., 2011). A 2-m long freeze core was obtained from the southern basin of Waite Lake from a water depth of 1.8 m in March 2009 (Galloway et al., 2010a). The sediment-water interface of the Waite Lake freeze was not captured by the freeze core. To obtain these surface sediments we returned to the same site in August 2011 and obtained a 36-cm long sediment core using a Glew corer with an internal barrel diameter of 6 cm (Glew, 1991; Glew et al., 2001).

3.2. Chronology

Twenty-five AMS radiocarbon ages were obtained from bulk sediment from the Danny's Lake sediment core. Ten AMS radiocarbon dates were obtained from nine bulk sediment samples and one terrestrial plant macrofossil from Waite Lake sediment core (obtained using the freeze corer). Three AMS ages were obtained from bulk sediments of the Waite Lake Glew core (Table 1). All samples were pretreated with a standard hydrochloric acid wash to remove carbonate material Faegri and Iversen (1989).

Analyses were performed using the accelerator mass spectrometer (AMS) at the ^{14}CHRONO Dating Laboratory at Queen's University, Belfast. Age depth relationships for the Danny's Lake sediment core and the Waite Lake sediment core (freeze core) were constructed using the computer program Bacon version 2.2 and the IntCal13 calibration curve (Figs. 2 and 3; Blaauw and Christen, 2011; Reimer et al., 2013; Crann et al., 2015). Radiocarbon ages younger than AD1950 were calibrated using CALIBomb (Reimer et al., 2004) with the NH_zone1.14c dataset (Hua and Barbetti, 2004). The age modeling procedure we used in Bacon is similar to that outlined in Blaauw and Christen (2005) but more numerous and shorter sections were used to generate a more flexible chronology (Blaauw and Christen, 2011).

A mean sediment accumulation rate of 70 yr/cm was used *a priori* in Bacon based on a summary of accumulation rates of sediment in lakes of the study region by Crann *et al.* (2015). Age depth relations in the Waite

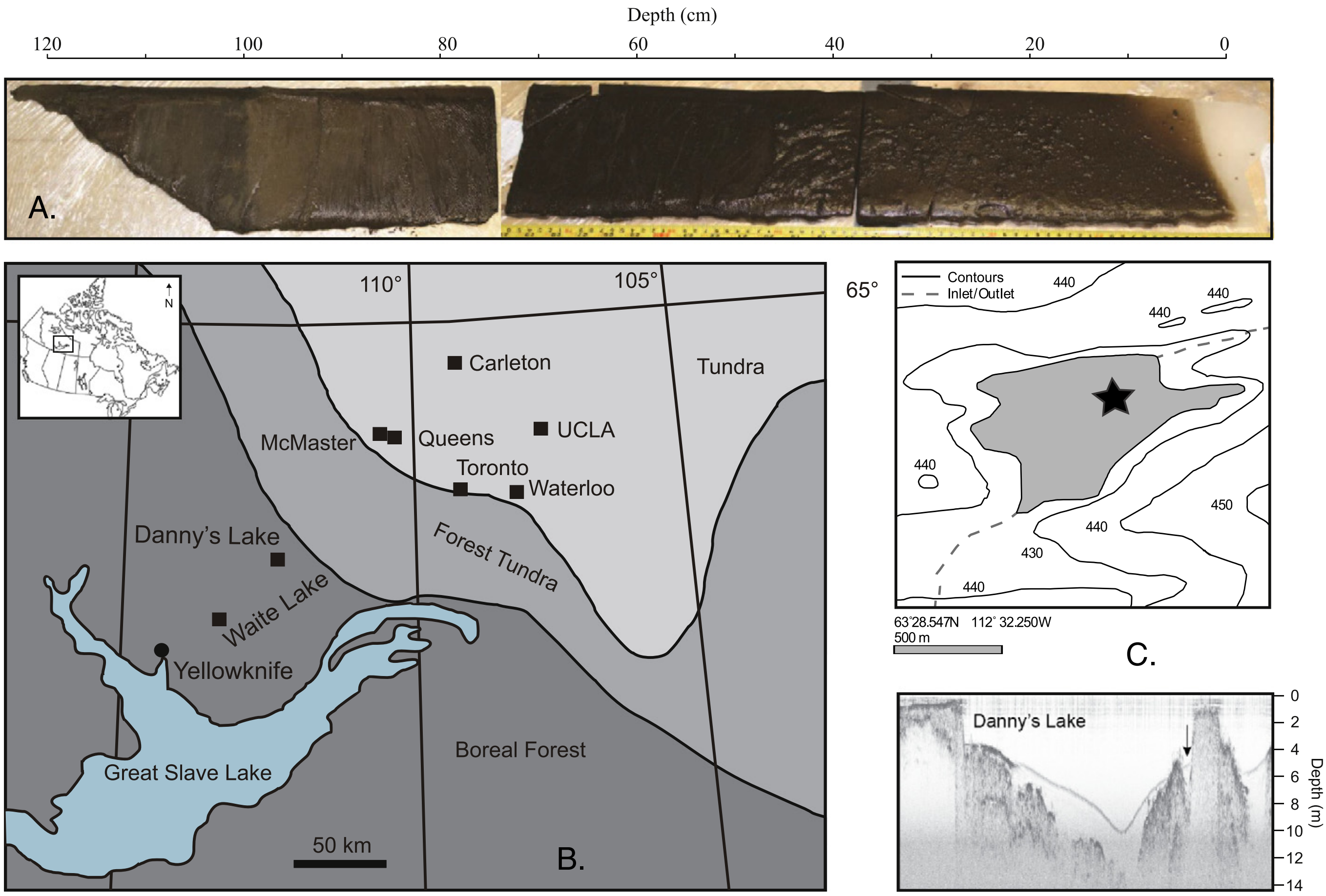

Fig. 1. A. Photograph of the Danny's Lake sediment core. B. Location of Waite and Danny's lakes (this study) coring sites in relation to other central Northwest Territories localities: McMaster (Moser and MacDonald, 1990), Queen's (Moser and MacDonald, 1990; MacDonald et al., 1993), Toronto (Pienitz et al., 1999), Waterloo (MacDonald et al., 1993), UCLA (Huang et al., 2004) and Carleton (Upiter et al., 2014) lakes. C. Bathymetry of Danny's Lake and core sampling site (star).

Table 1
Taxonomic authority and common names of Danny's Lake taxa.

Latin Name	Authority	Common Name
Pinus spp.	L.	Pine
Pinus banksiana	Lamb.	Jack Pine
Picea spp.	A. Dietr.	Spruce
Picea mariana	P. mill	Black Spruce
Picea glauca	(Moench) Voss	White Spruce
Abies balsamea	(L) P. mill	Balsam Fir
Larix spp.	P. mill	Larch
Larix laricina	Du Roi (K. Koch)	Tamarack
Juniperus spp.	L.	Juniper
Juniperus communis	L.	Common Juniper
Juniperus horizontalis	Moench	Creeping Juniper
Populus spp.	L.	Poplar
Populus tremuloides	Michx	Trembling Poplar
Populus balsamifera	L.	Balsam Poplar
Salix spp.	L.	Willow
Betula spp.	L.	Birch
Betula papyrifera	Marsh.	Paper Birch
Betula nana	L.	Dwarf Birch
Alnus spp.	P. mill	Alder
Alnus incana	L. (Moench)	Grey Alder
Alnus crispa	Ait. (Turrill)	Mountain Alder
Pteridium spp.	L.	Bracken
Botrychium spp.	Sw.	Moonwort
Sphagnum spp.	L.	Peat Moss
Lycopodium spp.	L.	Club Moss
Lycopodium clavatum	L.	Club Moss
Myrophyllum spp.	L.	Watermilfoil
Pediastrum spp.	Meyen (1829)	Green Algae

Lake Glew core were not modelled using the computer program Bacon because there were too few dates obtained for this short core (3 ages).

3.3. Palynology

Fift-seven 1-cm^3 aliquots of sediment were sampled every 2-cm for palynology using a microtome device throughout the length of each core (Macumber et al., 2011). No pollen and spore data was recovered from 46.4 to 36.3 cm (measured top to bottom) due to insufficient material. Sediments were extruded on site every 0.5-cm and sub-samples were obtained every 2-cm for palynological analysis. Forty-seven sub-samples between 20 cm and 131 cm of the 2-m long Waite Lake freeze core were obtained at near continuous 2-cm intervals. There was insufficient sediment volume from the upper 20cm of the core for palynological analysis. Sediments below 131 cm were not investigated because we chose to focus our higher-resolution study of Waite Lake on the latest Holocene when modern climate conditions were developed. Eighteen sub-samples were analyzed from the Waite Lake Glew core at continuous 2-cm intervals.

Processing of samples for palynology was done at the Geological Survey of Canada, Calgary, following methods described by Faegri and Iversen (1989) without hydrofluoric acid treatment. Processing involved hot baths of dilute hydrochloric acid and potassium hydroxide followed by acetolysis and staining with Safranin O. Slurries were mounted using liquid bioplastic. One tablet of *Lycopodium clavatum* spores (Batch No. 938,934; 10,679 spores/tablet) was added prior to processing to calculate palynomorph concentration (Stockmarr, 1971).

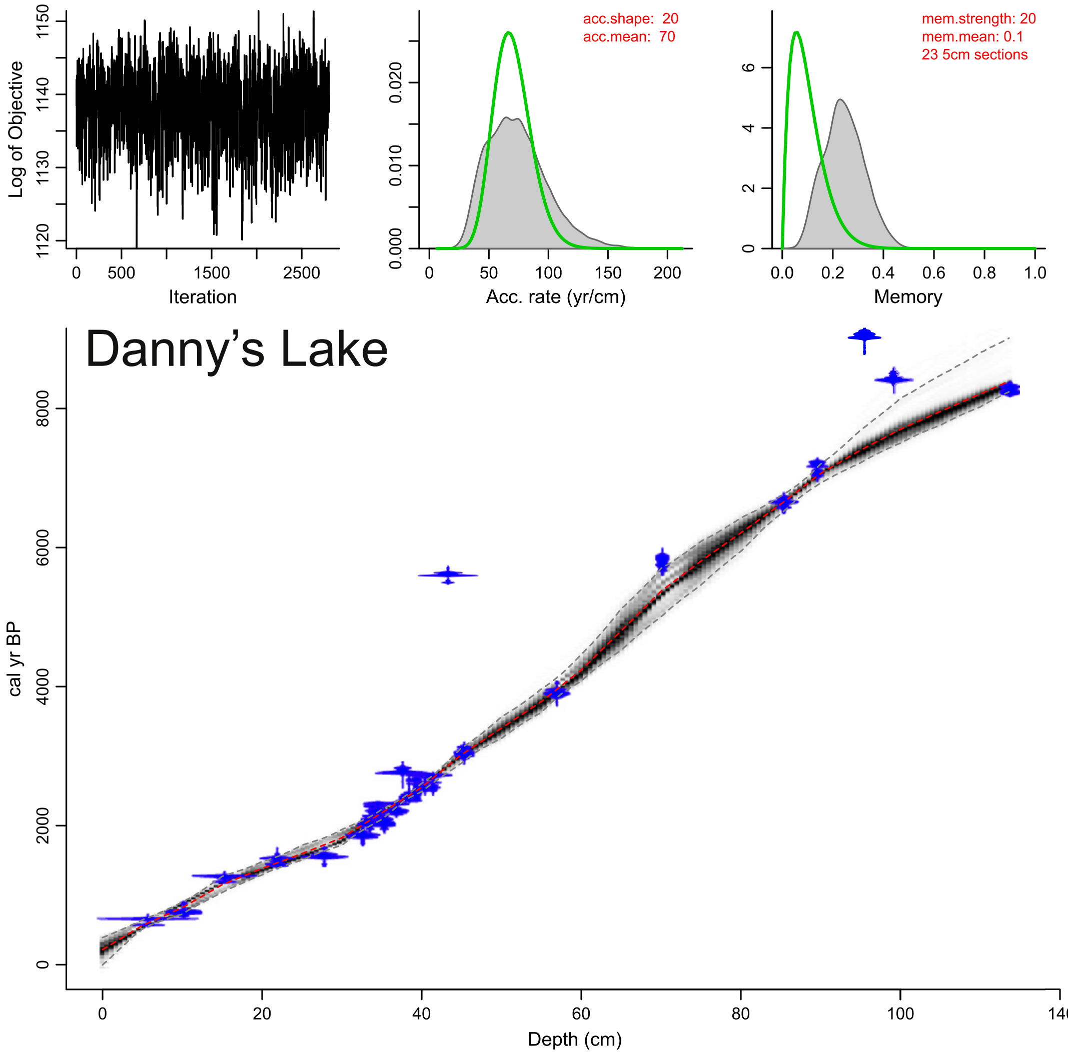

Fig. 2. Bayesian age-depth model developed using Bacon for Danny's Lake. On the top panel, leftmost plot shows that both MCMC runs were stable, middle plot shows the prior (curve) and posterior (filled histogram) distributions for accumulation rate (yr cm − 1), and the rightmost plot shows the prior (curve) and posterior (filled histogram) for the dependence of accumulation rate between sections. The large plot shows age distributions of calibrated ^{14}C ages and the age depth model (grey). Dark grey areas indicate precisely dated sections of the chronology, while lighter grey areas indicate less chronologically secure sections. Bottom graph shows modeled total chronological error range. Chronology reported in Table 1.

A minimum of 300 pollen and spores were enumerated in each sample. The colonial green alga *Pediastrum* and microscopic charcoal were also enumerated. All palynological material is curated at the Geological Survey of Canada. Relative abundances of pollen and spore taxa are based on a pollen sum that includes obligately terrestrial pollen and spores. Microscopic charcoal and *Pediastrum* abundances are expressed as a proportion of this pollen sum. Palynomorph accumulation rates (grains/cm^2/yr) are calculated using palynomorph concentration and an average sedimentation rate of 80 year/cm based on linear regression of the 18 calibrated radiocarbon dates used to generate the Danny's Lake Bacon model. An average sedimentation rate of 14 year/cm is calculated for Waite Lake sediment core (freeze core) (based on 10 AMS radiocarbon dates), and 28 years/cm for the Glew core (based on three AMS radiocarbon dates). Based on models outlined in Crann *et al.* (2015), average sedimentation rates for these sediment cores are consistent with regional data. Stratigraphically Constrained Incremental Sum of Squares Cluster Analysis (CONISS) based on square root transformed relative abundance palynomorph data of obligately terrestrial plants was used to aid in the delineation of pollen and spore assemblage zones of Danny's and Waite lakes palynostratigraphies (Grimm, 1987). Data are graphed using Tilia (Grimm, 1993-2004).

Pollen and spore identifications follow McAndrews *et al.* (1973) with the exception of *Picea* and *Betula*. Many authors have debated the defining characters of *Picea mariana* and *Picea glauca* pollen (e.g., Kapp, 1969; Birks and Peglar, 1980; Hansen and Engstrom, 1985; Lindbladh et al., 2002). In particular, average grain length measurements show a distinction between the maximum sizes of the two species but individual size ranges can overlap (Kapp, 1969; Brubaker et al., 1987). This overlap makes differentiation difficult. Hansen and Engstrom (1985) found that the sacci of *P. mariana* pollen taper distally, or are rounded distally and constricted at its attachment to the corpus, whereas the sacci of *P. glauca* are comparatively round to blunt. Lindbladh *et al.* (2002) described *Picea glauca* in similar terms, but noted that *P. glauca* was larger (>86.5 μm) and showed a high degree of exine verrucation.

In contrast, *P. mariana* has a smaller total grain size (<86.5 μm) and an undulating exine. However, since no *Picea* pollen in this study had exine undulation, we have classified *P. mariana* grains as specimens having noticeable bladder constriction and smaller than 86.5 μm in average grain length. *Picea* pollen larger than 86.5 μm average grain lengths with no bladder constriction are assigned *P. glauca*, following a combination of characters from Hansen and Engstrom (1985); Brubaker *et al.* (1987) and Lindbladh *et al.* (2002).

Betula pollen is sub-divided into *Betula pubescens*-type (tree birch), and *Betula nana*-type (dwarf birch) following Blackmore *et al.* (2003) when possible. At least 30 *Betula* pollen grains in each sample are

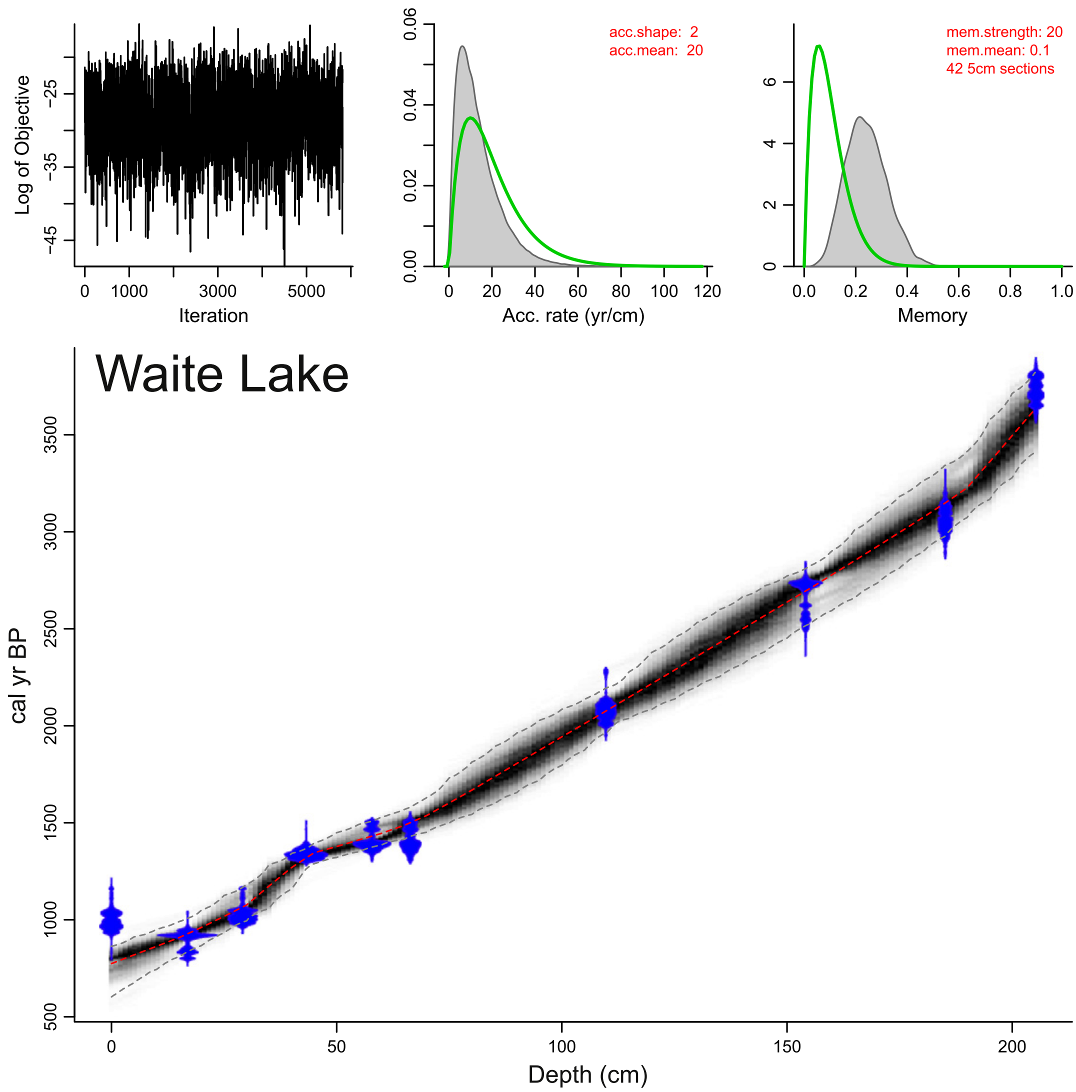

Fig. 3. Bayesian age-depth model developed using Bacon for Waite Lake. On the top panel, leftmost plot shows that both MCMC runs were stable, middle plot shows the prior (curve) and posterior (filled histogram) distributions for accumulation rate (yr cm − 1), and the rightmost plot shows the prior (curve) and posterior (filled histogram) for the dependence of accumulation rate between sections. The large plot shows age distributions of calibrated ^{14}C ages and the age-depth model (grey). Dark grey areas indicate precisely dated sections of the chronology, while lighter grey areas indicate less chronologically secure sections. Bottom graph shows modeled total chronological error range. Chronology reported in Table 1.

identified to the type level and a ratio of Dwarf/Tree *Betula* pollen was calculated. We attribute tree birch (*Betula pubescens*-type) to *Betula papyrifera* and dwarf birch to *B. nana* based on modern biogeography (Whitford, 2007). This was done to distinguish the different ecologies of tree and dwarf birches (discussed later). Differentiation of *Betula* was not attempted in our analyses of sediments from Waite Lake.

For pollen types difficult to identify to the species level using light microscopy, we base species designations on modern biogeography (Whitford, 2007). *Pinus* pollen identified in sediments of Danny's Lake and Waite Lake are attributed to *P. banksiana*. *Larix* pollen is attributed to L. *laricina*. Cupressaceae pollen is likely from *Juniperus communis* and *J. horizontalis*. We attribute *Populus* pollen to *P. tremuloides* and *P. balsamifera*. *Alnus* pollen is attributed to *A. crispa* and *A. incana*. The genus *Salix* may be represented by up to 9 different species in the study area, so we do not attempt to assign species to this *Salix* grains based on modern biogeography.

At Waite Lake, *Abies* pollen is attributed to *Abies balsamea* and Haploxylon type *Pinus* pollen has no known source plant in the study area. Both pollen types likely represent long distance anemophily or water transport. The closest population of *Abies balsamea* is in northern Alberta (Uchytil, 1991c), an area that is linked to the central Northwest Territories through the Mackenzie River watershed. It is possible that both *Abies balsamea* and Haploxylon type *Pinus* are being fed to Waite Lake through the Mackenzie River basin stream system.

Lycopodium ssp. Indigenous to the study region was differentiated from exotic spores added to pollen preparations based on differential stain acceptance (Stanley, 1966; Heusser, 1983). A listing of taxonomic authority and common names for taxa are shown in Table 2.

3.4. Fire History

Iversen (1941) was the first to recognize the utility of microscopic charcoal found in pollen preparations as a proxy for fires. Counts or surface area of microscopic charcoal are frequently collected along with pollen data to reconstruct fire history (Clark, 1988; MacDonald et al., 1991; Tinner et al., 1998). Microscopic charcoal ($<$100 μm) may be carried aloft during a fire and modelling suggests that particles can travel between 20 and 100 km before deposition (Clark, 1988; MacDonald et al., 1991; Whitlock and Millspaugh, 1996; Tinner et al., 1998; Ohlson and Tryterud, 2000, Gardener and Whitlock, 2001; Conedera et al., 2009). Therefore, microscopic charcoal recorded in the sediments of

Table 2
AMS radiocarbon dates from Danny's and Waite lakes. Bold indicates omitted outliers.

Lab ID	AMS or conv.	Depth range (cm)	^{14}C age (BP) ± 1c	Material Dated	5^{13}C %% (VDPB)	Cal BP ± 2c
Danny's Lake						
UBA-17,359	AMS	5.7	693 ± 21	Bulk sed.	-27.5	567–679
UBA-17,360	AMS	10.2	855 ± 23	Bulk sed.	-30.1	695–795
UBA-16,543	AMS	15–15.5	1329 ± 23	Bulk sed.	-26.3	1184–1299
UBA-17,361	AMS	21.9	1617 ± 25	Bulk sed.	-29.2	1416–1556
UBA-17,431	AMS	27.8	1659 ± 21	Bulk sed.	-27.8	1521–1615
UBA-16,544	AMS	32.6	1916 ± 25	Bulk sed.	-27.5	1818–1904
UBA-20,377	AMS	33.5	2071 ± 24	Bulk sed.	-24.7	1987–2120
UBA-20,378	AMS	34.2	2159 ± 24	Bulk sed.	-27.8	2061–2305
UBA-17,929	AMS	34.5	2257 ± 26	Bulk sed.	-30.2	2158–2343
UBA-20,376	AMS	35.3	2073 ± 28	Bulk sed.	-29.5	1986–2124
UBA-20,375	AMS	36.8	2248 ± 25	Bulk sed.	-29.5	2158–2339
UBA-17,432	AMS	37.6	2659 ± 32	Bulk sed.	-29.0	2742–2884
UBA-20,374	AMS	38.4	2392 ± 25	Bulk sed.	-27.6	2345–2488
UBA-20,373	AMS	39.3	2448 ± 33	Bulk sed.	-29.1	2358–2702
UBA-17,930	AMS	40.4	2549 ± 26	Bulk sed.	-28.6	2503–2748
UBA-20,371	AMS	41.4	2554 ± 28	Bulk sed.	-28.7	2503–2750
UBA-20,372	AMS	43.3	4863 ± 29	Bulk sed.	-24.7	5583–5652
UBA-16,545	AMS	45–45.5	2912 ± 24	Bulk sed.	-29.1	2964–3157
UBA-16,546	AMS	56.9	3604 ± 25	Bulk sed.	-26.2	3845–3975
UBA-16,547	AMS	70.1	5039 ± 51	Bulk sed.	-29.6	5661–5903
UBA-16,548	AMS	85–85.5	5834 ± 29	Bulk sed.	-31.3	6560–6733
UBA-17,931	AMS	89.5	6231 ± 34	Bulk sed.	-29.6	7016–7253
UBA-16,439	AMS	95.5	8112 ± 32	Bulk sed.	-27.3	8997–9125
UBA-17,932	AMS	99.1	7623 ± 38	Bulk sed.	-28.9	8370–8518
UBA-16,440	AMS	113.6	7450 ± 30	Bulk sed.	-24.9	8191–8346
Waite Lake Freeze Core						
UBA-18,474	AMS	0	1084 ± 41	Bulk sed.	-10.3	927–1066
UBA-16,433	AMS	16.9	995 ± 24	Bulk sed.	-18.6	800–961
UBA-16,434	AMS	29.1	1129 ± 22	Bulk sed.	-18.8	965–1076
UBA-16,435	AMS	43.2	1455 ± 23	Bulk sed.	-16.5	1304–1384
UBA-16,436	AMS	57.8	1519 ± 22	Bulk sed.	-21.1	1345–1514
Beta-257,686	AMS	66.3	1520 ± 40	Bulk sed.	-18.6	1333–1520
UBA-15,638	AMS	109.7	2107 ± 29	Twig	-31.7	1997–2149
Beta-257,688	AMS	154	2580 ± 40	Bulk sed.	-18.3	2498–2769
Beta-257,689	AMS	185	2920 ± 40	Bulk sed.	-18.0	2955–3210
Beta-257,690	AMS	205.1	3460 ± 40	Bulk sed.	-17.2	3633–3838
Waite Lake Glew Core						
UBA-18,968	AMS	17–17.5	1.0562 ± 0.003	Bulk sed.	-24.4	AD1956–1957
UBA-18,969	AMS	27–27.5	309 ± 22	Bulk sed.	-26.6	304–455
UBA-18,970	AMS	37–37.5	556 ± 26	Bulk sed.	-21.8	522–637

Danny's and Waite lakes are interpreted to represent regional fires that occurred during summer months.

4. Results

4.1. Sedimentology

Sediments preserved in the Danny's Lake sediment core are composed of organic-rich mud and are described in Macumber *et al.* (2011). Sediments obtained from Waite Lake freeze core are also composed of organic-rich mud. Visual properties of this freeze core are described in Galloway *et al*. (2010a). The Waite Lake Glew core is composed of material visually similar to that captured using the freeze core.

4.2. Chronology

The base of the Danny's Lake Sediment core was deposited between ca. 8610–8390 cal yr BP and the top of the Danny's Lake sediment between ca. 440–190 cal yr BP. Based on linear regression, the 2-cm sampling interval used for palynology is equivalent to ca. 160 years (Fig. 2). The sediment-water interface was observed to have been captured during core collection. Mixing of uppermost sediments or an old carbon effect due to dissolution of carbonates or incorporation of old carbon from other sources could have resulted in older than present material at 0 cm in this core (e.g., Hakansson, 1976; Boaretto et al., 1998; Bjorck and Wohlfarth, 2001). We have not altered our chronology to include a freshwater reservoir effect because this effect is variable over time (e.g., Philippsen and Heinemeier, 2013).

Age-depth relationships modelled for the Waite Lake sediment core (freeze) indicate that our palynological analysis of sediments represents the time between ca. 2530–2210 cal. yr BP to ca. 1090–920 cal. yr BP (Fig. 3). The 2-cm sampling resolution used for palynological analysis represents ca. 30 years. Linear regression for the Waite Lake Glew core indicate that sediments range in age from ca. 550–310 cal. yr BP to ca. (−70)-(−280) cal. yr BP. Capture of the sediment-water interface was observed upon extraction of the Glew core at this site. The 2-cm sampling resolution for palynological analyses is estimated to represent ca. 56 years, similar to the Waite Lake freeze core.

4.3. Palynology

4.3.1. Danny's Lake

The Danny's Lake freeze core contains numerous and well-preserved pollen and spores assigned to 19 taxonomic groups (Table 2). The colonial green alga *Pediastrum* is also present. Five pollen and spore assemblage zones are delineated using CONISS and visual inspection of relative abundance of pollen and spores of obligately terrestrial plants preserved in the Danny's Lake core. Zones are labelled DL-1 through DL-5 (Figs. 4, 5).

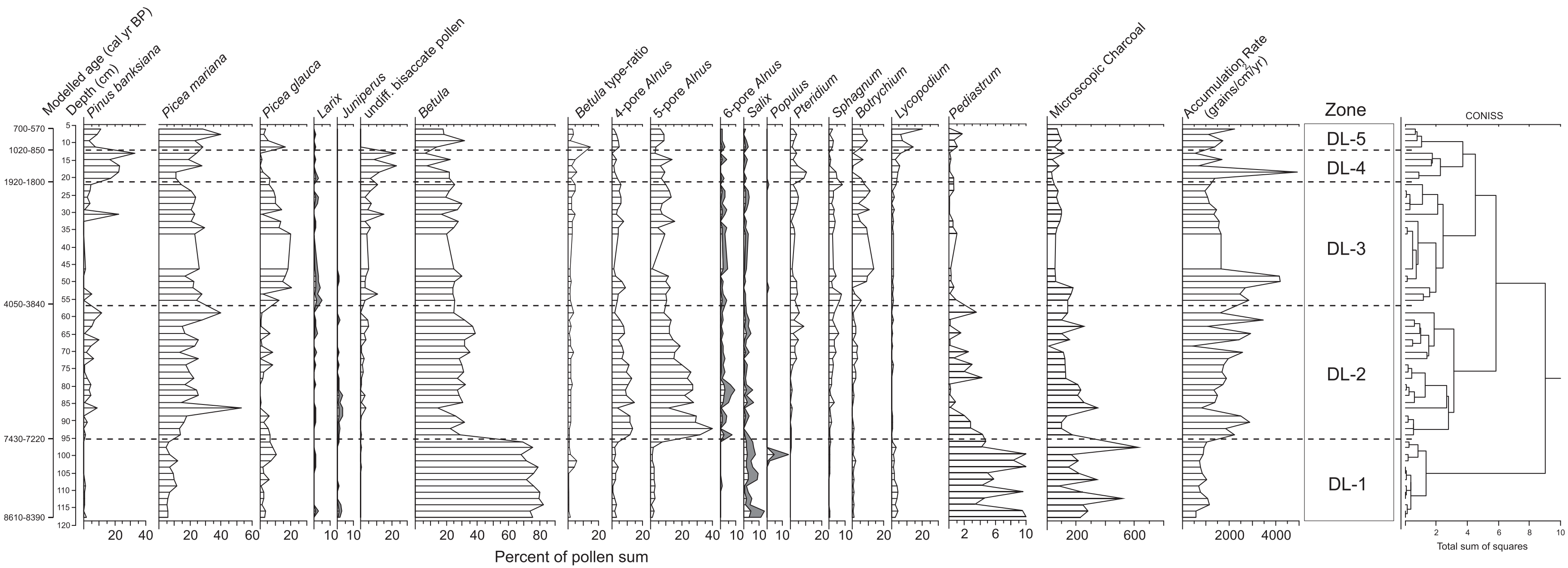

Fig. 4. Relative abundances of pollen and spore taxa preserved in sediments of the Danny's.

Danny's Lake Zone DL-1 (117.7 cm to 93.9 cm; ca. 8610–8390 to ca.7430–7220 cal yr BP) contain a palynoflora composed primarily of *Betula* (60–80%) and *P. mariana* (~15%) pollen. Minor components (~5%) include *P. glauca*, *Alnus*, and *Salix* pollen and *Lycopodium* spores. *Betula*-type ratio is low relative to overlying sediments, except between 105 and 100 cm (ca. 7990–7810 to ca. 7750–7560 cal yr BP), where it rises to about 10, reflecting a greater proportion of *B. nana*. *Pediastrum* occurs up to 10%. Pollen and spore accumulation rate in DL-1 ranges between 2000 and 6000 grains/cm^2/yr. Microscopic charcoal is present up to 700% of the pollen sum (Fig. 4).

Danny's Lake Zone DL-2 (93.9 cm to 55.3 cm; ca. 7430–7220 to ca. 4050–3840 cal yr BP) is characterized by an increase in *Alnus* pollen (up to 40%) and *P. mariana* pollen (up to 25%). *Pinus banksiana* pollen and *Sphagnum* and *Botrychium* spores increase to 10%. *Betula* pollen declines from ~70% in DL-1 to 35–40% in DL-2. The *Betula*-type ratio increases in this zone, suggesting higher proportions of *B. nana* relative to *B. papyrifera*. *Pediastrum* and microscopic charcoal ratios decline to 5% and 500% of the pollen sum, respectively. Pollen and spore accumulation rate increases gradually in this zone from 5000 to 7000 grains/cm^2/yr.

Danny's Lake Zone DL-3 (55.3 cm to 30.6 cm; ca. 4050–3840 to ca. 1920–1800 cal yr BP) is characterized by an increase in *P. glauca* (up to 20%) and *Larix* pollen (up to 5%), and *Sphagnum* and *Botrychium* spores (up to 15%). This coincides with a decrease in the relative abundances of *P. mariana* (down to 15%), *Alnus* (down to 20%) and *Salix* (<5%) pollen. Total *Betula* pollen remains similar to Zone DL-2 (35–40%), but the *Betula*-type ratio decreases. *Pediastrum* and microscopic charcoal continue to decrease to 2% and 300% of the pollen sum, respectively. No pollen and spore data was recovered between ca. 3180–3040 cal yr BP and ca. 2320–2220 cal yr BP due to insufficient material.

After ca. 2320–2220 cal. yr BP (36.3 cm), *P. banksiana* increases from <5% to 10%. Decreases in the proportion of *P. glauca* (down to 5%) pollen occur. Total *Betula* pollen remains constant between 20 and 30%, while the *Betula*-type ratio increases, with more *B. nana*. Microscopic charcoal is lower (~200%) than in Zone DL-2, and pollen and spore accumulation rate is consistently lower after ca. 3880–3650 cal yr BP (53.5 cm), down from 7000 grains/cm^2/yr in underlying sediments to about 2000 grains/cm^2/yr.

Danny's Lake Zone DL-4 (30.6 cm to 11.3 cm; ca. 1920–1800 to ca. 1020–850 cal yr BP) is characterized by an increase in *Pinus* pollen to 35% and *Lycopodium* and *Pteridium* spores while a decrease in *P. glauca* pollen (<5%) occurs. The *Betula*-type ratio gradually increases in Zone DL-4, indicating continued dominance of *B. nana* over *B. papyrifera*. Microscopic charcoal and pollen and spores accumulation rate remain similar to DL-3, near 100% and 2000 grains/cm^2/yr, respectively. One exception to this is at ca. 1370–1180 cal yr BP (18.5 cm), where total accumulation rate increases to 6000 grains/cm^2/yr.

The uppermost Danny's Lake Zone DL-5 (11.3 cm to 5.9 cm; ca. 1020–850 to ca. 700–570 cal yr BP) is characterized by an increase in *P. mariana* (up to 40%), *P. glauca* (up to 20%), and *Betula* (up to 30%) pollen and *Lycopodium* spores (20%). This coincides with a decrease in *P. banksiana* pollen down to 10%. Microscopic charcoal and pollen and spore accumulation rate remain similar to DL-4.

4.3.2. Waite Lake

The Waite Lake freeze and Glew cores contain well preserved pollen and spores assigned to 16 taxonomic groups (Table 2). *Abies* and diploxylon-type *Pinus* do not occur at present in the study area (Whitford, 2007) and their pollen may represent long-distance transport to Waite Lake. The Waite Lake pollen record is shorter than Danny's Lake but the higher resolution approach reveals low magnitude changes in the relative abundance and accumulation rate of palynomorphs. Four palynological assemblage zones are identified by CONISS and visual inspection in the Waite Lake freeze core, labelled WL-1 through WL-4. Two palynological assemblage zones are identified in sediments collected with the Glew core, labelled WL-5 and WL-6 (Figs. 7 and 8).

Palynoflora preserved in Waite Lake Zone WL-1 (131.2 cm to 107.3 cm; ca. 2530–2200 cal yr BP to ca. 2150–1920 cal yr BP) are characterized by pollen from *Abies* (20%), *P. glauca* (10%), *P. banksiana* (10%), *Betula* (15%), and *Alnus* (10%). Only one spore taxa is recorded (*Sphagnum* < 5%) in this zone. *Pediastrum* is present with a relative abundance near 5%. Microscopic charcoal varies between 400% and 900% of the pollen sum. Pollen and spore accumulation rate ranges between 1500 and 4000 grains/cm^2/yr.

Waite Lake Zone WL-2 (107.3 cm to 74.9 cm; ca. 2150–1920 cal yr BP to ca. 1740–1500 cal yr BP) is characterized by a decrease in *Pinus* pollen to <5% and a marginal increase in *Betula* pollen to near 20%, relative to Zone WL-1. The relative abundance of *Pediastrum* declines to 0% but increases to ~8% by the end of the zone. Microscopic charcoal abundances increase at the beginning of this zone to near 900% of the pollen sum and show a gradual decline throughout the zone to 600%. Pollen and spore accumulation rate is lower in this zone than in WL-1, between 1500 and 2000 grains/cm^2/yr.

Waite Lake Zone WL-3 (74.9 cm to 37 cm; ca. 1740–1500 cal yr BP to ca. 1300–1120 cal yr BP) is characterized by a marginal increase in *P. banksiana*-type pollen and a gradual increase in undifferentiated bisaccate pollen. *Pediastrum* peaks to a core maximum of ~10% at the onset of Zone WL-3 before declining 4% in the upper part of the zone. Microscopic charcoal abundance continues to decline in this zone and reach 300% of the pollen sum. Total accumulation rate of pollen and spores increase gradually throughout Zone WL-4 to reach 3000 grains/cm^2/yr.

Waite Lake Zone WL-4 (WL-4; 37 cm to 20 cm; ca. 1300–1120 cal yr BP to ca. 1100–920 cal yr BP) is characterized by marginal increases in the relative abundances of *P. glauca*, *Juniperus*, and *Betula* pollen. The relative abundance of *Pediastrum* occurs near 6% at the onset of Zone WL-4. Pollen and spore accumulation rate increases to a core maximum of 5000 grains/cm^2/yr near the top of the zone. Subtle changes in the relative abundances of *P. banksiana* and *Abies* pollen, both likely long distance transported, differentiate the basal zone of the Waite Lake Glew core (WL-5; 36 cm to 18 cm; ca. 550–310 cal yr BP to ca. 70–30 cal yr BP) from overlying WL-6 (18 cm to 0 cm; ca. 70–30 cal yr BP to ca. -70 to −280 cal yr BP. Pollen and spore accumulation rate is high (between 3000 and 4000 grains/cm^2/yr) in the lower part of Zone WL-5 relative to overlying WL-6, where rates occur between 1000 and 2000 grains/cm^2/yr.

5. Discussion

5.1. The early Holocene (ca. 8610–8390 to ca. 7430–7220 cal yr BP)

A birch-shrub tundra community likely surrounded Danny's Lake during the early Holocene, resulting in the deposition of large abundances of *B. papyrifera* and *Salix* pollen that are preserved in basal Danny's Lake sediments (King, 1993). *Picea mariana* and *Alnus* pollen occur near 5% in basal Danny's Lake sediments. Based on modern European pollen threshold values of Lisitsyna et al. (2011), pollen values near 5% indicate that these plants were present but uncommon on the landscape. Microscopic charcoal preserved in early Holocene aged sediments of Danny's Lake suggests that many regional fires occurred during this interval (Fig. 4). Fire occurrence was likely promoted by relatively warm and dry early Holocene conditions (Patterson et al., 1987; MacDonald et al., 1991; Conedera et al., 2009).

Fuel accumulation was probably less important than climate effects in a birch-shrub tundra environment, as fuel would be limited relative to more forested landscapes. Warmer climate at this time could have promoted more thunderstorms in the summer season, and therefore more ignition events (Kochtubajda et al., 2006). In addition to delayed migration following retreat of the Laurentide Ice Sheet in the central NWT (ca. 7000 cal. yr BP; Kaufman et al., 2004), the relatively frequent fires documented for the early Holocene at Danny's Lake may have maintained early successional taxa, such as *Betula*, while preventing more fire sensitive taxa such as *Picea* from flourishing (Ahlgren and Ahlgren, 1960; Rowe and Scotter, 1973). We record relatively low abundances of *Picea* pollen in this zone (Fig. 4), indicating that *Picea* trees were present regionally. A relatively dry early Holocene climate, indicated by the predominance of *B. papyrifera* over typically moisture-loving *Alnus* may also have been important in excluding *Picea* (Uchytil, 1991a; Matthews, 1992; Fryer, 2011; Fryer, 2014). Similar shrub-tundra communities are recorded at this time elsewhere in the central NWT (Moser and MacDonald, 1990; MacDonald et al., 1993; Seppa et al., 2003; Huang et al., 2004) but earlier in the Mackenzie Region of the territory at ca. 12,000 to 11,000 cal yr BP (Spear, 1993; Ritchie, 1984; Ritchie, 1985; MacDonald, 1987).

The later arrival time of birch-shrub tundra in the central NWT relative to the Mackenzie region is due to the delayed expression of Holocene Thermal Maximum as a result of persistence of the Laurentide Ice Sheet coupled with greater continentality of the central part of the territory (Berger and Loutre, 1991; Overpeck et al., 1987; Kaufman et al., 2004). In the early Holocene, low C/N ratios preserved in Danny's Lake sediments, coupled with relatively high abundances of the green alga *Pediastrum* at this time suggests that summer temperatures were warm, likely promoting lake productivity (Fig. 6; Griffith, 2014).

At high latitudes, lake productivity is related to air temperature because temperature controls the duration of the lake ice-free season and growth period for aquatic organisms (Willemse and Tornqvist, 1999; Jankovská and Komárek, 2000). An enrichment of $\delta^{13}C_{org}$ is recorded in the sediments of Danny's Lake during this interval (Griffith, 2014), suggesting strong evaporation and therefore, warm and dry conditions (Wolfe et al., 1996, 1999, 2003).

Holocene Thermal Maximum warming across sub-arctic North America is estimated to have been 1 to 2 °C due to a 10% increase in solar radiation relative to today (MacDonald et al., 1993; Edwards et al., 1996; Pienitz et al., 1999; Seppa and Birks, 2002; Kaufman et al., 2004; Clegg et al., 2010). While direct radiative forcing peaked between ca. 12,000 to 11,000 cal yr BP, warm conditions prevailed through the middle Holocene in many regions due to climatic feedbacks (Kaufman et al., 2004). Temperatures warmer than present by only 1 to 2 °C were sufficient to induce frequent large fires despite probable low fuel production due to the relatively dry conditions experienced in the region during this time.

5.2. The middle Holocene (ca. 7430–7220 cal yr BP to ca. 4050–3840 cal yr BP)

Picea mariana and *Larix* pollen increase near ca. 7430–7220 cal yr BP in the Danny's Lake record, suggesting that the catchment area began to become forested by locally occurring trees forming open spruce forest-tundra (King, 1993). Pollen and spore accumulation rate increases from 1000 grains/cm^2/yr to 3000 grains/cm^2/yr, indicating expansion of vegetation at this time, likely as a response to moistening and continued warm temperatures associated with the Holocene Thermal Maximum. The increased occurrence of pollen and spores of hygrophilous plants, such as *Alnus*, *B. nana*, *Sphagnum,* and *Botrychium*, suggests that climate was moister than the preceding interval. *Picea mariana*, *B. nana*, *Alnus crispa,* and *A. incana* are most often found on wet soils with poor drainage, such as swamps or bogs (Matthews, 1992; Tollefson, 2007; Fryer, 2011; Fryer, 2014).

Paleofire records frequently record an increase in fire frequency coinciding with *Picea mariana* invasion that may have been a result of highly flammable fuel structures (Uchytil, 1991d; Hu et al., 1993; Hu and Brubaker, 1996; Lynch et al., 2002). However, at Danny's Lake, microscopic charcoal ratios decline to 500% of the pollen sum at this time. This is likely an averaging effect as a result of using regional microscopic charcoal (Clark, 1988; MacDonald et al., 1991; Conedera et al., 2009) or could possibly be that *Picea mariana* did not have a large affect here due to the persistence of the ice sheet.

Beginning at ca. 7270–7070 (93.9 cm), a transition from fine silt to coarse silt as the dominant component in the sedimentary record is observed in the Danny's Lake sediment core (Macumber et al., 2011, Macumber, 2015). Spence and Woo (2008) found that the coarse silt sedimentary fraction is associated with spring melt overflow conditions into lake basins. However, the development of a more densely forested catchment at Danny's Lake at this time would have reduced hydraulic energy during the summer months because vegetation binds sediment making it less available to be eroded (Spence and Woo, 2008). Increased winter precipitation at this time could have resulted in greater snowpack whose melt provided sufficient hydraulic energy during freshet to carry coarser sedimentary components to the lake basin despite the influence of vegetation (Francus et al., 2008; Spence and Woo, 2008). Thus, we interpret the sedimentary change from fine silt to coarse silt to reflect relatively high winter precipitation and snow accumulation (Macumber, 2015).

A positive spike in $\delta^{13}C_{org}$ and negative excursion in C/N ratio occur in Danny's Lake sediments at this time (Griffith, 2014). These changes suggest a nutrient-driven rise in productivity due to the development of wetter conditions or longer ice-free season (Wolfe et al., 1996; Wolfe et al., 1999; Wolfe et al., 2003). This positive $\delta^{13}C$ excursion is immediately followed by a slight depletion of $\delta^{13}C$, interpreted to be due to increased flushing by more open hydrodynamic conditions (Griffith, 2014). A corresponding decrease in *Pediastrum* abundance at this level of the Danny's Lake core suggests a perturbation of planktonic algae communities that could be due to an increase in lake turbidity associated with increased seasonal runoff.

5.3. Middle Holocene treeline expansion

The expansion of *P. mariana* documented at Danny's Lake beginning at ca. 7430–7220 cal yr BP (Fig. 4 and 6) is indicative of the northeastward colonization by spruce in response to the continued warm but moistening mid-Holocene climate associated with the later stages of the Holocene Thermal Maximum (Moser and MacDonald, 1990; MacDonald et al., 1993; Huang et al., 2004; Kaufman et al., 2004). At the outset of spruce colonization, microscopic charcoal recorded at Danny's Lake decreases from 700% to 500% and remains relatively stable throughout ca. 7430–7220 to ca. 4050–3840 cal yr BP (DL-2). Due to resinous needles and cones, *P. mariana* often produces high-intensity fires that kill most or all trees in the stand (Fryer, 2014). Since microscopic charcoal abundances are decreasing during the time of spruce colonization, it is inferred that moister climate conditions led to fewer fires than experienced during the Early Holocene and in conjunction with favourable climate conditions, promoted the northward expansion of *Picea* and latitudinal treeline.

While treeline is documented to have reached Toronto, Waterloo, Queen's and McMaster lakes by ca. 5000 cal yr BP (Moser and MacDonald, 1990; MacDonald et al., 1993; Pienitz et al., 1999), a centennial resolution record from nearby UCLA Lake (Huang et al., 2004) suggests that *Picea* had reached this site as early as ca. 6500 cal yr BP. *Picea* is inferred to have reached Carleton Lake (~140 km east of UCLA Lake) by ca. 4500 cal yr BP based on changes in chironomid assemblages (Upiter et al., 2014). Diachroneity of *Picea* expansion between Danny's Lakes and these more northern sites suggest that northern treeline expanded at a rate of about 50 m/yr during the mid-Holocene in response to a temperature change of only 1–2 °C inferred from proxy records (Upiter et al., 2014).

To date, data from sites further north than Carleton Lake have not been published, with the exception of a record from TK-2 Lake (Seppa et al., 2003), located ~450 km northeast of Danny's Lake in adjacent Nunavut. There is no record of arboreal vegetation at TK-2 Lake (Seppa et al., 2003), constraining mid-Holocene treeline expansion to <66° N. To date, no other studies have attempted to estimate rates of Holocene treeline change, and therefore there are no other studies to compare our inferred rate of treeline migration for the central NT to. However, rates of vegetation change to climate variability can be quite rapid, occurring on a decadal scale, despite presumed lag response times of long-lived vegetation. For example, Galloway et al. (2010b) show rapid (28 year) response of temperate rainforest vegetation to a short-lived mid-Holocene climate perturbation.

5.4. The late Holocene (ca. 4050–3840 to present)

At ca. 4050–3840 cal yr BP, the Danny's Lake pollen record show that trees such as *P. glauca* and *B. papyrifera* began to replace *P. mariana*, *Salix* and *Alnus*, likely due to their superior shade tolerance and longevity (Uchytil, 1991a, 1991b; Moser and MacDonald, 1990; MacDonald et al., 1993; Huang et al., 2004; Fryer, 2014). Permafrost is an important influence in the distribution of plant communities. In the Yukon-Tanana uplands, Dingman and Koutz (1974) report that *P. glauca-B. papyrifera* communities are restricted to permafrost-free areas, such as stream margins where permafrost is absent (Arno and Hammerly, 1977). The vegetation community inferred for Danny's Lake suggests that that the establishment of *P. glauca* and *B. papyrifera* at Danny's Lake could reflect the establishment of permafrost free zones. Chironomid-inferred mean July air temperatures at Carleton Lake are 11.5 °C between ca. 4000 and 3000 cal yr BP and show that by the time *P. glauca -B. papyrifera* communities became established at Danny's Lake that climate had cooled by ~1° since maximum warmth of the Holocene Thermal Maximum (Upiter et al., 2014). A study of peats by Zoltai (1995) demonstrated that at ca. 6000 cal yr BP (approximately 2000 years earlier) permafrost was localized (small, isolated lenses in peats) near Danny's Lake and were sporadic (isolated islands) further to the north near UCLA and Carleton lakes (Zoltai, 1995).

It is likely that the southern limit of discontinuous permafrost documented at ca. 6000 cal yr BP during the height of the HTM began to shift to the south, beginning to approach modern position, with discontinuous permafrost surrounding Danny's Lake (Brown, 1967; Zoltai, 1995). While it is unknown how long it took for permafrost to reach its modern distribution in the central NT, it is possible that HTM warmth permitted expansion of *P. glauca* and *B. papyrifera* within overall cooling conditions due to a lag response time of ground thermal regime to climate and/or a lag response time of vegetation migrating from the south to Danny's Lake. Decreased microscopic charcoal abundance, down to 300% of the pollen sum, and an increase in *Sphagnum* and *Botrychium* spores at this time suggest that climate was becoming progressively moister (Ahlgren and Ahlgren, 1960). *Pediastrum* relative abundances and the organic content of Danny's Lake sediments decrease at this time (Griffith, 2014), suggesting a decline in lake productivity. This decline could be due to increased runoff and terrestrial erosion that led to increased turbidity in the water column, associated with moister conditions. No palynological data was collected between ca. 3180–3040 cal yr BP and ca. 2220–2320 cal yr BP due to insufficient sampling material.

After ca. 2200–2320 cal yr BP at Danny's Lake, *P. glauca* and *Larix* pollen decline and are replaced with pollen and spores from hygrophilous *B. nana*, *Alnus*, and *Botrychium*, indicating progressive moistening throughout this interval (Fig. 4). In the higher resolution decadal-scale Waite Lake palynological record that begins at ca. 2530–2200 cal yr BP (Fig. 5), subtle changes in the relative abundances of pollen are documented. Palynoflora composed primarily of arboreal taxa such as *Abies*, *P. glauca*, *P. banksiana*, as well as *Betula* and *Alnus* reflect a forested environment surrounding Waite Lake during the late Holocene. *Pinus banksiana* pollen declines in relative abundance at ca. 2150–1920 cal yr BP. *Pediastrum* disappears from the Waite Lake record and microscopic charcoal progressively declines from 900% of the pollen sum to a zone minimum of 350% at ca. 2010–1710 cal yr BP. These changes at Waite Lake coincide with a decrease in microscopic charcoal from 200 to 100% of the pollen sum at Danny's Lake, indicating that under this moister climate regime regional fires were also less common near the more northern Danny's Lake in comparison to Waite Lake, probably as a result of less fuel available from less dense vegetation cover and/or cooler air temperatures at the more northern site. Pollen and spore accumulation rate also decrease at Waite Lake at this time, indicating a reduced rate of pollen production. These palynological changes likely reflect vegetation reorganization associated with regional Neoglacial cooling. A sedimentological study of Danny's Lake sediments documents a further gradual decline of the fine silt component starting at ca. 2600 cal yr BP (Macumber, 2015). This component is associated with summer precipitation and would be expected to diminish under a cooling climate regime with shorter summer seasons.

5.5. Late Holocene treeline retreat

Following treeline expansion in response to the HTM, treeline retreat occurred across the North American sub-arctic between ca. 5000 and 3500 cal yr BP (Spear, 1993; MacDonald, 1983; Ritchie, 1984; Ritchie, 1985; Slater, 1985; MacDonald, 1987; Moser and MacDonald, 1990; MacDonald et al., 1993; Szeicz et al., 1995; Szeicz and MacDonald, 1995; Pienitz et al., 1999; Szeicz and MacDonald, 2001; Huang et al., 2004; Upiter et al., 2014). The chironomid record from Carleton Lake documents treeline retreat and establishment of tundra vegetation at ca. 4000 cal yr BP (Upiter et al., 2014). Pollen analysis indicates treeline had retreated from Toronto, Queens, Waterloo, McMaster and UCLA lakes by ca. 3500 to 3000 cal yr BP (Moser and MacDonald, 1990; MacDonald et al., 1993; Pienitz et al., 1999; Huang et al., 2004).

Treeline did not retreat south of Danny's Lake at this time (Fig. 6), but forest reorganization is apparent in the pollen record of this site. For instance, pollen of shrubby taxa such as *B. nana* and *Alnus* increase, while pollen of tree taxa such as *P. glauca* and *Larix* diminish in the pollen record. However, due to insufficient material for analysis, the timing of forest reorganization associated with treeline retreat at Danny's Lake can only be placed between ca. 3180–3040 cal yr BP and ca. 2220–2320 cal yr BP. Treeline retreat across the sub-arctic has been linked to decreasing summer insolation at high latitudes that decreased temperature during the growing season (Huang et al., 2004). Coincident with this treeline retreat, there is an expansion in the North Polar Vortex that would have resulted in cooler climate conditions. This has been documented in terrestrial dust records of the Greenland Summit ice core at ca. 3000–2400 cal yr BP (O'Brien et al., 1995). Average regional temperature increased by 1–2 °C during this time (Seppa and Birks, 2002; Clegg et al., 2010; Upiter et al., 2014).

5.6. The latest Holocene

At ca. 1370–1170 cal yr BP a brief increase of *P. banksiana* pollen at Waite and Danny's lakes may be in response to unusually cool conditions that perturbed boreal forest vegetation. During this time a fine sand component becomes important in the Danny's Lake sedimentological record, likely reflecting an increase in hydraulic energy during the spring melt (Macumber, 2015). Chironomid-inferred July temperatures show a late Holocene air temperature minimum of 10 °C to 11 °C around ca. 1300 cal yr. BP (Upiter et al., 2014). Climate cooling documented in the Danny's and Waite lakes palynological records at this time is broadly coeval with First Millennial Cooling that occurred between ca. 1690 and ca. 940 cal. yr BP in Alaska and on Baffin Island (Clegg et al., 2010; Thomas et al., 2011), which is associated with decreased solar forcing at this time (Wanner et al., 2011). Between ca. 1020–850 to 700–570 cal yr BP, *P. glauca* and *Betula* pollen increase in relative abundance, while pollen and spore accumulation rates decrease in the Danny's Lake sediment record.

The relative abundance of *Pediastrum* increases in both lake sedimentary records and C/N ratios decline in Danny's Lake sediments at this time (Griffith, 2014), suggesting that summer temperatures were relatively warm and promoted lake productivity. In the sedimentological record of Danny's Lake the fine sand component declines and a

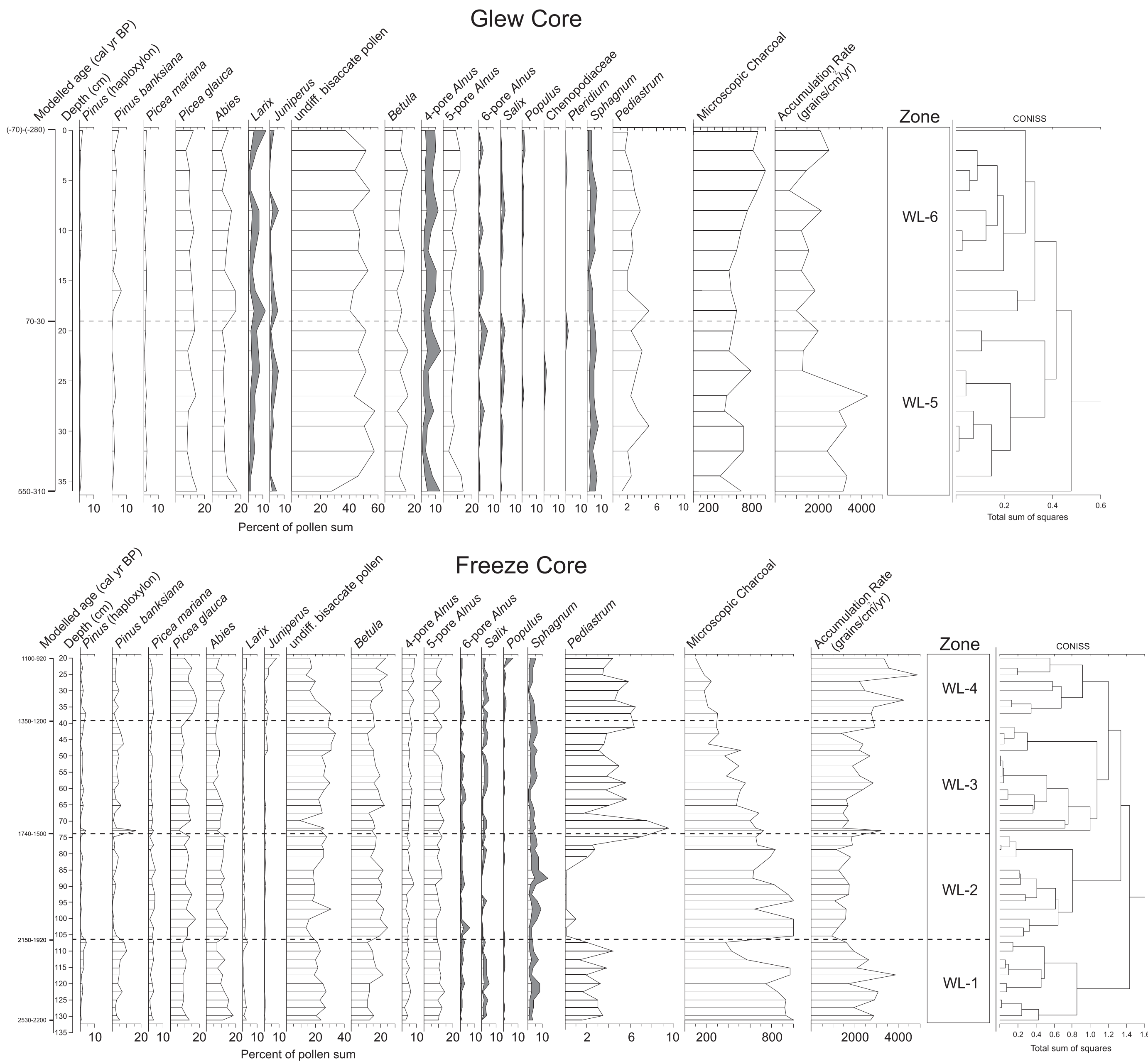

Fig. 5. Relative abundances of pollen and spore taxa occurring in one or more samples at Waite Lake in both the Glew Core (A) and Freeze Core (B). Zonation is based on stratigraphically constrained cluster analysis (CONISS) of pollen and spore taxa shown (Grimm, 1987). Chronology is from Table 1. Shaded areas represent 5% exaggeration.

sustained interval of the fine silt occurs between ca. 930–740 cal yr BP (Macumber, 2015). This is likely due to lower hydraulic energy available during spring melt and longer summer months that contributed greater amounts of fine silt. Chironomid-inferred mean July temperatures documented at Carleton Lake records are as high as 11.5 °C for this interval, a similar temperature to that inferred for the later phases of the HTM (Upiter et al., 2014). This event is time-correlative with the Medieval Warm Anomaly, a time of warming throughout the northern hemisphere that had a variable time range but generally persisted from ca.1000 to 700 cal yr BP (Lamb, 1965; Mann et al., 2009). The Medieval Warm Anomaly is thought to have been caused by anomalously high solar activity and/or variability in the ocean-atmosphere system (Jirikowic and Damon, 1994; Vaquero and Trigo, 2012). These warm conditions may have promoted primary production in Danny's Lake, suggested by the increase in *Pediastrum* and C/N ratios (Griffith, 2014), through longer ice free seasons and promotion of stable thermal regime in the lake. Enlargement of the areal extent of permafrost free zones may have promoted expansion of the *P. glauca* -*B. papyrifera* communities surrounding Waite and Danny's lakes.

The Waite Lake Glew core record spans from ca. 550–310 cal yr BP to the present. Stable boreal forest conditions are documented by the palynological record preserved in these sediments. After ca. 100 cal yr BP pollen accumulation rates decrease and at ca. 70–30 cal yr BP microscopic charcoal abundances rise to a maximum of 950% of the pollen sum, indicating that forest fires became more frequent in the 20th century. In general, typical moisture-loving plants such as *Sphagnum*, *Alnus*, or *Pteridium* do not show much, if any, change at this time in the pollen records presented from Waite Lake. Therefore, it is unlikely that moisture content had increased at this time. While no pollen and spores were analyzed for this interval at Danny's Lake, organic matter and C/N ratio display depletion trends, suggesting a decline in terrestrial vegetation surrounding the lake and possibly increased lake productivity

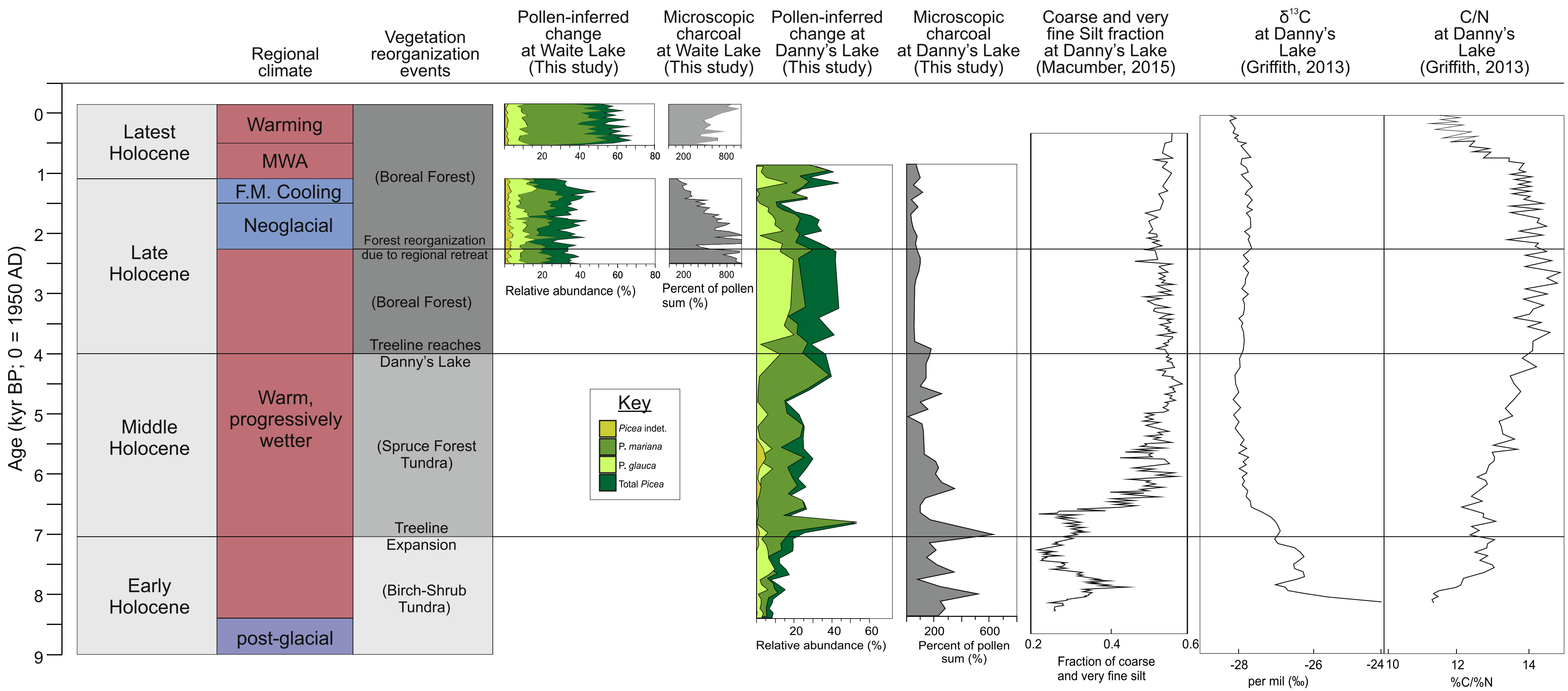

Fig. 6. Summary diagram showing interpreted regional climate and vegetation reorganization events alongside spruce pollen, microscopic charcoal, coarse and very fine silt fraction, $\delta^{13}C$ and C/N ratios of Danny's and Waite lakes.

(Griffith, 2014). Chironomid-inferred July temperatures at Carleton Lake increase to 12 to 13 °C, approaching or exceeding Holocene Thermal Maximum temperatures (Upiter et al., 2014). This combination of increased productivity in Danny's Lake and increased severity and frequency of forest fires at Waite Lake are likely the effects of 20th century warming on the region.

5.7. Latest Holocene treeline change

During the HTM, comparison of the Danny's Lake record to previous literature in the region shows that a temperature increase of 1 to 2 °C above present elicited a northward migration of treeline at a rate of about 20 yr/km. Warm conditions of about 1 °C during the Medieval Climate Anomaly also resulted in vegetation dynamics, but may have been of too short duration to have resulted in detectable treeline movement. Current temperatures in the central NT are now comparable to those experienced during the HTM and have exceeded those experienced during the Medieval Climate Anomaly. If temperatures stabilized it could be reasonably expected that the northern treeline would again advance northward into area currently occupied by tundra in the coming decades, as treeline had previously advanced past Carleton Lake (~200 km northeast of present treeline) during the Holocene Thermal Maximum. Further warming may result in more drastic change.

Increasing fire frequency documented for the 20th century at Waite Lake appears to be approaching regional fire frequency and severity documented during the Holocene Thermal Maximum at Danny's Lake. It is likely that with future projected warming that fire frequency and severity will continue to increase. As fuel sources increase with denser vegetation near modern treeline and ultimately, its northward movement, the area influenced by large forest fires in the central NWT will also expand.

6. Summary and Conclusions

We use pollen and spores and microscopic charcoal preserved in a ca. 8610–8390 cal year old sediment record from Danny's Lake and a 2530–2200 cal year old sediment record from Waite Lake located south of modern latitudinal treeline in the central Canadian sub-arctic to reconstruct treeline migration, vegetation dynamics south of treeline, and regional fire dynamics. Our study provides insight on rates of vegetation and treeline change and predicts the response of boreal vegetation and fire regimes to current and future climate warming. The early-Holocene post-glacial period was a time of warm, dry climate with frequent regional forest fires. Later successional taxa were likely present at Danny's Lake but frequent and/or severe regional fires likely suppressed succession, resulting in the persistence of a birch-shrub community. Middle Holocene vegetation change was driven by a shift to wetter climate with fewer fires that promoted expansion of *Alnus* and *P. mariana* surrounding Danny's Lake as boreal communities expanded northward.

Using our well-dated sediments and comparison to other sites, we estimate treeline expansion rates of ~50 m/yr in response to a 1–2 °C increase in July temperature during the HTM Treeline expansion that continued throughout the middle Holocene, transforming the landscape surrounding Danny's Lake into boreal forest at ca. 4050–3840 cal yr BP. Treeline expansion halted and began to retreat at northern sites after ca. 4000 cal yr BP in response to the development of cooler climates associated with the Neoglacial. Forest reorganization occurred at more southern sites as well. Tree taxa such as *P. glauca* and *Larix* diminish, while pollen of shrubby taxa such as *B.nana* and *Alnus* increase. However, due to insufficient material for analysis, the timing of forest reorganization associated with treeline retreat at Danny's Lake can only be constrained between ca. 3180–3040 cal yr BP and ca. 2220–2320 cal yr BP.

Further development of moist conditions and decreased forest fire activity after 2220–2320 is associated with widespread First Millennial Cooling (ca. 1690–940 cal yr BP). This cooling trend was punctuated by an episode of increased lake productivity and forestation in response to the warming contemporaneous with the Medieval Climate Anomaly (ca. 1000–700 cal yr BP). Conditions following the Medieval Climate Anomaly were relatively stable until the 20th century, where warming has likely driven an increase in fire activity. The Waite and Danny's lake sedimentary records document below- treeline boreal forest dynamics and provide insight on regional responses of sub-arctic terrestrial ecosystems to hemispherical climate events.

While it is clear that forest reorganization and expansion occurred in response to mid-Holocene climate change across the North American sub-arctic, local factors (e.g., permafrost) also created heterogeneity in plant community responses to increased temperatures. The central Canadian sub-arctic was the location of much forest reorganization during the Holocene, and further studies of the area will likely refine our understanding of rates of treeline expansion in the region to inform the rate at which northern environments are, and will, respond to current and predicted climate variability.

Lake core. Zonation is based on stratigraphically constrained cluster analysis (CONISS) of pollen and spore taxa shown (Grimm, 1987). Chronology is from Table 1. Shaded areas represent 5% exaggeration.

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