Original Article

Holocene treeline changes in the Canadian Cordillera are controlled by climate and topography

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Abstract

Aim: Even though ongoing climate change is expected to lead to an upward shift of treelines in mountain areas, evidence for widespread treeline advances remains scarce, implying secondary controls on treeline dynamics at the local scale. We aim to determine if vegetation change in response to past warm periods was regionally synchronous or if local factors such as topography, geomorphology or fire caused divergent local responses.

Location: The Canadian Cordillera in south-eastern British Columbia (Canada).

Methods: We analyzed post-glacial sediments from three lakes at or just below the present treeline for macrofossils, pollen and charcoal to infer past local forest composition, density, dynamics and fire disturbance.

Results: At two lakes (Windy and Redmountain), tree macrofossil concentrations were highest in the warmer-than-present Early Holocene (11’700 – 7000 cal. BP), indicating higher forest density and treeline position during this time period. At the third lake (Thunder), macrofossil concentrations were low during the Early Holocene and reached maximum values in the mid-Holocene (7000 – 3000 cal. BP). The divergent vegetation dynamics and species composition at Thunder Lake suggest that moisture availability may have limited the establishment of closed forests on steep south-facing slopes or shallow soils in the Early Holocene.

Main Conclusions: Summer temperature was the main driver of treeline dynamics over millennial to decadal timescales. Closed forests, however, occurred only in areas of adequate moisture availability, which is controlled by topography and geomorphology. We therefore expect a rapid upward shift of treelines during the 21st century in response to warmer temperatures, but only where deep soils or favourable aspects provide sufficient moisture for tree growth. Upward forest expansion will therefore be patchy and occur first in favourable microsites.

Keywords: British Columbia, climate change, fire history, forest dynamics, macrofossils, moisture availability, palaeoecology, pollen, timberline, vegetation history

Introduction

Climate change in mountain areas is expected to lead to an upward shift of vegetation zones due to thermal control of the upper range limits in many montane and alpine plant species (Körner, 2003; Pauli *et al.*, 2012). Changes in the upper limit of mountain forests (i.e. treeline) are of particular interest for ecosystem managers and global change researchers due to pronounced differences in ecosystem services, microclimate and species pool between alpine meadows and closed subalpine forests (Holtmeier, 2009; Körner, 2012). The upward migration of treeline often leads to a reduction in available area for montane and alpine species due to topographical constraints (Theurillat & Guisan, 2001; Elsen & Tingley, 2015), resulting in the extinction of endemic species in extreme cases. Anticipating future range shifts that could threaten biodiversity and ecosystem services is therefore of vital importance.

Although global warming is more pronounced at high altitudes and latitudes (IPCC, 2013), treeline advances are not uniform. A review of treeline changes by Harsch *et al.* (2009) found evidence for an upward shift of treelines in only half the studies. Besides temperature, factors such as local disturbances (e.g. fire), competition, land-use legacies, geomorphology or topography might play an important role as well (Holtmeier & Broll, 2005; Malanson *et al.*, 2007; Kharuk *et al.*, 2010; Leonelli *et al.*, 2011; Greenwood *et al.*, 2014; Ameztegui *et al.*, 2016; Liang *et al.*, 2016). For example, Macias-Fauria & Johnson (2013) could only successfully model tree presence in the Canadian Rocky Mountains at high resolution (10 m) and over a large area (> 100 km^2), when using geomorphic as well as climatic variables. Using the same statistical model with future climate scenarios, they also showed that geomorphology and topography will severely limit the upward expansion of mountain forests. Holtmeier and Broll (2005) even argued that at the landscape and local scale, topography is the dominant driver of treeline dynamics and that local site conditions are not likely to change with future climate warming.

One way of evaluating the impact of ongoing and future climate change on mountain forests is by studying treeline changes since the last ice age. Summer temperatures during the

Early Holocene thermal maximum (ca. 11’000 – 8500 years before present) were ca. 2-4 °C warmer than present in Western Canada (Chase *et al.*, 2008; Walker & Pellat, 2008; Gavin *et al.*, 2011), similar to climate projections for the end of the 21st century (IPCC, 2013). The analysis of macrofossils, i.e. plant remains such as leaves or seeds preserved in lake sediment, has proven to be a reliable tool for the reconstruction of past treelines due to high spatial resolution (Birks, 2001; Tinner, 2007). Macrofossil abundance has also been linked to tree abundance in the landscape and has been used to infer past changes in forest density (Dunwiddie, 1987; Blarquez *et al.*, 2012).

Previous palaeoecological studies have mainly focused on climatic controls of treeline changes such as temperature (e.g. Rochefort *et al.*, 1994; Pisaric *et al.*, 2003; Mensing *et al.*, 2012). In this study, we were particularly interested in the following research questions: 1) Does subalpine forest react synchronously with climatic changes at our study sites, and 2) What is the role of secondary factors such as fire, topography and/or geomorphology in treeline dynamics during past warm periods? To address these questions, we analyzed lake sediments from three lakes at or just below treeline in British Columbia, Canada, for pollen, macrofossils, and charcoal. We then compared these records with independent summer temperature reconstructions based on fossil species assemblages of non-biting midges (Chironomidae) (Chase *et al.*, 2008). Our proxy records of treeline dynamics and summer temperature variations are from the same sediment cores, thus minimizing chronological issues in the assessment of treeline responses to climatic change.

Materials and Methods

Study sites

The three study sites - Windy Lake, Thunder Lake and Redmountain Lake (informal names) - are small (3 – 20 ha), subalpine lakes in the Canadian Cordillera (Fig. 1, Tab. 1). These lakes are all located within the uppermost forest zone in interior British Columbia, the Engelmann spruce - subalpine fir zone (ESSF). Climate in the ESSF is cold and wet, with most of the precipitation falling as snow. Mean annual temperatures (MAT) range from +2 to -2°C and growing seasons are short (< 3 months). Mean annual precipitation (MAP) is highly variable and ranges from 400 to 2200 mm (Coupé *et al.*, 1991). The vegetation in the ESSF is dominated by *Picea engelmannii* Parry ex. Engelm. (Engelmann spruce) and *Abies lasiocarpa* (Hook.) Nutt. (subalpine fir) with *Pinus contorta* Dougl. ex Loud. var. *latifolia* Engelm. ex S. Wats. (lodgepole pine) in drier areas or after fire disturbance. Other tree species in this zone include *Pinus albicaulis* Engelm. (whitebark pine) in drier areas and *Alnus viridis* (Chaix) DC. subsp. *sinuata* (Regel) A. Löve & D. Löve (slide alder) in wetter areas or avalanche chutes. At low elevations (< 1500 m a.s.l.), forests are dominated by *Tsuga heterophylla* (Raf.) Sarg. (western hemlock) and *Thuja plicata* Donn ex D. Don (western redcedar). The ESSF includes subalpine parkland at its upper elevation, with clumps of trees occurring together with heath, meadows and grassland. Treeline elevation ranges from 2300 m a.s.l. in the southern part of the ESSF to 1700 m a.s.l. in the northern part of the forest zone (Coupé *et al.*, 1991).

All three lakes are located in glacial cirques; however, local topography differs with regard to the steepness and aspects of surrounding slopes (Fig. 1). Windy Lake is located in the Selkirk Mountains at 1813 m a.s.l. On the south and east side of the lake, slopes are fairly steep (> 30°) with avalanche tracks interrupting the otherwise closed forest (Figs 1 & S1.1). Thunder Lake lies at 1539 m a.s.l. in the Cariboo Mountains. Steep south- to east-facing slopes with an elevation gain of ca. 800 m border the lake. Closed forest exists only on the east side of the lake and along ridges sheltered from avalanches. The northernmost study site is Redmountain Lake at

1590 m a.s.l. in the central Canadian Rocky Mountains. The lake is surrounded by fairly gentle terrain with steep slopes only on its south side. It is the only lake located above timberline with lush meadows and small clusters of *Abies lasiocarpa* around the lake. The pollen record of selected taxa from Redmountain Lake was previously published (Gavin *et al.*, 2009). A detailed description of the study sites is given in Table 1 and can also be found in Chase *et al.* (2008).

Sampling methods and chronology

We retrieved sediment cores from the three lakes using a 5 cm diameter Livingstone piston corer in the summers of 2002 and 2003. At each lake, two overlapping cores were taken at the deepest point of the lake basin, split horizontally in the laboratory and combined to a single master core using visual correlation of distinct sediment layers. Because of poor correlation of parallel core drives at Thunder Lake, subsamples for analysis were taken from a single core drive, resulting in a hiatus at ca. 100 cm sediment depth.

The age-depth models of the three lakes (Fig. 2) are based on a total of 16 AMS radiocarbon dates from terrestrial plant remains as well as three distinct tephra layers (Chase *et al.*, 2008). All dates were calibrated to years before present (cal. BP) using the INTCAL13 calibration curve (Reimer *et al.*, 2013). The age-depth models were calculated with clam (Blaauw, 2010) using Monte-Carlo sampling with 1000 iterations and Stineman interpolation (for Windy Lake and Redmountain Lake) or a monotonic spline (for Thunder Lake).

Pollen, macrofossil and charcoal analyses

We processed a total of 143 subsamples of 1 cm^3 (Windy: 49, Thunder 32, Redmountain 62) for pollen analysis following standard procedures with HCl, KOH, HF, acetolysis and mounting in silicone oil (Fægri *et al.*, 1989). To calculate influx and concentration, we added a known number of *Lycopodium* spores to the subsamples before chemical treatment (Stockmarr, 1971). We identified pollen under a light microscope at 400x magnification using published keys (e.g. Fægri *et al.*, 1989) and the reference collection at the University of Oregon. We identified a minimum of 350 terrestrial pollen grains per sample. Pollen percentages were then calculated based on the sum of all terrestrial pollen types. We subdivided the pollen diagram into local pollen assemblage zones using constrained hierarchical clustering and identified the number of significant zones with the broken-stick model (Grimm, 1987) using R 3.1.3 (R Core Team, 2015) with the package 'Rioja' (Juggins, 2015).

For macrofossil and macroscopic charcoal analysis, we sieved a total of 422 continuous sediment samples of 5 to 150 cm^3 (Windy 130, Thunder 160, Redmountain 132) with a mesh size of 250 µm after pretreatment with sodium hexametaphosphate. Macrofossils and charcoal were identified under a stereomicroscope at 10-50x magnification using published keys (Dunwiddie, 1985) as well as the reference collection at the University of Oregon. To allow for comparability between samples and lakes, we calculated macrofossil and charcoal concentrations (number cm^{-3}) and influx (number cm^{-2} yr^{-1}). The temporal resolution of the macroscopic charcoal record was too low for quantitative peak analysis.

Results and Interpretation

Windy Lake

The first needle of *Abies lasiocarpa* appears at ca. 11'800 cal. BP at Windy Lake (Fig. 3). Needles of *Pinus albicaulis* and *Picea engelmannii* occur shortly afterwards (11'700 and 11'400 cal. BP, respectively). By 11'300 cal. BP, macrofossil concentrations and influx increase and show additional distinct peaks throughout the Early Holocene at 10'700, 9700 – 10'000, 9200 – 9500, 8500 – 8800, 7800 – 8300 and 7100 – 7300 cal. BP. Macrofossil concentrations and influx decrease after 7000 cal. BP and stay at low values for the rest of the Holocene. The macrofossil assemblage is dominated by *Picea engelmannii* together with *Abies lasiocarpa* throughout the entire Holocene. *Pinus contorta* is only present in the Early Holocene (11'700 – 7000 cal. BP).

Charcoal concentration and influx at Windy Lake are highest in the Early Holocene (11’700 – 7000 cal. BP), with a conspicuous peak at 9800 cal. BP. Several smaller charcoal peaks are evident in the Early and mid-Holocene, whereas charcoal concentration and influx stay at low values with no distinct peaks in the Late Holocene (4000 cal. BP – present).

High values of *Artemisia* pollen and low values of tree pollen (< 80%) indicate that the lake was surrounded by alpine tundra before 12’000 cal. BP (Fig. S1.2). The first appearance of arboreal macrofossils at 11’800 cal. BP and the pronounced increase in macrofossil concentration and influx after 11’300 cal. BP document the establishment of trees and subalpine forest at Windy Lake. High values of macrofossil concentration and influx suggest that dense subalpine forest surrounded the lake in the Early Holocene, whereas a subsequent decrease points to a more open forest composition since 7000 cal. BP. The local species composition as recorded by macrofossils stayed fairly constant throughout the entire Holocene, suggesting similar forest composition to present-day Engelmann spruce – subalpine fir zone (ESSF).

Thunder Lake

Abies lasiocarpa and *Pinus albicaulis* needles are present in the oldest samples of Thunder Lake at 12’650 cal. BP (Fig. 3). After this brief initial occurrence, arboreal macrofossils are absent in the sediment record for more than a millennium before *Pinus contorta* needles appear at 11’000 cal. BP. *Abies lasiocarpa* and *Pinus albicaulis* macrofossils appear again at 10’600 and 10’000 cal. BP. The first needle of *Picea engelmannii* occurs at 8700 cal. BP. Macrofossil concentration and influx remain low and are dominated by *Abies lasiocarpa* throughout the Early Holocene (11’000 – 7500 cal. BP) before steadily increasing and reaching a peak in the mid-Holocene at 5000 cal. BP. The abundance of *Picea engelmannii* needles in the macrofossil record markedly increases after 7000 cal. BP. After the hiatus, macrofossil concentration and influx decrease to low values around 1500 cal. BP, increase again for c. 800 years and drop to very low values for the last 350 years of the record. *Pinus albicaulis* and *Pinus contorta* needles occur throughout the entire Holocene. Macroscopic charcoal concentrations and influx stay at relatively low values throughout the Holocene, but markedly increase after 1500 cal. BP and stay at high values for more than 1000 years, before decreasing to very low values at the end of the record.

The presence of trees in the Late Glacial as suggested by the needles found in the oldest samples of the record would imply a higher regional treeline prior to the Younger Dryas, followed by an absence of arboreal macrofossils for the Younger Dryas cold period (c. 12’900 – 11’700 cal. BP). The age estimate of the oldest two samples is poorly constrained, however, as it is an extrapolation into inorganic sediments below the lowest radiocarbon date of ca. 11’000 cal. BP. Due to low pollen concentration, the pollen record does not extend to the Late Glacial (Fig. S1.3). At the beginning of the Holocene, the presence of *Pinus contorta* needles and the high percentages of *Pinus* pollen point to an open lodgepole pine forest at the lake (Figs 3 & S1.3). At ca. 10’600 cal. BP *Abies lasiocarpa* established around the lake, as indicated by the presence of macrofossils and the increase in pollen percentages. The species composition and density of the subalpine forest changes significantly after 7500 cal. BP when an increase in macrofossil concentrations and pollen percentages suggest a higher abundance of *Picea engelmannii* around the lake. The conspicuous increase in macroscopic charcoal from 1500 – 400 cal. BP indicates a drastic change in local fire regimes during the Late Holocene.

Redmountain Lake

The first needle of *Abies lasiocarpa* in the sediment record of Redmountain Lake occurs at 9800 cal. BP (Fig. 3). Macrofossil concentration and influx increase by 9500 cal. BP, with the first presence of a *Picea engelmannii* needle. Macrofossil concentration and influx reach the highest values in the Early Holocene (9500 – 7500 cal. BP) before steadily decreasing for the rest of the Holocene. After 3500 cal. BP, macrofossils occur only irregularly and at very low values. The macrofossil assemblage is dominated by *Abies lasiocarpa* and *Picea engelmannii* in the Early Holocene, whereas later, it mostly consists of *Abies lasiocarpa* needles. Macroscopic charcoal concentration and influx values reach highest average values in the Early Holocene, but are highly variable with many distinct peaks throughout the entire record.

Low macrofossil concentrations, as well as low pollen percentages of *Picea* and *Abies,* suggest that Redmountain Lake was either surrounded by alpine tundra or very open treeline forest from deglaciation until 9600 cal. BP (Figs 3 & S1.4). The high concentrations of *Abies lasiocarpa* and *Picea engelmannii* needles indicate closed forest around the lake during the Early Holocene. Macroscopic charcoal also reaches its highest concentrations during the Early Holocene, pointing to increased local fire activity in this period. Increasing pollen percentages of herbs such as Poaceae and Cyperaceae together with low coniferous macrofossil concentrations point to the establishment of the present-day parkland vegetation in the Late Holocene, i.e. after 3500 cal. BP.

Discussion

Climate and topography as drivers of local vegetation dynamics

We use the abundance of macrofossils as an indicator for local tree abundance around our study sites. The quantitative interpretation of plant remains found in lake or mire sediments has a long tradition in Europe and North America (see e.g. Birks, 2001 and references therein). Even though macrofossil abundance of different species in the lake sediment depends on different processes such as production, dispersal, deposition and preservation, Dunwiddie (1987) showed a statistically significant quantitative relationship between conifer needles in surface samples from the Pacific Northwest and the basal area of tree species surrounding the sampling sites. Similarly, Blarquez *et al.* (2012) developed a calibration function to estimate past tree biomass in the landscape based on the annual accumulation rate of conifer needles in the European Alps. We are therefore confident in interpreting the abundance of conifer needles as an indicator of forest density around our study sites. We concede that local events such as snow avalanches or landslides could cause an extremely high influx of macrofossils into the lake and would result in extraordinarily high macrofossil concentrations within a single sample. Indeed, one sample of Redmountain Lake at 6550 cal. BP contained 39 *Abies lasiocarpa* needles, compared with an average of two needles per sample for the entire core. Pollen influx or pollen percentage ratios have also been used to infer local vegetation and, more specifically, the location of treeline (e.g. Pisaric *et al.*, 2003; Mensing *et al.*, 2012). These metrics did not agree with the macrofossil analyses at our study sites (Fig. S1.5), most likely due to different dispersal and within-lake depositional processes. In contrast to pollen, macrofossils provide direct evidence of local tree presence and abundance. Thus we discuss vegetation dynamics at our sites primarily based on macrofossil data.

The macrofossil concentrations at Windy Lake are linearly correlated with the chironomid-inferred temperature reconstruction at both millennial to centennial scales ($r = 0.52$, $P < 0.001$, for the entire record; Fig. S1.6). The timing of tree establishment at 11’800 cal. BP agrees with the rapid warming of up to 6°C (summer temperature) at the transition from the cold Younger Dryas to the warm Early Holocene (Chase *et al.*, 2008). The highest summer temperatures of the record, from ca. 11 – 9 ka, are matched by the highest macrofossil concentrations and influx values, suggesting a more productive and extensive forest around the lake (Fig. 3). Loss-On-Ignition (LOI) analysis shows very low values of organic content in the sediments of Windy Lake during the Younger Dryas, a rapid increase to high values during the Early Holocene and intermediate values during the mid- and late Holocene (Fig. 2a). This pattern suggests higher terrestrial and/or aquatic productivity during the Early Holocene than before and after, consistent with the temperature and macrofossil records. The slow cooling from the Early to Late Holocene as a result of decreasing summer insolation is reflected in a decrease in total arboreal macrofossil concentration and influx (Fig. 3).

Short-term fluctuations in solar activity, possibly linked to summer temperature, coincide with variations in the macrofossil record as well (Fig. 3). Especially during the Early and Late

Holocene, peaks and dips in the macrofossil concentration and influx correspond to high and low solar activity (Solanki *et al.*, 2004). While solar forcing of decadal and centennial-scale climate is far from fully understood, evidence that it is linked to local site variability has been reported from many regions (e.g. Hu *et al.*, 2003; Beer & van Geel, 2008; Eichler *et al.*, 2009). In particular, a nearby study (Gavin *et al.* 2011) noted an anti-phase correlation between solar insolation and biogenic silica production in Eleanor Lake during the Early Holocene, although the seasonal sensitivity of the climate proxy is difficult to interpret. The Windy Lake results suggest that forests were in dynamic equilibrium with climate and responded to temperature changes with minimal lag times. During decadal to centennial warm periods, forest productivity and/or density increased at the elevation of Windy Lake. Conversely, during grand solar minima, colder temperatures led to a decrease in forest productivity and possibly also treeline elevation. Interestingly, this relationship is more pronounced during the Early and Late Holocene, probably due to higher variability in incoming solar irradiation (Fig. 3).

At Redmountain Lake, the presence of closed subalpine forest during the Early Holocene also suggests higher-than-present summer temperatures during this time period. This finding is in agreement with high organic content of the sediments (Fig. 2f) as well as elevated summer temperatures and local vegetation dynamics at Windy Lake farther south. The later establishment of subalpine forest at Redmountain Lake than at Windy Lake can be explained by its location at higher latitudes. Closed forest could only establish around this site when summer temperatures reached a maximum after 9900 cal. BP (Fig. 3), even though the chironomid-inferred July temperature reconstruction at Redmountain Lake (Fig. S1.5) suggests that summer temperatures never reached current levels during the Holocene (Chase *et al.*, 2008). Indeed, other studies suggest that the Holocene thermal maximum was much weaker or even absent at higher latitudes, e.g. in Alaska (Clegg *et al.*, 2011). Nevertheless, the agreement among the macrofossil records at Redmountain and Windy Lake, and the temperature reconstruction from Windy Lake, suggests that warm summer temperatures during the Early Holocene resulted in the establishment of closed forests at Windy and Redmountain lakes.

In contrast to Windy and Redmountain Lake, the macrofossil record at Thunder Lake shows the highest concentrations during the mid-Holocene (Fig. 3). High organic content of the mid-Holocene sediments from Thunder Lake supports the interpretation of denser/more productive forests during this period (Fig. 2e). Reconstructed summer temperatures from the same sediment core, however, do not suggest different trends at Thunder Lake than at the other two sites. Indeed, the continuous presence of conifer needles (mostly *Abies lasiocarpa*) indicates that summer temperatures were already warm enough during the Early Holocene for the establishment of trees around the lake. Other factors than summer temperature evidently played an important role in the local vegetation dynamics at Thunder Lake.

The very low concentrations of *Picea engelmannii* macrofossils during the Early Holocene and its increase after ca. 7500 cal. BP when the climate became cooler and wetter in the region (Hebda, 1995; Bennett *et al.*, 2001; Walker & Pellatt, 2008; Galloway *et al.*, 2011; Mihindukulasooriya *et al.*, 2015), suggests that moisture availability limited the establishment of dense forests around Thunder Lake in the dry Early Holocene. In contrast to *Abies lasiocarpa* or *Pinus albicaulis*, *Picea engelmannii* is susceptible to drought during the growing season and does not grow well on poorly established soils (Burns *et al.*, 1990). Thunder Lake has steep slopes on its north and northwest side, where present-day forest cover is low or absent (Figs 1 & S1.1). With shallow soils and a warm and dry climate during the Early Holocene, trees were probably limited to the less steep, south side of the lake (Fig. S1.1). Progressive soil development and an increase in precipitation due to changing atmospheric circulation patterns in the mid-Holocene (Shuman & Marsicek, 2016), might have allowed *Picea engelmannii* and *Abies lasiocarpa* to establish all around the lake. This hypothesis would explain the highest macrofossil concentration during the mid-Holocene. An alternative hypothesis would be lower avalanche activity during the mid-Holocene. High influx values and pollen percentages of *Alnus* (most likely *Alnus viridis*) suggest high regional abundance in avalanche runs during the Early Holocene. High avalanche activity on the steep south-facing slopes around Thunder Lake would prevent the establishment of closed forest. Increased avalanche activity due to cold winters and unstable snowpack in the Early Holocene has also been suggested to explain the late establishment of subalpine forest in the Western Olympic Mountains, USA (Gavin *et al.*, 2001). Another factor that could directly impact macrofossil concentrations in the sediment is a change in lake size (Birks, 2001; Tinner, 2007). Due to the very positive water balance at high elevations in the study area, we expect that the lakes have always been controlled by the outlet elevation and therefore were never smaller in size.

Regional vegetation dynamics at the treeline in British Columbia

The divergent local vegetation dynamics at our three study sites agree with other palaeoecological studies in the region (Table 2, Fig. 1). High-elevation study sites in the Pacific Northwest show highest macrofossil concentration either during the Early Holocene (Reasoner & Hickman, 1989; Pellatt & Mathewes, 1994; Pisaric *et al.*, 2003) or during the mid-Holocene (Reasoner & Hickman, 1989; Spooner *et al.*, 1997; Pellatt *et al.*, 2000; Heinrichs *et al.*, 2001, 2002; Pisaric *et al.*, 2003). The absence of a clear geographical or altitudinal pattern to the maximum abundance of recorded macrofossils suggests that local factors such as topography or geomorphology played an important role besides climate.

During the warm and dry Early Holocene, available moisture during the growing season was probably too low for tree growth on steep south-facing slopes and poorly developed soils. Closed subalpine forest could only establish where geomorphic processes created deep alluvial soils, such as at the bottom of glacial valleys like at Moose Lake (Gavin *et al.*, 2001) or Lake O’Hara (Reasoner & Hickman, 1989), or at predominantly north-facing slopes with lower evapotranspiration such as Louise Pond (Pellatt & Mathewes, 1994) or BC2 Lake (Pisaric *et al.*, 2003). This is in agreement with recent studies suggesting that soil moisture can limit seedling establishment at the treeline (Resler, 2006; Malanson *et al.*, 2007; Müller *et al.*, 2016).

With decreasing summer solar insolation, cooler summer temperatures, progressive soil development and most importantly a shift to wetter conditions after ca. 8000 cal. BP, available soil moisture became high enough for trees to establish on south-facing slopes and poorly developed soils. This in turn could have started a positive feedback loop, with increased litter production leading to the build-up of organic rich soils that in turn enhanced local forest productivity. Subalpine lakes in the region with maximum forest productivity in the mid-Holocene are indeed either located on exposed ridges or mountaintops with little alluvial soil-accumulation such as Martins Lake (Gavin *et al.*, 2001), 3M Pond (Pellatt *et al.*, 2000), Crater Lake (Heinrichs *et al.*, 2002) or Buckbean Bog (Heinrichs *et al.*, 2001), or in glacier forefields such as Opabin Lake (Reasoner & Hickman, 1989) or Susie Lake (Spooner *et al.*, 1997).

Fire history

High abundance of macroscopic charcoal in the sediments of Windy Lake during the Early Holocene points to a fire regime driven by climate and fuel availability, with increased fire activity during warm and dry periods with highest forest density. In the Late Holocene (4000 cal. BP – present), when fuel availability was lower and climate was colder, the absence of distinct charcoal peaks suggests only low-severity fires. Redmountain Lake shows highest charcoal concentrations during the Early Holocene as well, indicating again a mostly climate-driven fire regime with higher severity fires due to increased fuel availability. Pronounced charcoal peaks throughout the record show recurring fire events during the entire Holocene, despite low fuel availability and cooler temperatures in the Late Holocene.

At Thunder Lake, a marked increase of charcoal concentration and influx during the last 2000 years indicates that the fire regime was not primarily driven by climate or fuel availability in the Late Holocene. Even though there were documented warm and dry phases during this time period, the climate was generally colder and wetter than during the Early Holocene (Hebda, 1995). A possible explanation for the divergent fire regime at Thunder Lake compared with Windy and Redmountain Lake could again be the different topography with steep south-facing slopes. A recent study in the ESSF zone of the Columbia Mountains concludes that aspect is an important controlling factor of fire regimes with shorter fire return intervals on south-facing slopes (Courtney Mustaphi & Pisaric, 2013). An increase in fire activity during the late Holocene has also been documented at other sites in the Pacific Northwest (Walsh *et al.*, 2015). The authors hypothesize that either an increase in El Niño/Southern Oscillation (ENSO) frequency or human impact might have increased biomass burning in the late Holocene (Walsh *et al.*, 2015). Indeed, peaks in local biomass burning in the Pacific Northwest during the last 6000 years seem to coincide with periods of frequent ENSO events (Walsh *et al.*, 2015), even though there is only weak evidence for a link between ENSO and wildfire activity in the last century (Gedalof *et al.*, 2005; Meyn *et al.*, 2010). The drastic increase in fire activity between 1500 – 400 cal. BP at Thunder Lake also coincides with maximum population density in the Pacific Northwest (Walsh *et al.*, 2015). The use of fire for ecosystem management in Native American cultures is well documented (e.g. Boyd, 1999; Lepofsky & Lertzman, 2008). In subalpine areas, fire was often used to increase huckleberry yield, an important food source. Even though there is no direct evidence for the involvement of humans, the drastic change in fire regime had a profound impact on the surrounding vegetation, as indicated by the presence of a significant pollen zone boundary at this time (Fig. S1.4). The highly divergent fire histories at the three study sites suggests that even though climate was an important driver of fire frequency at millennial scales, local factors such as fuel availability, topography and human impact can override climatic controls of fire activity.

Conclusions

Climatic controls or more specifically summer temperatures are the most important driver of treeline dynamics in the Canadian Cordillera over long timescales and large spatial scales. Our palaeoecological records indicate that subalpine tree species responded to the rapid increase in summer temperatures at the Younger Dryas – Early Holocene transition with an immediate upward shift of their range and established around the three lakes as soon as summer temperatures reached a critical threshold. Changes in solar activity, possibly affecting summer temperature, also have a discernible impact on mountain forests on shorter timescales (decades to centuries). Our results suggest that forest productivity and most likely treeline position as well, can rapidly respond to changes in summer temperature. The upward expansion of forest due to increasing summer temperatures is also controlled by secondary factors such as local topography and geomorphology. Our results show that the establishment of closed forest at higher elevations during the abrupt climate warming at the end of the last ice age is only possible if moisture availability is high enough. This means that ongoing and future climate warming will lead to a rapid upward shift of treeline, but forest establishment above present elevations will be patchy and depend on the availability of soils deep enough to sustain tree growth. The upward shift of mountain forest will therefore most likely not be uniform and occur first on favourable sites with adequate moisture availability.

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Supporting Information

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

Appendix S1: Supplementary Figures

Biosketch

Christoph Schwörer is currently a postdoctoral research associate at the University of Bern, Switzerland. He is interested in long-term vegetation dynamics and climate change impacts in mountain environments. His research combines palaeoecological methods such as pollen, charcoal and macrofossil analyses with spatially explicit dynamic vegetation modelling.

Author contributions: D.G.G, I.A.W. and F.S.H. conceived the study and obtained initial funding, C.S. performed the macrofossil and charcoal analyses, D.G.G. performed the pollen analysis, C.S. and D.G.G. interpreted the results and C.S. led the writing with contributions from all co-authors.

Editor: Mark Bush

Tables

Table 1 Geographic and climatic characteristics of the three study sites in the Canadian Cordillera. Climate data from the 1981-2010 norm period, calculated with the Climate BC tool (Wang *et al.*, 2012). MAT = mean annual temperature, MAP = mean annual precipitation sum

	Windy Lake	Thunder Lake	Redmountain Lake
Elevation (m a.s.l.)	1813	1539	1590
Latitude (° N)	49.81	52.23	53.92
Longitude (° W)	117.88	119.35	121.29
Lake size (ha)	3.2	19.7	5.9
Lake depth (m)	3.9	2.9	2.8
MAT (°C)	2	1.2	0.8
Mean July T (°C)	12.5	11.7	11.1
Mean January T (°C)	-6.3	-8.1	-8.3
MAP (mm)	1290	1828	1548
Dominant tree species	*Abies lasiocarpa, Picea engelmannii*	*Abies lasiocarpa, Picea engelmannii*	Parkland, *Abies lasiocarpa*
Treeline elevation (m a.s.l.)	2200	1900	1800
Timberline elevation (m a.s.l.)	2000	1700	1500

Table 2. Inferred highest forest density and topography from additional study sites in the Canadian Cordillera. Sites included in the table are those with continuous macrofossil records that span the Holocene. Sites are ordered chronologically by the timing of the maximum macrofossil concentration in sediments.

Site name	Elevation (m a.s.l)	Latitude	Longitude	Aspect	Topography	Peak in macros (cal. BP)	Reference
Louise Pond	650	53°25'	131°45'	NW	small depression on steep north-facing slope	11’500-9500	Pellatt & Mathewes 1994
Windy Lake	1813	49°49'	117°53'	N-NW	cirque lake with steep slopes	11’500-8000	this study
Lake O'Hara	2015	51°21'	116°20'	S-SW	valley bottom	11’500-7000	Reasoner & Hickman 1989
BC2	1635	58°28'	124°28'	E*	level plateau	10’500-9500	Pisaric *et al.* 2003
Moose Lake	1508	47°53'	123°21'	W*	valley bottom	10’500-7500	Gavin *et al.* 2001
Redmountain Lake	1590	53°55'	121°18'	N*	cirque lake in mostly gentle terrain	10’000-8000	this study
Dead Spruce Lake	1378	58°34'	124°32'	NW *	depression on gently sloped ridge	9000-5000	Pisaric *et al.* 2003
Crater Lake	2120	49°11'	120°05'	-	level plateau	8400-4200	Heinrichs *et al.* 2002
Martins Lake	1415	47°42'	123°32'	W	small depression on exposed ridge	7800-5800	Gavin *et al.* 2001
3M Pond	1950	49°59'	121°13'	S*	small depression on exposed ridge	7600-3800	Pellatt *et al.* 2000
Opabin Lake	2280	51°21'	116°20'	SW	glacier forefield, talus slopes	7500-4500	Reasoner & Hickman 1989
Thunder Lake	1539	52°14'	119°21'	S-E	cirque lake with steep slopes	7000-2500	this study
Susie Lake	1417	57°48'	131°12'	NE	moraine dammed lake in valley bottom	6500-4500	Spooner *et al.* 1997
Buckbean Bog	1810	49°07'	119°41'	-	level plateau on mountain top	5900-3800	Heinrichs *et al.* 2001

* mostly level terrain

Figures

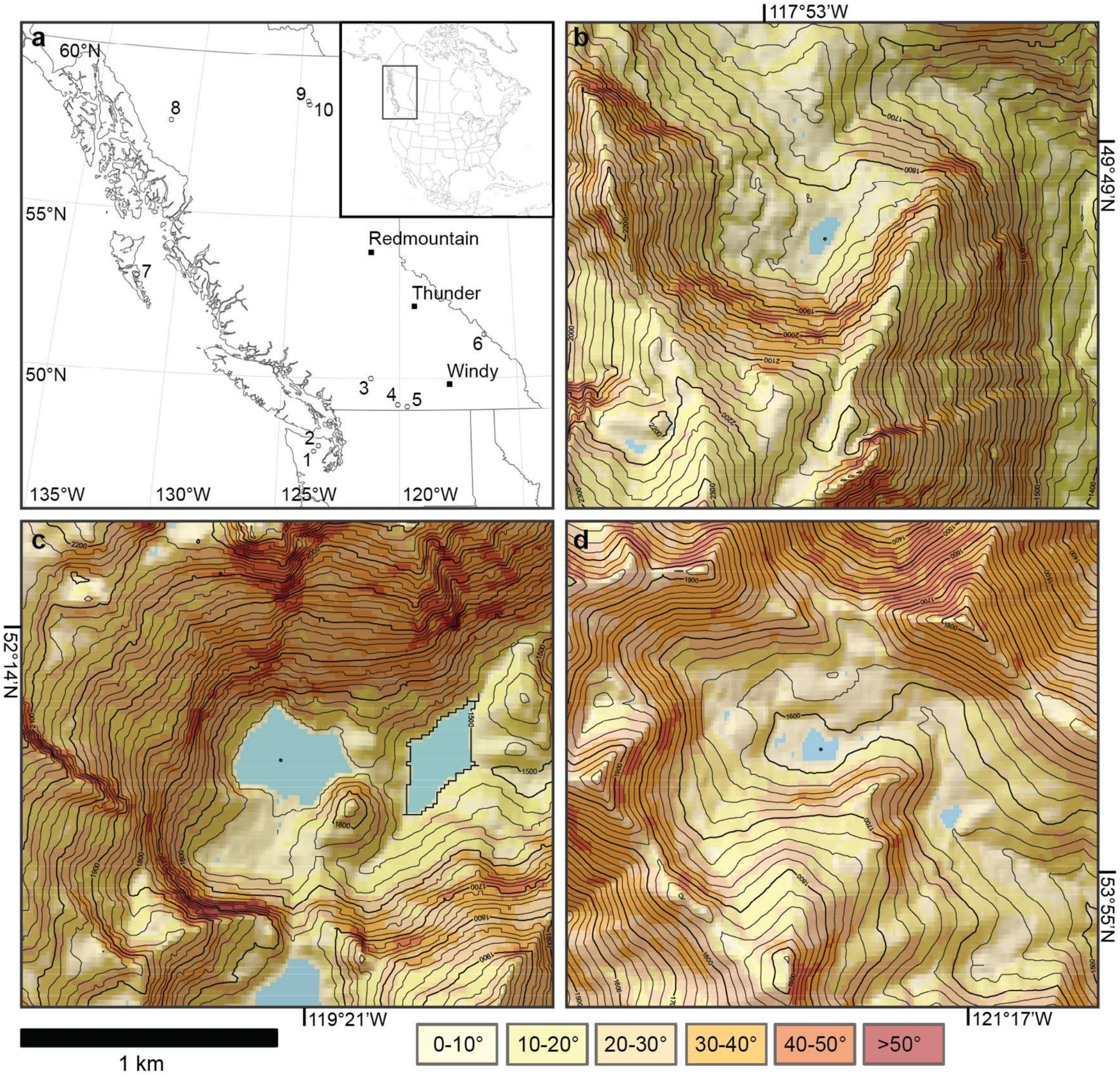


Fig. 1 a) Location of our three study sites in British Columbia, Canada and other palaeoecological sites in the region: 1. Martins Lake (Gavin *et al.*, 2001), 2. Moose Lake (Gavin *et al.*, 2001), 3. 3M Pond (Pellatt *et al.*, 2000), 4. Crater Lake (Heinrichs *et al.*, 2002), 5. Buckbean Bog (Heinrichs *et al.*, 2001), 6. Lake O'Hara and Opabin Lake (Reasoner & Hickman, 1989), 7. Louise Pond (Pellatt & Mathewes, 1994), 8. Susie Lake (Spooner *et al.*, 1997), 9. Dead Spruce Lake (Pisaric *et al.*, 2003) and 10. BC2 Pond (Pisaric *et al.*, 2003). The inset shows the location of the study region in North America. b-d) Shaded relief maps of the three study sites showing slope steepness and elevation contours. b) Windy Lake, c) Thunder Lake and d) Redmountain Lake

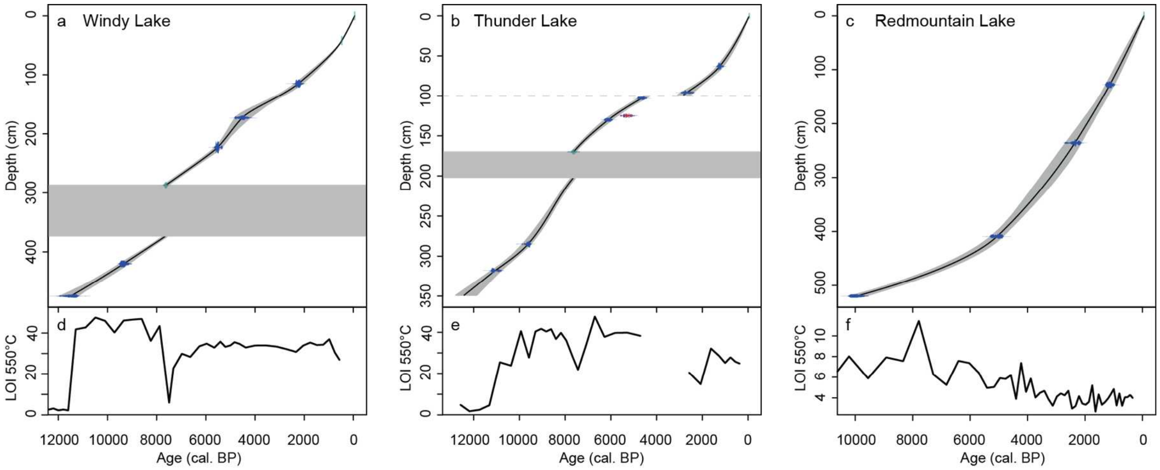


Fig. 2 Age-depth models of a) Windy Lake, b) Thunder Lake and c) Redmountain Lake with the probability distributions of the ^{14}C ages. Horizontal grey bars show the Mazama tephra. Grey area is the 95% probability distribution of the age-depth model based on Monte-Carlo sampling with 1000 iterations. Radiocarbon dates are presented in Chase *et al.* (2008). Lower graphs (d,e,f) show Loss-On-Ignition at 550 °C, which is a measure of the organic content of the sediment.

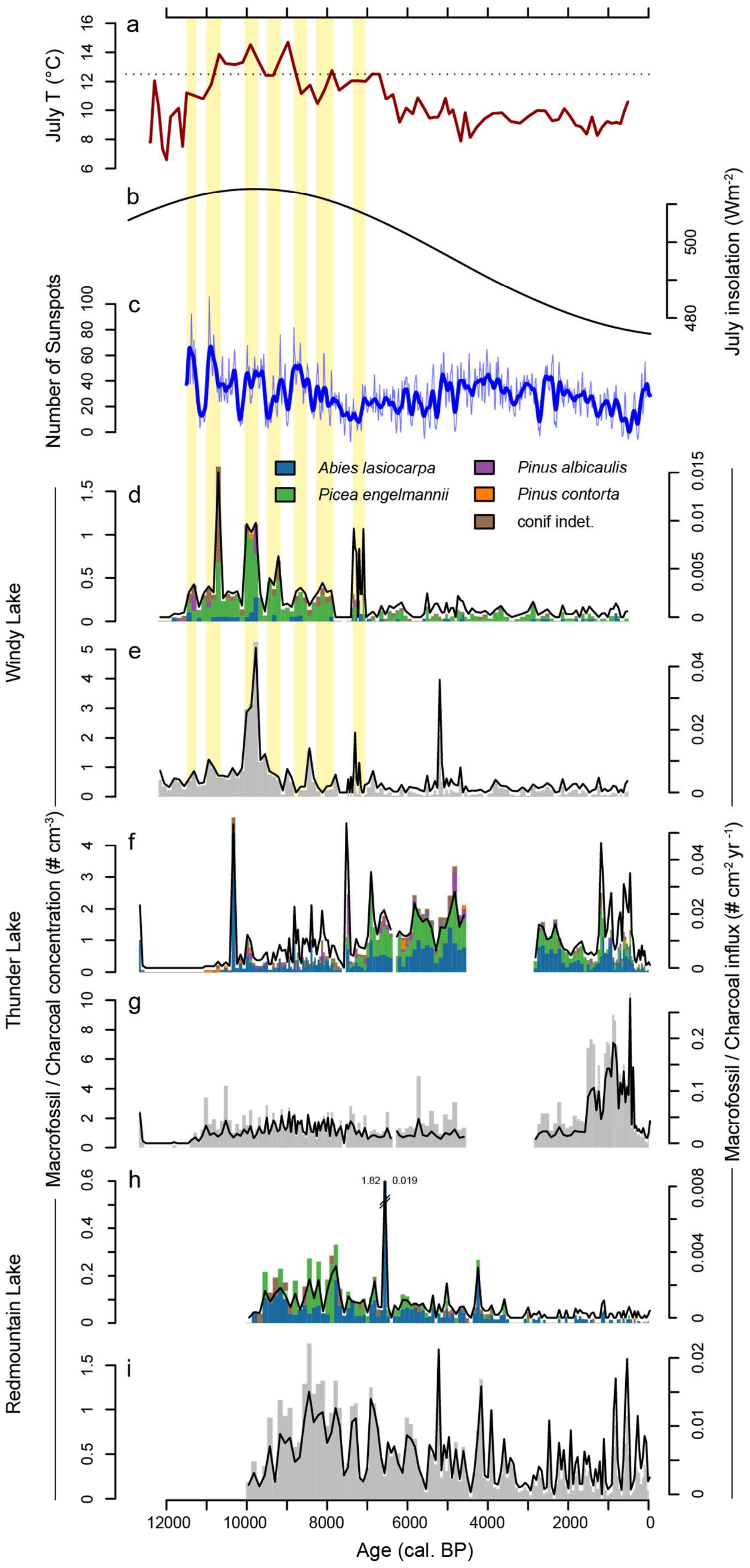
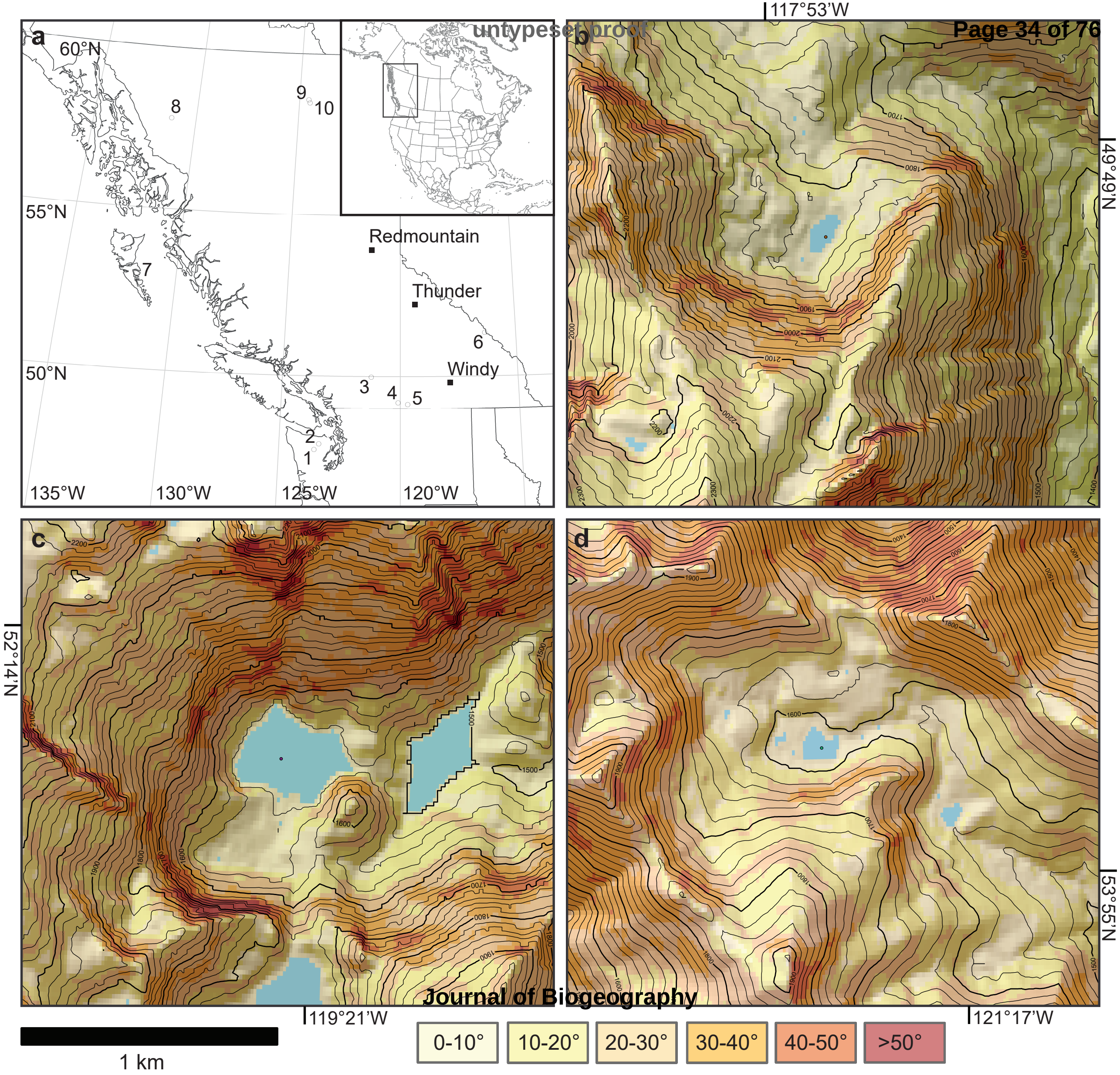

a
July T (°C)
6
8
10
12
14
16
b
July insolation (Wm^{-2})
480
500
c
Number of Sunspots
0
20
40
60
80
100
Abies lasiocarpa
Picea engelmannii
Pinus albicaulis
Pinus contorta
conif indet.
d
e
f
g
h
i
Windy Lake
Thunder Lake
Redmountain Lake
Macrofossil / Charcoal concentration (# cm^{-3})
Macrofossil / Charcoal influx (# cm^{-2} yr^{-1})
1.82
0.019
12000
10000
8000
6000
4000
2000
0
Age (cal. BP)

Fig. 3 Comparison of palaeoclimate indicators with reconstructed local vegetation and fire history from Windy, Thunder and Redmountain Lake. a) Reconstructed July temperatures based on chironomid assemblages from Windy Lake (Chase *et al.*, 2008). Dashed horizontal line indicates present-day July temperature for the reference period 1981 – 2010 at Windy Lake, calculated with the Climate BC tool (Wang *et al.*, 2012). b) July solar insolation at 50° N latitude (Laskar *et al.*, 2004). c) reconstructed number of sunspots as a measure of solar activity, where a high number of sunspots indicates high solar activity (Solanki *et al.*, 2004). d, f, h) stacked coniferous macrofossil concentrations (bars) and influx (solid line) of Windy, Thunder and Redmountain lakes, respectively. e, g, i) macroscopic charcoal concentration (grey bars) and influx (solid line) of Windy, Thunder and Redmountain lakes, respectively. Yellow vertical bars indicate peaks in macrofossil concentrations at Windy Lake.


a
60°N
55°N
50°N
135°W
130°W
125°W
120°W
1
2
3
4
5
6
7
8
9
10
Redmountain
Thunder
Windy
b
117°53'W
49°49'N
c
52°14'N
119°21'W
d
53°55'N
121°17'W
1 km
0-10°
10-20°
20-30°
30-40°
40-50°
>50°

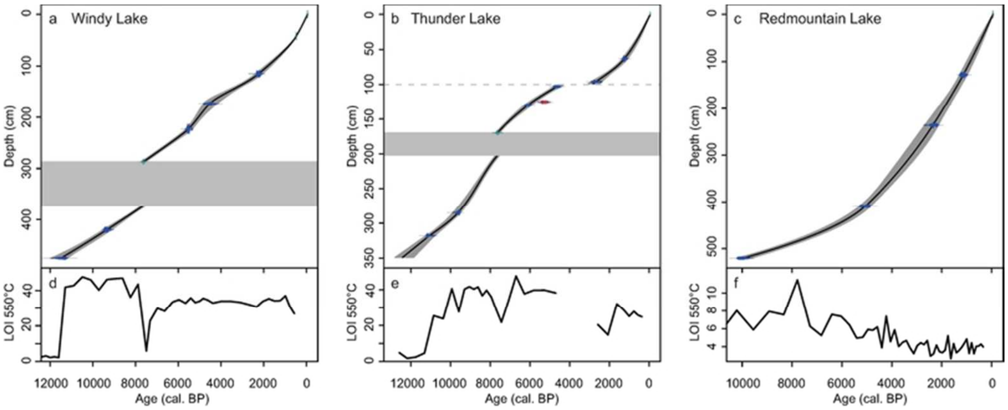


Fig. 2 Age-depth models of a) Windy Lake, b) Thunder Lake and c) Redmountain Lake with the probability distributions of the 14C ages. Horizontal grey bars show the Mazama tephra. Grey area is the 95% probability distribution of the age-depth model based on Monte-Carlo sampling with 1000 iterations. Radiocarbon dates are presented in Chase et al. (2008). Lower graphs (d,e,f) show Loss-On-Ignition at 550 °C, which is a measure of the organic content of the sediment.

Fig. 2

68x27mm (300 x 300 DPI)

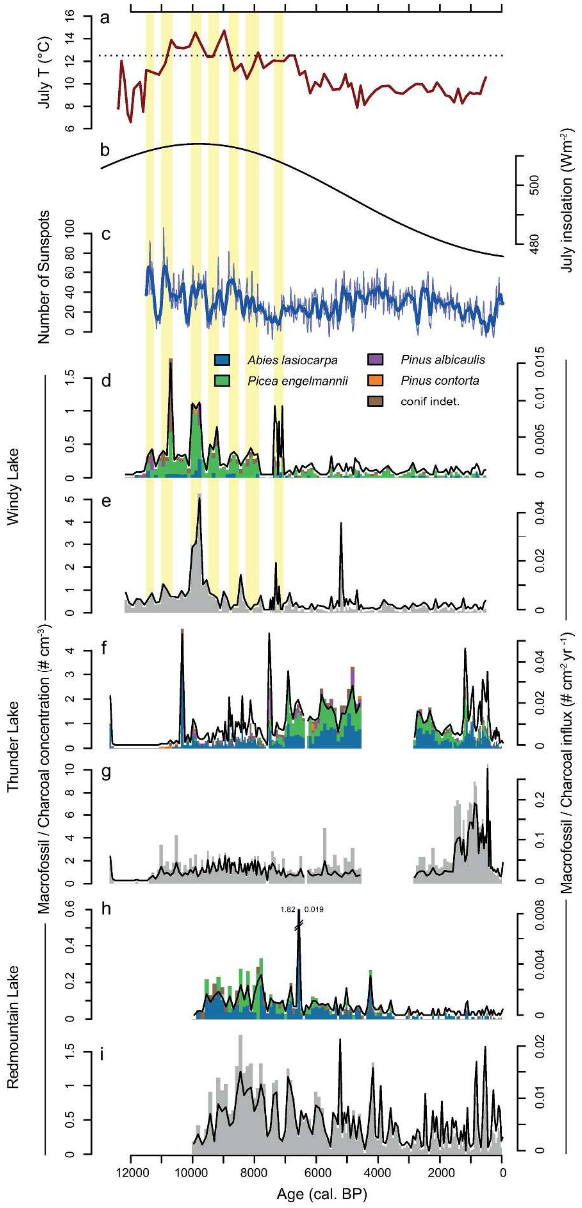


Fig. 3 Comparison of palaeoclimate indicators with reconstructed local vegetation and fire history from Windy, Thunder and Redmountain Lake. a) Reconstructed July temperatures based on chironomid assemblages from Windy Lake (Chase et al., 2008). Dashed horizontal line indicates present-day July temperature for the reference period 1981 – 2010 at Windy Lake, calculated with the Climate BC tool (Wang et al., 2012). b) July solar insolation at 50° N latitude (Laskar et al., 2004). c) reconstructed number of sunspots as a measure of solar activity, where a high number of sunspots indicates high solar activity (Solanki et al., 2004). d, f, h) stacked coniferous macrofossil concentrations (bars) and influx (solid line) of Windy, Thunder and Redmountain lakes, respectively. e, g, i) macroscopic charcoal concentration (grey bars) and influx (solid line) of Windy, Thunder and Redmountain lakes, respectively. Yellow vertical bars indicate peaks in macrofossil concentrations at Windy Lake.

Fig. 3

220x364mm (300 x 300 DPI)

Appendix S1

Journal of Biogeography

Holocene treeline changes in the Canadian Cordillera are controlled by climate and topography

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Supplementary Figures

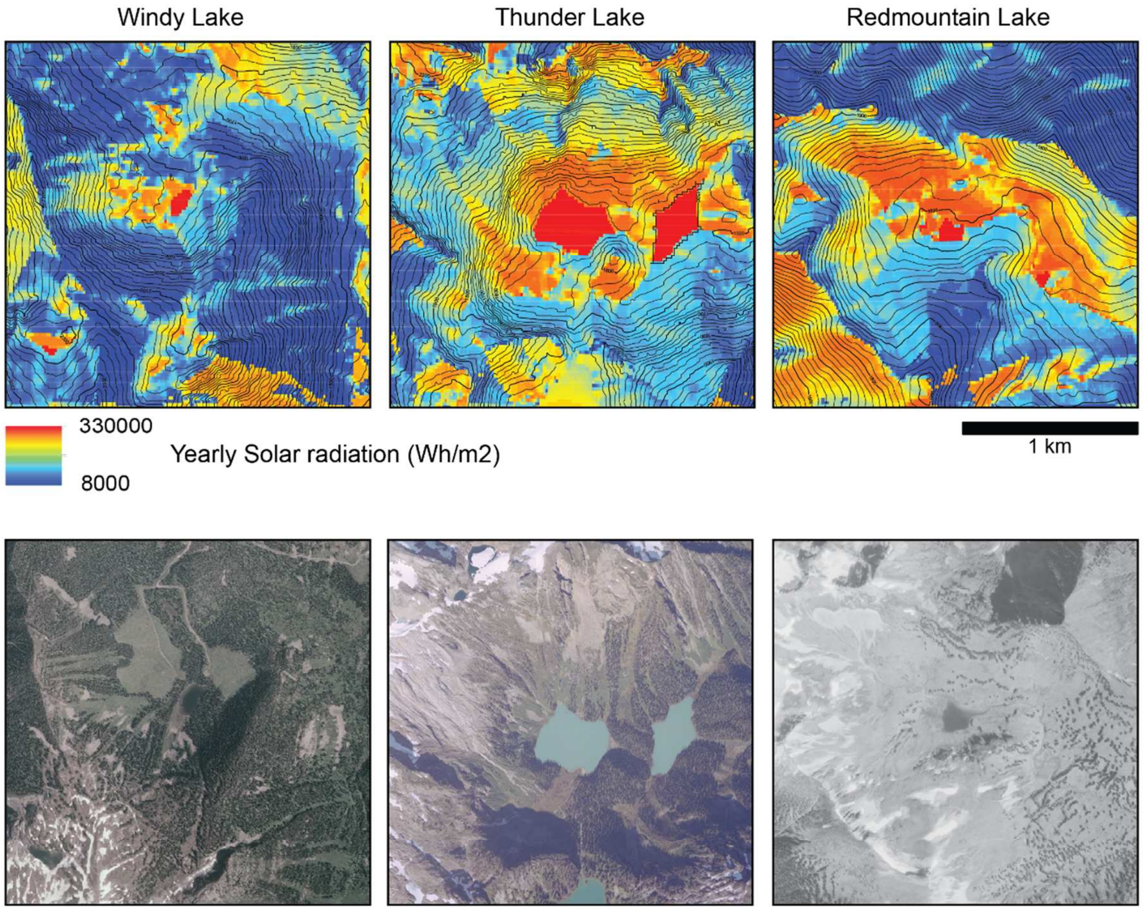

Fig. S1.1: Gridded yearly solar radiation (top row) for the three study sites as well as aerial images showing present-day vegetation cover.

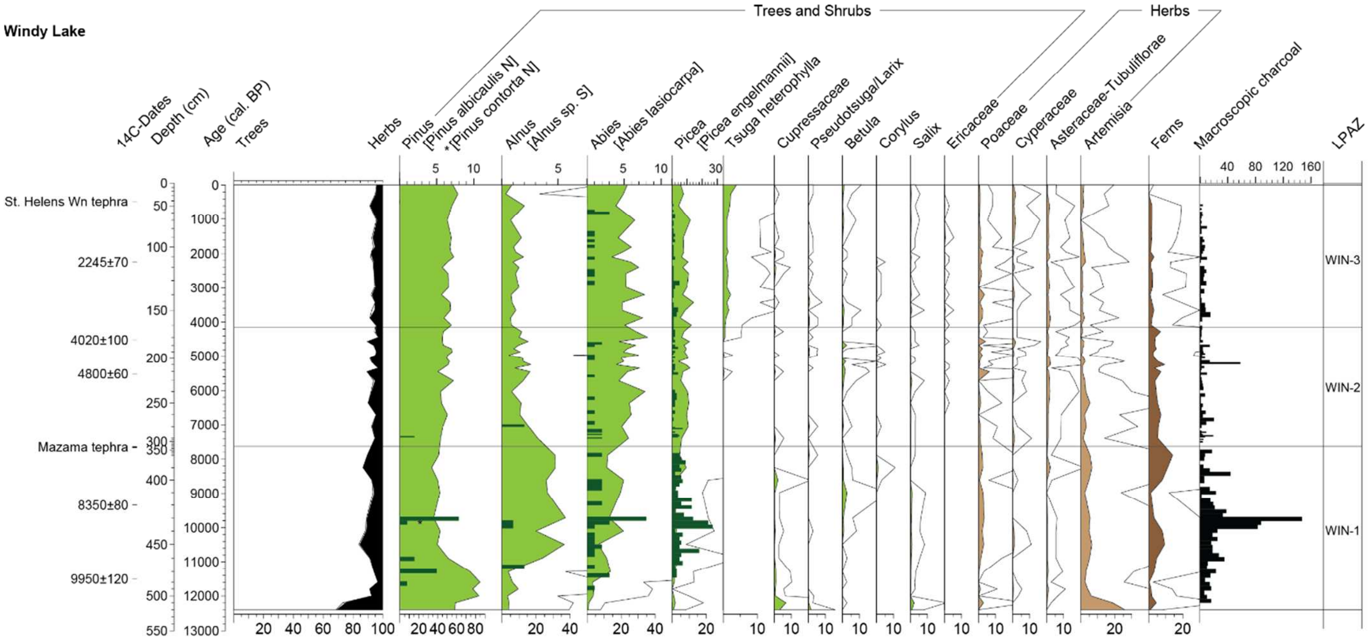

Fig. S1.2 Combined pollen percentage and macrofossil concentration diagram of Windy Lake. The pollen percentages are based on the terrestrial pollen sum. Empty curves show 10x exaggeration. Macrofossil and charcoal concentrations are calculated for a standard volume of 28 cm^3. *LPAZ* = Local pollen assemblage zones, N = needles, S = seeds

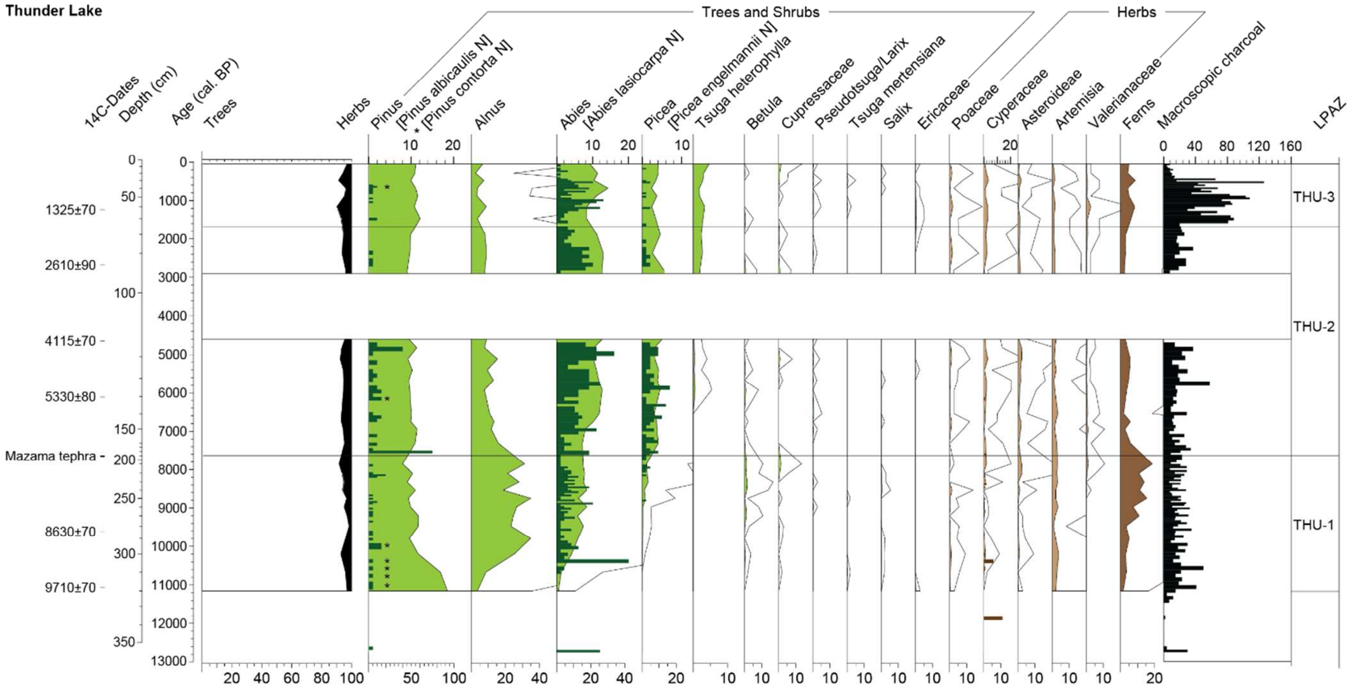

Fig. S1.3 Combined pollen percentage and macrofossil concentration diagram of Thunder Lake. The pollen percentages are based on the terrestrial pollen sum. Empty curves show 10x exaggeration. Macrofossil and charcoal concentrations are calculated for a standard volume of 12 cm^3. *LPAZ* = Local pollen assemblage zones, N = needles, S = seeds

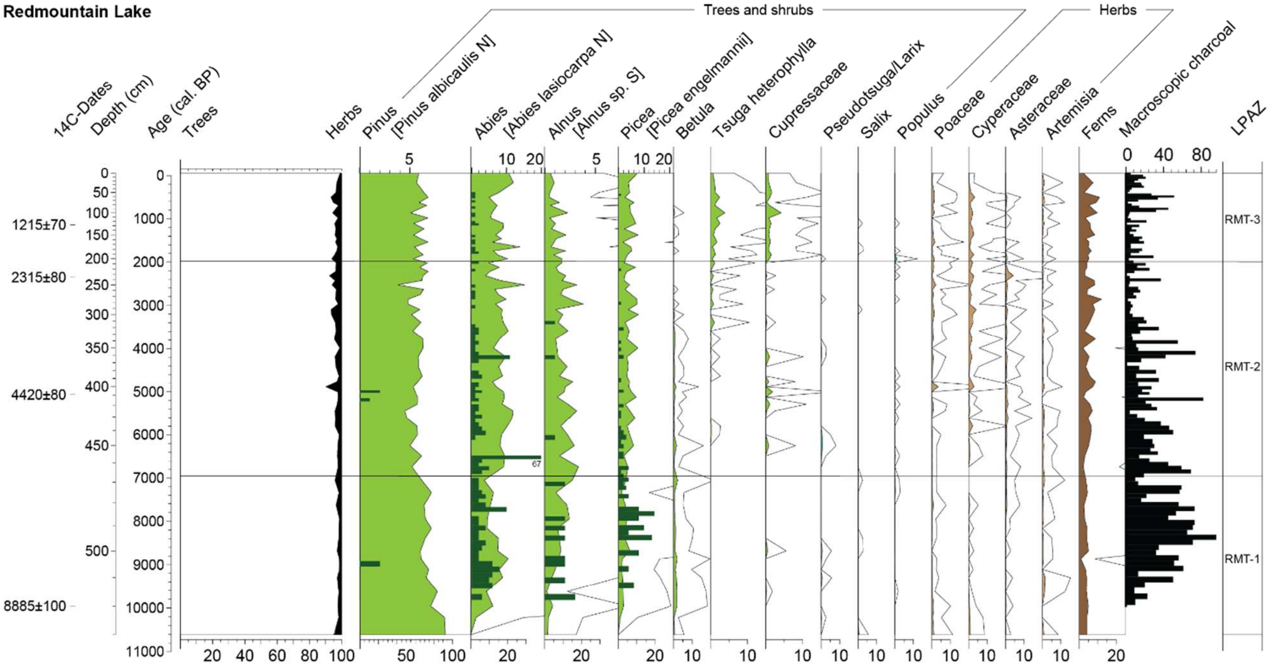

Fig. S1.4 Combined pollen percentage and macrofossil concentration diagram of Redmountain Lake. The pollen percentages are based on the terrestrial pollen sum. Empty curves show 10x exaggeration. Macrofossil and charcoal concentrations are calculated for a standard volume of 55 cm^3. *LPAZ* = Local pollen assemblage zones, N = needles, S = seeds

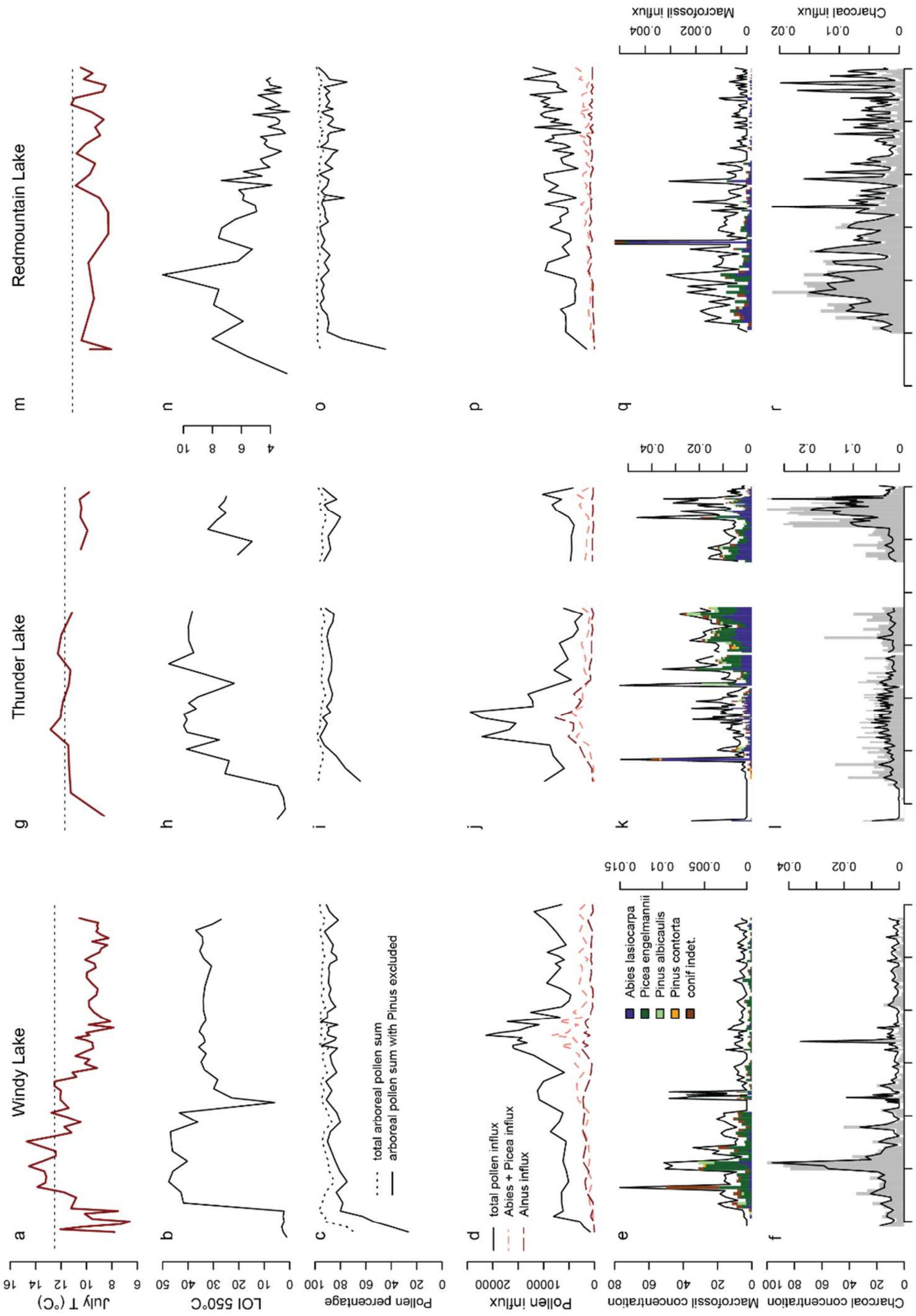

Fig. S1.5 The chironomid-inferred July temperature reconstructions from Chase et al. (2008) for the three study sites (a, g, m) compared to various indicators of past treeline and forest density. Loss-On-Ignition at 550 °C (b, h, n) is a measure of the organic content of the sediment, a portion of which is derived from soil organic matter. The total arboreal pollen sum as well as the total arboreal pollen sum calculated with *Pinus* pollen excluded (c, i, o) is a measure of the percent pollen from trees; *Pinus* is removed in one case because it is regionally dispersed over long distances. Total pollen influx values as well as influx values of fir + spruce and alder (d, j, p) is a measure of total pollen input rate into the lake and should reflect regional tree abundance, but is also affected by within-lake depositional processes and dating errors. Stacked coniferous macrofossil concentrations and influx (solid line) (e, k, q) are repeated from Fig. 3 in the main text. Macrofossils represent vegetation at scales of 10's to 100's of metres and thus represent vegetation in the immediate catchment. Macroscopic charcoal concentration (grey bars) and influx (solid line) (f, l, r) also is repeated from Fig. 3 in the main text and represents local biomass burned.

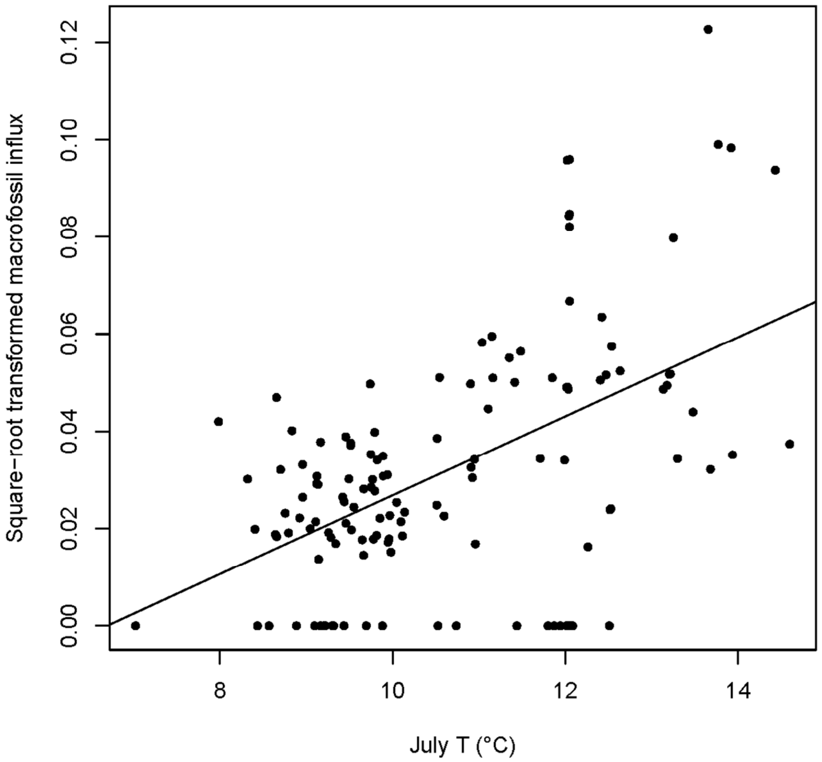

Fig. S1.6 Square-root transformed influx of tree macrofossils (cm^{-2} yr^{-1}) at Windy Lake versus chironomid-inferred July temperatures. The line shows the significant linear correlation ($r = 0.52$, $P < 0.001$).

Sediment from high-elevation lakes such as Redmountain Lake has been used to reconstruct treeline changes in the Canadian Cordillera (Photo: Dan Gavin).

173x130mm (300 x 300 DPI)