The role of fire in the mid-Holocene arrival and expansion of lodgepole pine (*Pinus contorta* var. *latifolia* Engelm. Ex S. Watson) in Yukon, Canada

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Abstract

In northwest Canada, *Pinus contorta* (lodgepole pine) has been migrating northwards and westwards for millennia. Its regeneration is currently enhanced by fire, which may act as a trigger for local population expansion. Using Holocene charcoal records from four small (<10 ha) lakes in southern Yukon, we investigated the relationship between long-term *Pinus* population dynamics and fire. Fossil stomata extracted from dated lake sediments indicate pine was present at low densities in southern Yukon forests by ~6000 cal yr BP. At each site, the main population expansion (indicated by an increase in *Pinus* pollen from <5% to values as high as 60%) occurred 2000->4000 yr after the first local appearance of *Pinus*, suggesting a long period of stasis at low densities. Population increases—based on pollen accumulation rates—occurred at different times at the four sites. Estimated expansion periods were ~2500-800 years, and population doubling times were ~150-600 years, similar to previous estimates. Estimated fire return intervals (FRIs) fluctuated over time. At all sites the *Pinus* expansion began during a phase with a relatively short FRI, but only one difference between the mean FRIs before and during the *Pinus* rise were not statistically distinguishable. Nor was the subsequent higher abundance of pine associated with shorter FRIs. It is unlikely that regional pine expansion is primarily linked to changes in climate or a climate-mediated fire regime, although it may have been triggered at individual sites during a period of high fire frequency. The long period of stasis at low population densities suggests intrinsic control of population growth; possibly *Pinus* expansion was initially constrained by lowered reproductive fitness (Allee effect) and/or interaction with local site-based factors.

Keywords: *Pinus contorta* ssp. *latifolia*, migration, Holocene, fire, Allee effect, Yukon.

Introduction

The circumpolar boreal forest is the second largest forest ecosystem on the planet and a resource of global significance, both environmentally and economically. It plays an important role in feedbacks between land surface and atmosphere (Bonan et al., 1992, Chapin et al., 2000, French et al., 2000): large carbon stores, fires, and a dynamic ecotone with tundra mean that alterations of forest distribution, species composition or the disturbance regime are likely to have major impacts on climate via the surface energy budget and atmospheric chemistry (e.g. Levis et al., 1999). Effects of climate warming are associated with modified growth rates of dominant tree species (e.g. *Picea glauca* [white spruce], Barber et al. 2000), increases in area burned (e.g. Chapin et al., 2000) and higher fire frequencies (Kasischke et al., 2010; Kelley et al., 2013). Vegetation change, seen as change in species abundances and/or distributions, can feed back to the fire regime by modifying flammability and fuel source availability (Lynch et al., 2002; Lloyd et al., 2004; Brubaker et al., 2009).

Understanding how transformations of vegetation composition and disturbance regime occur through time is, therefore, high on the agenda of global change studies. A classic problem is that processes such as forest-tree recruitment and population expansion occur over longer timescales than are observable by modern ecological techniques (i.e., centuries or longer).

Similarly, fire disturbance is best quantified as fire frequency over time or average fire return interval over multi-century to millennial timescales, but modern estimates are typically based on decadal timescales. In Yukon, the slow Holocene (~10,000-year) migration of lodgepole pine *(Pinus contorta* var*. latifolia* Engelm. ex S. Watson*)* into spruce *(Picea)*-dominated boreal forest (MacDonald and Cwynar, 1985, 1991; Strong and Wills, 2013) provides a natural long-term experiment through which we can examine how fire and vegetation interact as pine invades boreal forest. While a minor seral species on moist substrates, it is dominant on warm, well-drained sites. Reproduction is fire-dependant, with many ecotypes requiring heat for cones to open. Near its modern range limits in central Yukon, populations generally increase in burned-over areas at the expense of pre-existing species (Johnstone and Chapin, 2006), suggesting its current spread is facilitated by fire.

In this study we used dated pollen and charcoal records and stomatal counts from four small (<10 ha) southern Yukon lakes to describe the dynamics of late-Holocene pine expansion and its relation to fire disturbance on millennial timescales. Specifically we used the records to i) compare long-term (Holocene) trends in fire occurrence with recent observations; ii) test whether pine expansion was associated with increased fire events or clusters of events; and iii) test whether local fire frequencies were higher after pine attained co-dominance. The resulting data also revealed a long pre-expansion phase in pine population dynamics, which may have implications for future migration patterns.

Fire in the boreal forest of north-west North America

Fire is the main disturbance in the northern boreal forest and dictates much of the vegetation mosaic (Rowe and Scotter, 1973). The main tree species have different structural and functional relations with fire. *Picea mariana* (black spruce) has semi-serotinous cones that are triggered by fire to open and release seeds, meaning that it tends to establish early post-fire dominance in a burned area. *Picea glauca* (white spruce) depends on survivor trees to recolonize or invade burned areas. Seral hardwoods such as paper birch and aspen (*Betula neoalaskana, Populus tremuloides*) distribute seeds widely and opportunistically invade after fire; they also have the ability to survive fires via re-sprouting. *Pinus contorta* typically has serotinous cones that release seeds upon heating, and much seed dispersal is localized to burned areas. However, Cwynar and MacDonald (1987) argue that seed aerodynamics allow (uncommon) long-distance dispersal via fire plumes.

In the boreal forest, *Pinus contorta* (also referred to here as pine) stands typically experience low-intensity ground fires, which can suppress competition from slower-growing understorey species, but stand-replacing crown fires are common in drought conditions or when there is high fuel build-up (Bourgeau-Chavez et al., 2000). Immediately post-fire, an initial herb and shrub stage quickly progresses to overall dominance by pine seedlings and saplings. In the absence of periodic fires, pine tends to be replaced by more shade tolerant species between ~50 and 200 years post-burn. Usually however, before this stage is achieved a stand-thinning or stand-replacing fire occurs, and dominance of pine is maintained. If the canopy becomes open enough, pine will also regenerate in the understory and thus maintain dominance (Bourgeau-Chavez et al., 2000). Johnstone and Chapin (2003) observed that in mixed stands near the current northern limit, the proportion of pine increases with each recurring fire, suggesting a link between population expansion and fire occurrence.

Johnstone and Chapin (2003) citing Eis et al. (1982) report that in northern British Columbia white spruce does not overtop pine for at least 100 years after fire due to slower growth rates, and even longer would be required for spruce to exclude pine competitively from stands. Thus, short fire return intervals (<150 years) should favour pine, all else being equal. At the northern range limit of pine, intense fires and a fire return interval of <25 years can maintain succession in the hardwood (aspen) stage (Johnstone and Chapin,

2006) —although fire is not always a prerequisite for aspen dominance in boreal forest settings (Cumming et al., 2000)—and such short return intervals are not the norm.

Late-Quaternary history of Pinus contorta in Yukon

Much of the modern range of *Pinus contorta* was glaciated until ~10,000 yr BP (MacDonald and Cwynar, 1985; Anderson, 2004). The interior race, var. *latifolia* now occupies territory east of the coastal Cordillera. Where it existed during the Wisconsin glaciation is not fully known. Boreal trees may have survived in unglaciated areas of northern Yukon; however, a lack of fossil pollen evidence, no early-Holocene expansion and a likely unfavourable glacial-age climate argue against the existence of pine here (MacDonald and Cwynar, 1985). More probably, pine was confined to south of the ice sheets (Terasmae, 1973; Wheeler and Guries, 1982; Brubaker et al., 2005). Using pollen data MacDonald and Cwynar (1985, 1991) reconstruct a northward migration initiated south of the Laurentide ice limits at ca. 12,000 yr BP. In contrast, there is evidence of early (~10,000 yr BP) establishment and/or refugia for the coastal race of *Pinus contorta* (var. *contorta*) along the Pacific coast of Alaska (Peteet, 1991).

An early model based on allozyme data (Wheeler and Guries, 1982) placed populations in two separate refugia that recently rejoined at the border of British Columbia and Yukon. More recently, Marshall et al (2002) used chloroplast DNA microsatellites to investigate the genetic structure of *P. contorta* across its modern range and concluded that the taxon probably underwent rapid spread across much of the range beginning 12,000 years ago. Genetic patterns suggest that within the last ~3000 yr geographically related genetic differentiation has arisen, particularly near the northern range edge. The data also suggest an increasing trajectory in population size as small founder populations expanded over time.

Pine first expanded in the southern Yukon at ~3000 yr BP (MacDonald and Cwynar, 1985), reaching its present northern limit in the Central Yukon approximately 120 years ago (Schweger et al., 1987). Strong and Hills (2013) reviewed current pine pollen records for western Canada with a focus on topographic constraints to migration. They highlight a broad and relatively rapid spread to northern British Colombia in the first half of the Holocene (to ca 6ka BP); subsequently spread slowed and featured locally disjunct areas of pine separated by extensive regions of high ground. The implication is that higher-elevation climates constrained northward movement to a few key routes, possibly slowing migration rates. Pine may still be migrating northwards, as there is no evident climatic control at its present northern limit and it can grow healthily further north and west of its current natural range (Johnstone and Chapin, 2003).

Holocene climate change and **Pinus contorta**

The main Holocene driver of temperature in Yukon is the early-Holocene (~11-ka) summer insolation maximum and subsequent decline (Bartlein et al., 1992; Kaufman et al., 2004; Bartlein et al., 2014). The first part of the Holocene was characterized by greater seasonality; winters warmed and summers cooled in the later Holocene (ca. 5000-0 ka BP; see Cwynar and Spear, 1991). In the St. Elias Range, there is evidence for glacier fluctuations in the last several millennia (summarized by Anderson et al. 2007); these appear to be spatially complex and related to the position of the Aleutian low (thus at least partly precipitation-driven). Lake-level records show coherent pattern of low levels prior to ca. 10,000 yr BP across eastern Alaska and Yukon; these are considered to be primarily a function of lower precipitation (Abbott et al., 2000; Barber and Finney 2000; Anderson et al., 2005; Anderson et al., 2007). Subsequently in Yukon, lake-levels rose, most likely reflecting higher precipitation, reaching their maximum ca. 4000-2000 yr BP. Records from Marcella Lake (Anderson et al., 2005) and Jellybean Lake (Anderson et al.,

2007) indicate a shift to more arid conditions in the last 1200 years in the southern Yukon, which fits with both Cwynar's original interpretation of expanding steppe vegetation at Marcella at this time (Kettlehole Pond, Cwynar 1988), and with diatom records from central Yukon (Pienitz et al., 2000).

According to the climate envelopes for *Pinus contorta* developed by Thompson et al. (1999), the temperatures of the warmest and coldest months in Yukon lie well within temperature envelope, but if winter means are as cold as -20 to -30°C, lodgepole pine nears its lower precipitation limit. Increasing precipitation and/or winter warming ~4000 yr BP may, therefore, have been conducive to the general spread of pine from northern British Columbia to southern Yukon (winter mean ~ -20°C). However, sensitivity to these climate variables is not reflected in modern growth responses in Yukon populations (Miyamoto et al., 2010).

The long-distance signal in* Pinus *pollen and use of stomatal records

In the northern boreal forest of northwest North America *Pinus* and *Picea* produce abundant pollen and disperse it widely making it particularly difficult to determine from pollen values whether trees occur at a site (Anderson and Davis et al., 1991; Brubaker, 1994; Binney et al., 2011). Bennett (1983, 1986) showed that pollen influx to small sites approximates population trajectories, and the “tail” of low pollen values preceding a marked rise can be interpreted as establishment of scattered individuals followed by a major population increase. This model is used, for example, by Cwynar and MacDonald (1991) as the basis for charting the progress of pine across western Canada, and by Giesecke and Bennett (2004) and Giesecke (2005) in a similar exercise for *Picea abies* (Norway spruce) in Scandinavia. Furthermore, studies have shown that macrofossils and, in particular, records of stomata, often confirm the presence of nearby trees when the pollen percentages are low (e.g. Cwynar and Spear, 1991; Hansen et al., 1996; Pisaric et al., 2000). The frequent preservation of stomata, one of the most resistant components of conifer needles, confers practical advantages over plant macrofossil analysis as stomata can be part of routine pollen counts, but it should be noted that site-specific constraints may work against the consistent determination of local species’ presence: the likelihood of stomata being in a particular lake is enhanced by the presence of inflowing streams (Froyd, 2002) and the possibility of needle-fragment transport via fire plumes (Pisaric, 2002).

[figure 1 approximately here – location)

Methods

Study area

Yukon (Fig. 1) was only partly glaciated during the last glacial maximum. Lobes of the Cordillerian and Laurentide ice sheets advanced and retreated repeatedly in the southeast Yukon until ~10,000 yr BP, depositing glacial drift (Anderson, 2004). The climate is cold continental; Pacific Ocean influences are attenuated by the Cordillera to the southwest. Average January temperatures range from -20°C in the south to -30°C in the north, and average July temperature is ~15°C (Phillips, 1990). The southeast receives ~250 mm of precipitation annually; precipitation varies spatially and with elevation.

Below treeline, vegetation is dominated by boreal forest (Viereck and Little, 1975; Viereck et al., 1986). The forest mosaic reflects topography, successional stage, and forest fire history (Viereck, 1983; Viereck et al., 1992; see above). Four conifers occur in the southern and central Yukon: *Picea glauca*, *Picea mariana*, *Larix laricina* (tamarack), and *Pinus contorta* var. *latifolia* Seral hardwoods include *Betula neoalaskana*, *Populus tremuloides*, and *Populus balsamifera* (cottonwood). *Alnus crispa* (alder) and many species of *Salix* (willow) are common understorey shrubs.

Site Descriptions

Salmo Lake: (60^o 26’ 44 N, 133^o 33’ 41 W; elevation 866m ASL) is one of three small ponds located within dead ice topography in a small east-west trending valley (Fig. 1). The oval basin has one steep bank and simple bathymetry culminating in a flat bottom at ca. 8m. The basal lithology displays an abrupt contact between coarse sand and overlying organic sediments, dated to ~11,000 yr BP, probably marking local deglaciation. To the north the terrain is sandy and dominated by pine, to the south, west, and immediately around the lake spruce dominates. An extensive area of low-lying muskeg (black spruce) is present in the river valley to the west.

Haircut Lake: (60^o 30’ 56 N, 133^o 12’ 20 W; elevation 1000m ASL; Fig. 1) has an area of ~10 ha and lies in a basin approximately 30m below the surrounding terrain. The bottom is largely flat at ~8.0m, but the basin sides shelve steeply near the shore. A small inlet enlarges the catchment to the south. A small ponded-up outlet is present at the northern end, but has no visible current. The age of the basal sediment is ~7.5 ka; the lake may have formed from blocking of the outlet during the Holocene. Its steep surrounds are completely dominated by dense pine forest with very little under-storey vegetation, and deciduous tree species and shrubs are largely limited to the shoreline.

Marcella Lake: (60º 4’ 25 N, 133º 48’ 28 W; elevation 697m ASL) is a kettle pond located on a terrace of unconsolidated till and outwash related to a former melt-water channel (see Cwynar, 1988 [Kettlehole Pond]; Anderson et al., 2005; Fig. 1). The lake is approximately 4.0 ha in area. It has simple bathymetry, and the deepest point (9.7 m) is located centrally. It lies ~20 m below the surrounding terrain within a well defined 0.8-km^2 catchment. The catchment is dominated by pine and aspen, with open vegetation dominated by *Artemesia frigida* (small sagebrush) and grasses on well-drained, south-facing slopes. Spruce is present on the shoreline and extensive spruce forests occupy the river floodplain 1-2 kilometres to the west. Anderson et al. (2005) discuss the core stratigraphy, pollen record and dating in detail; sedimentation began ~10,000 yr BP.

Dragonfly Lake: (60º 48’ 43 N, 135º 20’ 24 W; elevation 760m ASL), the northernmost site, is situated approximately 20 km northwest of Whitehorse (Fig. 1). It is a small, shallow pond about 6.0 ha in area containing marl-rich sediments. The basin has one steep bank to the south-west. The simple bathymetry consists of a small deeper (~ 2 m) area, roughly in the centre, surrounded by a ~1-m deep ring. An abrupt onset of organic sedimentation marks local de glaciation at ~10,700 yr BP. The surrounding vegetation is mostly dominated by spruce, but individual pines are present nearby and pine stands occur in the Whitehorse area. At the time of coring pale yellow cloudy water colour suggested high internal productivity.

Sediment sampling and analyses

We obtained sediment cores from the deepest part of each lake using a modified 5cm-diameter Livingstone piston corer (Wright et al., 1984); these were stored at ~4°C in the laboratory. We described sediment stratigraphy visually, and for each 1-cm of the core we obtained values for loss-on-ignition at 550°C and magnetic susceptibility (using a Bartington O-ring). Data are available from the corresponding author.

Chronology: Dated samples consisted of sieved terrestrial macrofossils, charcoal or extracts of bisaccate pollen (obtained via heavy-liquid separation and centrifuging). Radiocarbon dates are reported as conventional radiocarbon years BP (AD 1950), and calendar age determinations are based on the INTCAL04 calibration data set (Reimer et al., 2004), reported as at the 1-σ range and median age. The radiocarbon sample depths were measured from the water surface and reported as such in Table 1. For plotting pollen and charcoal accumulation and time-series analyses, age models were adjusted to zero at the surface sample, correcting for the ~50-yr difference between the 1950 radiocarbon age and the age of the topmost sediment, and depths are reported with 0 cm equivalent to the sediment surface. Age-depth models were constructed using a spline interpolation and are pinned to the eastern lobe of the White River Ash (WRA) tephra, which was present in all records and has been well dated to ~1150 yr BP (Lerbekmo, 2008). Chronological information on the records is given in years before present (yr BP) unless otherwise indicated.

Pollen and stomata: Pollen samples were prepared and mounted using conventional methods (Faegri and Iversen, 1989) and used for pollen analysis and the determination of stomatal presence. A known amount of exotic *Lycopodium clavatum* spores was added to each sample to enable the calculation of pollen accumulation rates (PARs) based on the age model and exotic count. Pollen counts were usually ≥300 terrestrial pollen grains, but in a few samples the count was lower. For Salmo and Marcella, trends in the probable proportions of pollen of *Picea mariana* and *P. glauca* were determined using a simple size discrimination (see online supporting material). The mean body width of mixed modern samples of pure *Picea glauca* was ca 7.5 µ larger than that of a mixed sample of pure *Picea mariana* ($p \leq 0.001$). Inferred trends based on size were checked for selected samples using Hansen and Engstrom's (1985) morphometric criteria.

For most or all levels within the 'pine tail' (low levels of *Pinus* pollen), and for selected levels above and below, slides continued to be screened for the presence of stomata at x20 magnification after the pollen count was complete. Spores of the exotic marker were tallied simultaneously. Counts ceased at the positive identification of a pine stoma in a sample. If no pine stoma was found, scanning ceased when a total of 2000 exotic spores had been recorded. Stomata of *Picea* were also distinguished and recorded; finding a *Picea* stoma did not stop the count.

Bennett (1983) used an exponential function to describe population expansion based on PAR values. A logistic fit is perhaps more appropriate ecologically (e.g. Giesecke, 2005); however, the high variability of our PAR data and the relatively low sample number at some sites meant the pine expansion for our study sites was best described by an exponential curve over the period of increase (see also MacDonald and Cwynar, 1991). We used the window of best fit for an exponential function: the set of samples giving the highest R^2 from low values to the sample above which the pine PAR curve evened out or declined. Doubling time was estimated from the slope of the straight line fitted to the plot of ln(PAR) against time. At Dragonfly lake, the rapid expansion was covered by few samples and (relatively) poorly described by an exponential function; we therefore also fitted a straight line to the main pollen rise.

Charcoal: Cores were sampled contiguously. We used 1 ml of sediment taken at 1-cm intervals. Samples were placed in 10% tetra-sodium pyrophosphate solution for 24 hours to deflocculate the sediment and bleached in 6% hydrogen peroxide to whiten any other organic material. The material was then passed through 250-µ and 125-µ nested sieves using distilled water to gently disaggregate any remaining clumps. Samples were scanned at x20 magnification for locating fragments, with charcoal identification confirmed at x40 magnification. All charcoal fragments present in the sample were counted. Both particle count and area were tallied, and comparisons showed that particle count was a satisfactory measure of charcoal concentration per cm^3 of sediment. Charcoal accumulation rates were calculated using concentration and age-depth models.

We used the Char-Analysis v.1.2 software to analyze the charcoal time series (Higuera, 2009; Higuera et al., 2009). The software distinguishes background influx from peaks by creating a threshold through the time series of charcoal data, and it provides a statistical probability that distinctions are valid. Experimentation with different parameter values assessed the sensitivity of the method to these data. In all runs, the results were fairly similar and robust. We chose a 10-year initial data interpolation to create a dataset with uniform time steps less than the sampling resolution of the records. We used a 500-yr local smoothing window to distinguish charcoal peaks and a 1000-year moving window to estimate fire return interval and its approximate reciprocal, fire frequency.

Results

Chronology

All sites possess near-millennial resolution radiocarbon dating (Table 1), which provides robust chronologies. All age-depth relationships are near-linear, except for Marcella (Fig. 2). Three samples were omitted from the age models. In none of the sediment cores are there stratigraphic or physical features that might explain the aberrant ages. SUERC-11735, a conifer needle, appears to be displaced downward in Salmo. At Marcella, sample CAMS-11558 is omitted as it is significantly older than the WRA tephra located slightly below it. The Haircut sample CAMS-120918 is also too old in relation to other dates.

Table 1. Radiocarbon dates given as original 14C age, 1-sigma calibrated ranges and median calibrated age. Italicised dates were omitted from the final age-depth models as they were considered anomalous. Pollen samples consisted of *Picea glauca*, *P. mariana, and Pinus contorta* concentrates. Dates from Anderson et al. (2005) are indicated thus.**

Site	Publication Code	Depth (cm)	Sample Material	Conventional Radiocarbon Age	Calibrated Age 1σ range (years BP)	Median Age (years BP)
Salmo	CAMS 120913	862-863	Pollen	2750 +/- 35	2789 – 2869	2829
	SUERC-11736	905-905.5	Charcoal	3579 +/- 39	3820-3982	3901
	SUERC-7206	941-943	Pollen	4810 +/- 31	5473-5551	5512
	SUERC-11735	*960.5-961*	*Charcoal and charred needle*	*4691 +/- 40*	*5317-5482*	*5399*
	Poz-16782	1000	Pollen	7030 +/- 50	7745-7959	7852
	SUERC-7023	1024-1024.5	Wood	8090 +/- 49	8928-9135	9034

	CAMS 120914	1048-1048.5	Leaf and wood fragments	10090 +/- 100	11586-11825	11705
Marcella	CAMS-115580	50-51	Charcoal	1080 +/- 35	932-1057	1080
	CAMS-115581	*50*	*Terrestrial vegetative fragments*	*3570 +/- 35*	*3821-3975*	*3898*
	CAMS-96832**	101	Wood	2365 +/-40	2351-2454	2351
	CAMS-73144**	198	Wood	5330 +/- 40	6038 - 6183	6070
	CAMS-73145**	241	Wood	7370 +/- 110	8069 - 8310	8180
	CAMS-96834**	466	Wood	8605 +/- 40	9543 - 9608	9546
	OS-12131**	520	Wood	9090 +/- 55	10220-10333	10220
Haircut	CAMS-120917	879-881	Pollen	610 +/- 40	620-650	635
	SUERC-11412	904-905	Pollen	1952 +/- 35	1825-1952	1888

	CAMS-120918	*921-923*	*Pollen*	*3940 +/- 70*	*4287-4445*	*4366*
	SUERC-11409	942-944	Pollen	3122 +/- 35	3257-3408	3332
	SUERC-7831	956.5-957.5	Charcoal	3659 +/- 52	3846-4095	3955
	SUERC-11407	990-991	Pollen	5581 +/- 35	6297-6413	6355
	SUERC-7834	1012-1013	Charcoal	6935 +/- 113	7585-7916	7768
Dragonfly	SUERC-11406	240-241	Pollen	606 +/- 35	543-655	599
	CAMS-120915	280-282	Pollen	1155 +/- 35	1051-1091	1071
	Poz-16785	365-366	Pollen	2870 +/- 30	2918-3078	2998
	SUERC-11404	426-427	Pollen	4050 +/- 35	4422-4625	4523
	SUERC-11403	456-457	Pollen	4529 +/- 35	5049-5194	5121
	SUERC-7828	523-525	Charcoal and wood fragments	5816 +/- 88	6502-6695	6598

Poz-16783	566-567	Pollen	6950 +/- 40	7685-7860	7772
SUERC-7829	627-628	Charcoal, wood and *Carex* seeds	8294 +/- 147	9124-9463	9293
CAMS-120916	674-675	Wood and leaf fragments	9480 +/- 90	10586-10798	10692

Vegetation history

Detailed vegetation histories of the sites are available in Franklin-Smith (2007). Here we focus on changes in the tree species composition of the boreal forest relevant to the mid-/late-Holocene pine invasion. Note that the definition of the beginning of the *Pinus* zone according to the pollen percentage diagram (determined by visual inspection) is not identical to the period of population increase, which is derived from fitting a curve to the PARs (see below); values of PARs do not always mirror percent patterns.

Salmo Lake: Four zones are delimited by visual inspection in the percentage pollen diagram of Salmo Lake (Fig. 3); this site has near-basal date of ~11,700 yr BP and is used as the example of regional vegetation development. All sites follow a similar trajectory of Holocene vegetation development.

[Figure 2 near here—age-depth plots]

The basal deciduous zone covers the period from local deglaciation until the rise of *Picea* pollen (~11,700-9900 yr BP). The pollen is dominated by that of herbs and deciduous shrubs, with *Betula* attaining dominance by the zone end, reflecting post-glacial colonization of open ground and the establishment of woody deciduous vegetation cover.

The subsequent *Picea* zone (9900-6500 yr BP) begins with an abrupt rise in pollen values of *Picea* and is dominated by pollen of *Picea* and *Betula*. At Salmo, the *Picea* pollen is mostly attributable to *P. glauca*; the zone reflects establishment of white-spruce dominated evergreen conifer forest with an admixture of deciduous hardwoods. *Picea* but not *Pinus* stomata were found in this zone.

The *Pinus* “tail” zone (6500-2850 yr BP) is characterized by low but consistent presence of *Pinus* pollen (<5-15%) and the occurrence of *Pinus* stomata at most screened levels. The pine tail may reflect long-distance transport, but various estimates, summarized by Strong and Hills (2013), suggest that this level of pollen abundance signifies the presence of pine at low densities in the regional vegetation (see below). Between 6000 and 4000 yr BP there is a change in *Picea* grain size, with more grains attributable to *Picea mariana*.

[Figure 3 –Salmo Lake pollen record—near here]

The *Pinus* zone is the most recent pollen assemblage zone (2850 yr BP to present). It is characterised by *Pinus* pollen abundances up to 60% and reflects the establishment of pine as a co-dominant boreal forest species. *Pinus* stomata are present in screened levels.

Haircut, Marcella and Dragonfly: The other lake records are represented by summary *Pinus-Picea* diagrams (Fig. 4a, b, and c). The vegetation trends recorded at Salmo Lake occur in each lake pollen sequence, except that Haircut Lake (Fig. 4a) does not record the deciduous zone. Here, the earliest pollen zone, beginning about 7500 yr BP, is dominated by *Picea*, with *Betula* and *Salix,* and is consistent with an established spruce-dominated forest (*Picea* determinations were not made). From ~6000 yr BP *Pinus* stomata are recorded, coincident with the appearance of *Pinus* pollen in low abundances (2-10%). The pine tail zone at Haircut Lake lasts until 3400 yr BP when a rise in *Pinus* pollen and a rapid decline of *Picea* and *Betula* mark the beginning of the pine zone.

The Marcella lake pollen record (Figure 4b) is that of Anderson et al. (2005) plus new data covering the top 50 cm (~1000 yr). The pollen record and chronology at Marcella are less secure than that of the other three sites because a slumped portion of sediment interrupts the record; however, when corrected for the slump, the record is mainly consistent with another from this site (Cwynar, 1988). It contains a short deciduous zone (10,000-9500 yr BP). The *Picea* pollen increase at the beginning of the spruce zone at ~9500 yr BP is abrupt, suggesting a relatively rapid transition to evergreen coniferous forest dominated by *P. glauca*. Some *P. mariana* may have been present in the early spruce forest (SI Figure 1); after ca. 6000 yr BP it increases in importance (in Cwynar's [1988] record *P. mariana* peaks between 7000 and 5000 yr BP). *Pinus* is consistently present from ~5000 yr BP, and its pollen also occurs intermittently in older sediments at very low levels. *Pinus* stomata are present from ~7500 yr BP. The main rise in *Pinus* pollen begins at ~2500 yr BP; *Pinus* pollen values remain high to the present.

[Figure 4a, b, c—Haircut, Marcella, Dragonfly—near here]

Dragonfly Lake has similar pollen zones to Salmo and Marcella (Figure 4c). Sedimentation began about 11,000 years ago, and the basal deciduous zone ends at 9800 yr BP with an abrupt rise in *Picea* pollen; both *Picea* species occur throughout the record, with more dominance of *P. mariana* in the last two millennia. The first appearance of *Pinus* stomata marks the beginning of the *Pinus* "tail" at about 5000 yr BP. *Pinus* pollen is present consistently from 4800 yr BP. The record shows strong temporal asynchrony compared with the other sites with respect to the main *Pinus* rise, which occurs abruptly at 1100 yr BP. The later pine increase at this, the farthest north-west of the four study sites, is consistent with the patterns reported by MacDonald and Cwynar (1991) and Strong and Hills (2013).

Pollen accumulation rates. Fig. 5a shows PARs in the *Pinus* tail and *Pinus* zones for each site and Fig. 5b the exponential curves used to estimate population growth parameters. Table 2 presents estimated expansion period and doubling time for each site. Salmo, Haircut and Marcella data fit an exponential model well (R^2>0.9). Dragonfly Lake has a slightly poorer fit (R^2=0.86): there are rather few samples in the pine rise, and the PARs may be affected by an excursion in the age model at the WRA, which coincides with the steepest PAR increase. A straight line was also fitted to the Dragonfly data; the fit was no better (R^2 = 0.8119; Table 2), but the estimated time periods are considerably shorter (and likely more reasonable, given the steepness of the

PAR curve). Estimates of expansion period and doubling time vary. The longest expansion period is at Salmo (~2500 yr) and the shortest at Haircut (~1000 yr). Estimated PAR doubling times range from ~575 years at Dragonfly (exponential estimate) to ~160 at Haircut.

[Figure 5a and b –PARs and exponential curves—near here]

Table 2. Details of pine population expansion (values rounded to 5 yr)

Site	Population expansion period (Cal yr BP)	Duration (yr)	Doubling time (yr)
Salmo	4420-1910	2515	460
Haircut	3465-2510	955	160
Marcella	2480-1250	1230	225
Dragonfly	2045-435	1610	575
Dragonfly (linear)	1220-435	785	360

Charcoal records and inferred fire histories

Fig. 6 shows time series for charcoal accumulation and identified peaks for each site using a 500-year smoothing window. Note that in Figures 6 and 7, the zones 4-1 marked on the diagrams represent deciduous period (Dragonfly only), *Picea* with the *Pinus* “tail”, the *Pinus* expansion period defined by the PARs, and the post-expansion period, respectively, not the original named pollen zones defined by the pollen frequencies.

All sites record continuous charcoal presence, except for samples prior to the *Picea* rise and a few samples in the *Picea* zone at Marcella Lake. Median charcoal concentrations (pieces cm^{-3}) are higher at Salmo and Haircut (47 and 25, respectively), and lower at Dragonfly and Marcella (15 and 13, respectively). Signal-noise ratio (effectiveness of peak identification) estimates for segments of each time series are reported in the supplemental information (SI Figure 2). The signal-noise ratio is above the threshold value for reliability (3.0) for most of the record at each site. Peak distribution is irregular: there are short (ca 500-yr) “quiescent” periods with low charcoal values and no peaks at all sites, but these are not synchronous. In the Salmo record, there is one period with no identified peaks from ~2500-1500 yr BP. Charcoal abundance (as shown by accumulation rate) varies strongly through time at each site, but not in parallel.

[Figure 6 near here]

In charcoal Zone 4 (deciduous, only shown for Marcella and Dragonfly) the signal-noise ratio is low, reflecting low charcoal counts and a threshold near zero. Few peaks were identified; the majority of peaks that fail to qualify as signal occur in this zone. The deciduous-*Picea* transition (charcoal zone 4 to 3) shows features more peaks and higher charcoal accumulation, likely reflecting the major increase in flammable biomass with the beginning of spruce dominance. Particularly high accumulation characterizes the *Pinus* rise and early *Pinus* zone (charcoal zones 2 and 1) at Marcella and Dragonfly, but this is attributable, at least in part, to a brief change in the slope of the age models related to the WRA.

[Figure 7 a-d near here]

Table 3: Fire regime estimates and uncertainties for the four sites

	Charcoal Zone 3 (pre-expansion)			Zone 2 (*Pinus* expansion)			Zone 1 (post expansion)		
	mFRI	upper CL	lower CL	**mFRI**	upper CL	lower CL	**mFRI**	upper CL	lower CL
Salmo	**243**	291	199	**280**	438	168	**162**	219	115
Haircut	**191**	230	153	**150**	227	94	**183**	266	113
Marcella	**247**	296	200	**145**	180	107	**222**	303	128
Dragonfly	**146**	170	121	**134**	186	89	**n**	n	n

Charcoal records during **Pinus** *population expansion*

Figures 7 a-d show peak identification, estimated fire return interval and estimated fire frequency for each site. Table 3 shows fire return intervals and 95% confidence intervals estimated by Char-Analysis for charcoal zones 3, 2, and 1. The long-term (Holocene) fire return intervals are consistent with other charcoal-based estimates from northern boreal forest values, mostly falling within the range ~ 300 to ~100 yr (see Higuera et al. 2009; Kasischke et al. 2010; Kelly et al. 2013). During the expansion phases at all sites except Salmo, there is a tendency for fire return interval to be relatively short, and fire frequency relatively high, compared with the overall record (mean fire return interval in the expansion phase is 150 years or less, but 280 at Salmo; Table 3). At each site there is fire activity at the beginning of pine expansion (evidenced by several charcoal peaks). No pine expansion begins in a “quiescent” period lacking peaks. However, at Salmo, much of the latter half of the *Pinus* increase features a particularly long fire return interval. At all sites but Salmo, fire return intervals lengthen in the last 500 years of the record, which may be partly an artefact, as the age models fail to account for any reduced compaction of the near-surface sediment.

Discussion

Pattern of spread of **Pinus contorta** *in the southern Yukon*

As Godwin (1975) pointed out, the ecological processes of species' arrival, establishment and population expansion are distinct events, and only the two latter can be distinguished in the fossil record (Froyd, 2005). It is important that reconstructions of post-glacial plant migrations based on palynological data focus on both; otherwise inferred ecological properties, such as dispersal capability, the time elapsed between individual arrival and population expansion, and the mode of population spread are affected (see, for example, Bennett, 1988; Birks, 1989; Giesecke and Bennett, 2004; Giesecke, 2005).

The presence of low populations of *Pinus* over several millennia starting ~7000-5000 yr BP at each site is interpreted from stomata that are assumed to be from decomposed pine needles of local origin. This would not hold if stomata were regularly reaching the lakes via long-distance transport. Fluvial input from large catchments is not an issue, as all lakes have extremely small catchments and three are closed basins. Another possibility is aerial transport via forest fire convection columns as suggested by Cwynar and MacDonald (1987). Pisaric (2002) confirmed that needles and other plant fragments can be moved 20 km (and possibly further) by fire-related atmospheric transport; in his study many fragments, but not all, showed some degree of charring. However, the stomata we observed were not obviously charred.

A model invoking a moving front of high pine populations approaching, delivering stomata via fires, and then passing each site does not fit other observations (see below). Rather, these results support the findings of Peteet (1991), Fossitt (1994) and Froyd (2005) that it is possible for *Pinus* to be present at a site and yet be represented by extremely low pollen frequencies. Furthermore, the dates of first appearance of stomata and of the pine rise differ by centuries to millennia with no clear directional pattern (except that the population expansion at Dragonfly, the northernmost site, is latest; Table 2). The southernmost site, Marcella, records early small populations, but the pine expansion is later than at Salmo and Haircut to the north. This pattern is also consistent with spread via founder populations, rather than as a dense moving front (see Giesecke, 2005). Thus, model that best fits the pattern of Holocene pine invasion into the southern Yukon features a long period (2000 - >4000 years as detected by stomata) when *Pinus* was present as scattered individuals or small stands, then an asynchronous triggering of local population increases.

Our estimated period of exponential expansion varies between <1000 and ~2500 years and population doubling times between ~150 and ~600 years (Table 2, Fig. 5). These figures compare well with the estimates of MacDonald and Cwynar (1991), who report a range of 80-1100 years for doubling times across the range of pine, with shorter times typical of Yukon sites. In their study, populations at southern sites showed relatively gradual rates of increase (over several millennia) from initially fluctuating low levels. In Yukon, the population increase happened much faster (~1000 years). They suggested this difference may reflect physiography and habitat availability (better establishment opportunities northward), and, possibly, slowly varying climate. What differs in our study is the stomatal record linked to the tail of extremely low pollen values suggesting a long period of low population size (3000-4000 years) in northern sites also.

The role of fire and lodgepole pine migration

The lakes are small, so the spatial resolution of their vegetation and fire records is limited, each sensing events in their catchments and immediately adjacent terrain. This, coupled with the heterogeneous regional vegetation and fire mosaic, produces individually distinct records (see Gavin et al. 2006). The observed patterns nevertheless make regional ecological sense: identified peak frequency and charcoal accumulation (indicating fire events and burned biomass, respectively) increase with the establishment of spruce forest in the early Holocene at Salmo, Marcella and Dragonfly; subsequently the timeaveraged fire return intervals vary slowly, mostly lying between ~350 and ~100 years. These Holocene rates are in keeping with other long-term estimates (e.g., Lynch et al. 2002; Higuera et al. 2009) but lower than those reported recently from Yukon (e.g. Johnstone and Chapin 2006) and other likely anomalous C20th fire regimes (Kasischke et al. 2010; Kelly et al. 2013). However, on occasion two or more fire events within a century are evident in the charcoal record, and there are multi-century periods with no identified fires, suggesting high century-scale variability in fire patterns. Temporal matches of peak clusters, quiescent periods or changes in fire frequency among the four records are not evident, suggesting no regional, long-term control of fire regimes, such as climate, has been operating.

Our data support a model of fire-assisted expansion of pine but show no evidence that local pine dominance or co-dominance subsequently altered fire regimes. The observed fire regimes are consistent with conditions that would allow small pine populations to increase, as observed in the modern boreal forest (Johnstone and Chapin 2003)—if other conditions were conducive to pine growth. From Table 3, it can be seen that fire return times trend lower during the *Pinus* expansion (except at Salmo), though their 95% confidence limits overlap those of the preceding period (except at Marcella). *Pinus* began to increase when the estimated fire return interval was 150 years or less (~250 years at

Salmo), i.e. during a period of relatively frequent fire events that would have favoured *Pinus* competitively (Johnstone and Chapin, 2003). However, periods of equally short fire return intervals within the earlier part of the *Pinus* “tail” at Haircut and Dragonfly saw no pine expansion (Figures 7b and d). Conversely, at Salmo, after an initial cluster of fires there were relatively few fire events during expansion. This may explain why its population growth curve is shallow, with a long (>2000 yr) expansion period and doubling time (462 yr; see Table 2). Subsequently, neither larger local pine populations nor the overall drying trend in southern Yukon during the past 1000 years (see above) can be linked to regional changes in the fire regime: trends are weak and contradictory (at Dragonfly the period after *Pinus* rise is too short to estimate fire statistics (see Figs. 7d; Table 3).

There is also no evidence that the mid-Holocene (7000-4000 yr BP) regional increase of *Picea mariana* at Marcella and Salmo was linked to higher charcoal influx (charred biomass) or fire frequency, as it is in some interior Alaskan records (Lynch et al 2002; Brubaker et al. 2009). However, the study sites are located away from low-lying and poorly-drained portions of the landscape that are dominated by *P*. *mariana*, with, consequently, little possibility of direct charcoal influx from black-spruce dominated areas.

Invasion of patchy landscapes and the Allee effect

The time taken for pine to reach co-dominance in closed boreal forest, which was already dominated by species with similar structural-functional characteristics, appears not to be primarily a function of dispersal ability or of burn availability. Rather it may reflect intrinsic biological controls on expansion rate, with eventual population release facilitated by a suitable fire regime and, possibly, other local site factors.

This pattern could be explained by elements of the Allee effect (Taylor and Hastings 2005). Rare long-distance seed dispersal restricts the degree of gene flow and genetic variation available among individuals in an area and consequently reproductive fitness (Gieseke 2005; Taylor and Hastings 2005). Furthermore, although pollen can be widely dispersed, at low overall population densities, pollination rates of female cones may be low. As the species typically outcrosses and exhibits inbreeding depression (Sorenson 2001), time would be needed to build sufficient genetic variation within a population of widely dispersed *Pinus contorta* individuals to enable population growth. Thus, the observed stasis at low population size for millennia may reflect genetic constraints operating within the large-scale trajectory of Holocene migration. Furthermore, in heterogeneous landscapes “range-pinning” operates, where individuals are also required to disperse between limited suitable habitat patches, i.e., recently burned areas on suitable substrates, or topographic constraints on suitable habitats (Taylor and Hastings 2005, Strong and Hills, 2013). Direct environmental-genetic constraints may have also played a role, whereby poorly-adapted ecotypes took time to adapt to relatively unfavourable conditions in southern Yukon, although clear environmental differences from regions directly to the south are not apparent. Overall, the fossil-based history of pine in southern Yukon aligns quite well with the phylogeographic patterns reported by Marshall et al (2002) that suggest relatively recent (last ~3000 year) population expansions from low numbers, followed by some local differentiation of populations near the northern range margin.

The operation of elements of the Allee effect can be broadened to post-glacial boreal forest dynamics in general. It was invoked by Giesecke (2005), for example, to explain the relatively slow Holocene expansion of *Picea abies* (Norway spruce) across Scandinavia. Here *Pinus sylvestris* (Scots pine) spread extremely quickly into deglaciated regions in the early Holocene, a reciprocal taxonomic pattern to that seen in Yukon. Some records of late-Quaternary boreal tree migration encompass invasions of more open landscapes (e.g. Picea glauca in western Canada (Ritchie and MacDonald, 1986). In the absence of competition from similar functional types, and thus control by patch dynamics over establishment, the Allee effect might be expected to be greatly reduced. Thus, observations of rapid spread in the palaeorecord may be linked with a low degree of intrinsic constraint on population growth. This may be as influential as the dispersal kernel shape (Clark, 1998) or the presence of refugial “booster” populations (see, e.g., Birks and Willis 2008; Stewart et al 2009). Early Holocene expansions may reflect the initial advantage gained by one of several possible species with similar functional characteristics (see West 1980), whereas individuals of species arriving later are faced with restrictions such as swamping by other species’ pollen and patchy habitat availability.

Conclusion

Given the likelihood that climate warming will promote range changes in many species, insight into the ecological dynamics that promote or constrain population increases as species occupy new territory is important. During the Holocene *Pinus contorta* spread widely as individual trees into the extant spruce forest of Yukon, but populations were prevented from expanding for millennia, probably by biological constraints on reproductive success. Expansion of local populations was likely facilitated by the regime of frequent fires, which is reflected in recent observations. Future population growth rates might be affected by a large increase in fire frequency (climatically and/or anthropogenically driven) or by other human influence (e.g., planting, inadvertent seed dispersal, provision of new colonization sites by physical disturbance), but the Holocene perspective suggests that biological constraints on immediate population expansion are also important, and these are unlikely to change even with substantial warming.

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Figure Captions

Figure 1. Study area location and aerial views of the four sites.

Figure 2. Plots of calibrated radiocarbon dates for the four sites showing the 1-σ range about the median. Dates used in age models are grey filled circles. The age at the surface (assumed as 1950 AD) is shown as a black filled circle with no uncertainty bars. The White River Ash (see Lerbekmo, 2008) is marked by a black rectangle. Samples omitted from age models are marked by black triangles and discussed in the text. The original ^{14}C dates are listed in Table 1.

Figure 3. Pollen diagram for key taxa at Salmo Lake illustrating details of the regional forest history. Zones were defined by eye and named to illustrate key vegetation changes. Stomata are shown as present or absent, and all levels screened for stomata are indicated.

Figure 4a. Summary pollen-stoma diagram for Haircut Lake.

Figure 4b. Summary pollen-stoma diagram for Marcella Lake. The data are partly from Anderson et al. (2005).

Figure 4c. Summary pollen-stoma diagram for Dragonfly Lake.

Figure 5a. The pollen accumulation rate (PAR) curves plotted against time for each site, scaled to the same time axis.

Figure 5b. The exponential curves fitted to the PAR values. R^2 values are shown. For Dragonfly, the alternative linear fit is shown as a dashed line (R^2 = 0.8119).

Figure 6. Charcoal accumulation time series and peak identification for the four sites. Peaks not identified as signal are shown as grey filled circles under the series. Zone 3 is pre-pine expansion; zone 2 is the pine expansion; zone 1 is post-pine expansion. At Marcella and Dragonfly we also defined Zone 4 (early deciduous), but charcoal values are low in this zone, making it difficult to define peaks.

Figure 7 a-d. The charcoal time series for each site, showing, from top downwards, identified charcoal peaks, peak magnitude, estimated fire return interval with 95% confidence intervals, and smoothed estimated fire frequency.

The population expansion window for *Pinus* is shown as a rectangle across the time series, and the beginning of the *Pinus* “tail” is shown by a dashed vertical line.

Online supplementary material

Figure S1 shows variation in *Picea* grain-size measurements with time for Salmo and Marcella Lakes.

Figure S2 shows for each site a sample of signal-noise ratios (SNRs: reliability of peak identification) estimated by Char-Analysis for the charcoal peaks determined using a 500-yr window to define peak threshold. Each graph represents a non-overlapping segment of the charcoal accumulation time series. The vertical line intersecting the x-axis represents the local threshold value of charcoal accumulation. The distribution plotted to the left represents noise, that to the right local fires; the y-axis shows proportional contributions of the sample charcoal values. SNR values >3.0 indicate a good separation of signal from noise.

Figure 1

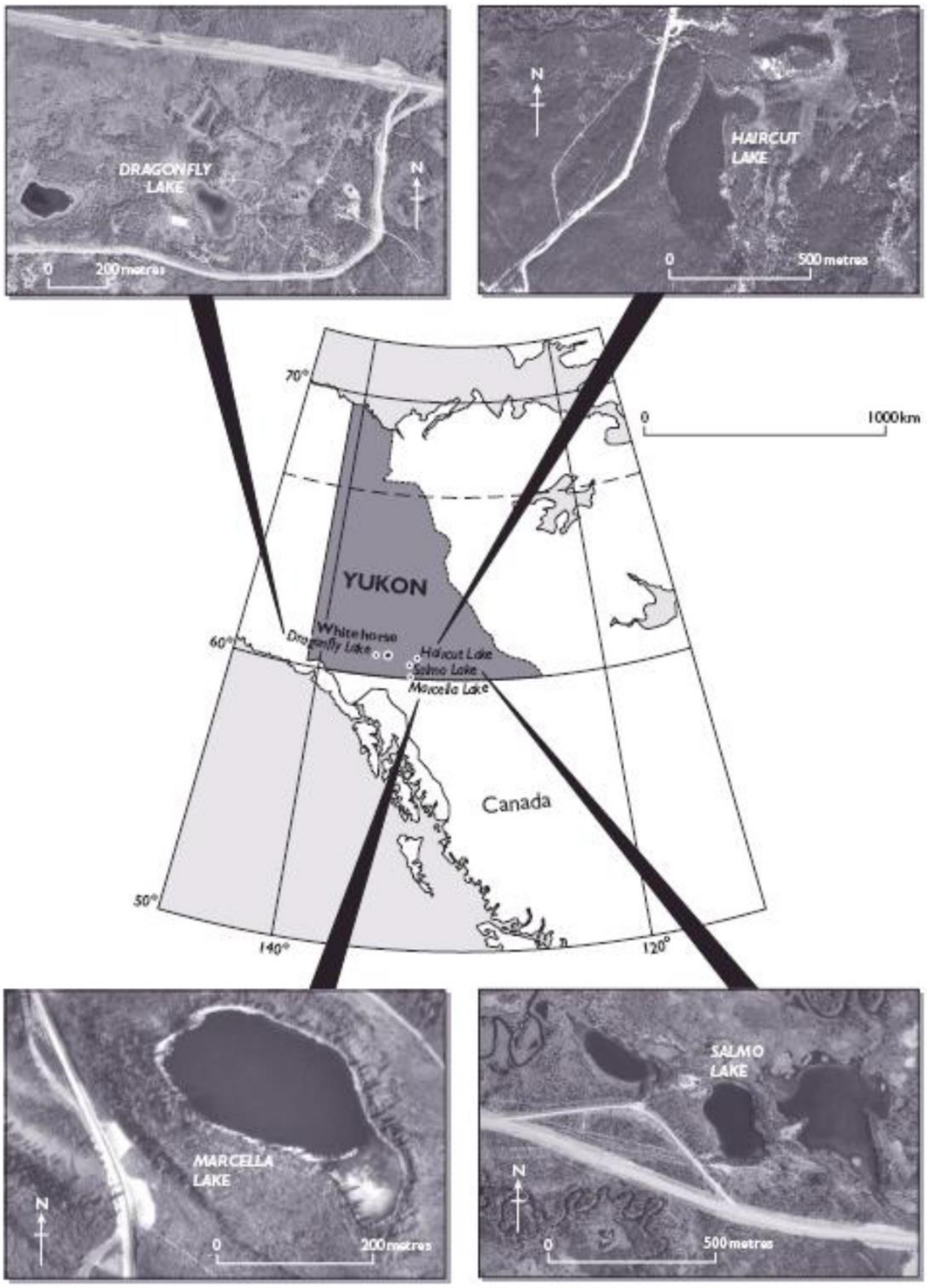

DRAGONFLY LAKE
N
0
200 metres
N
HAIRCUT LAKE
0
500 metres
70°
0
1000 km
YUKON
Whitehorse
Dragonfly Lake
Haircut Lake
Salmo Lake
Marcella Lake
60°
Canada
50°
140°
120°
MARCELLA LAKE
N
0
200 metres
SALMO LAKE
N
0
500 metres

Figure 2

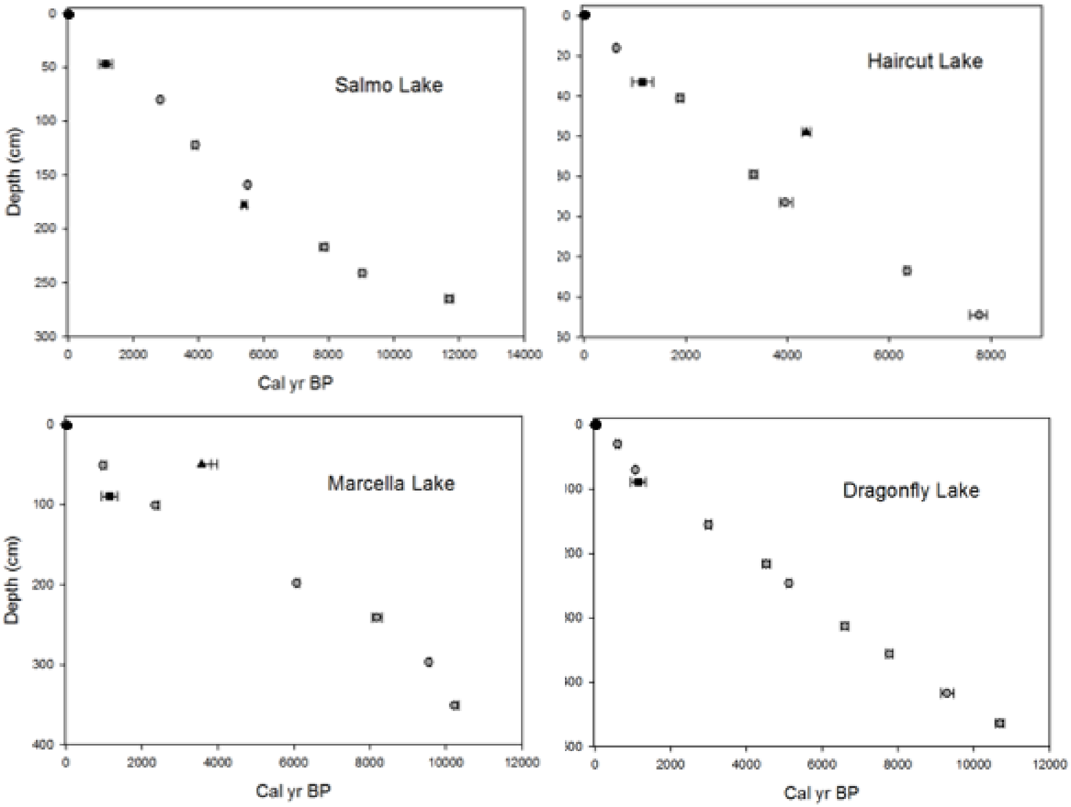
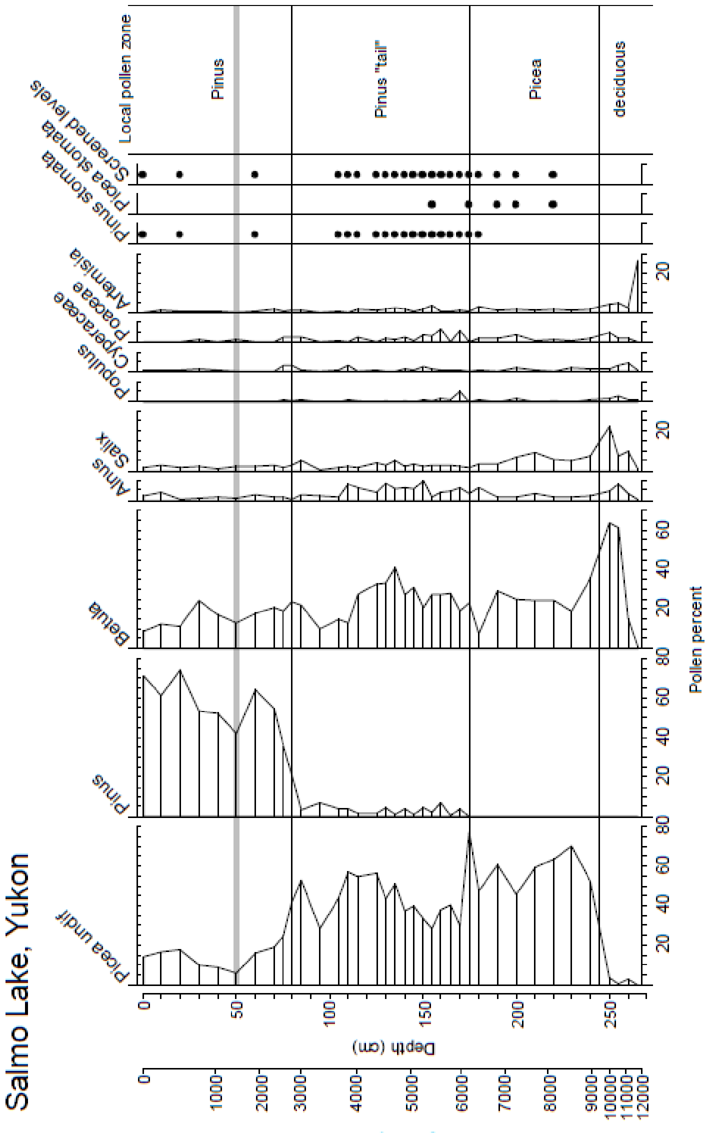
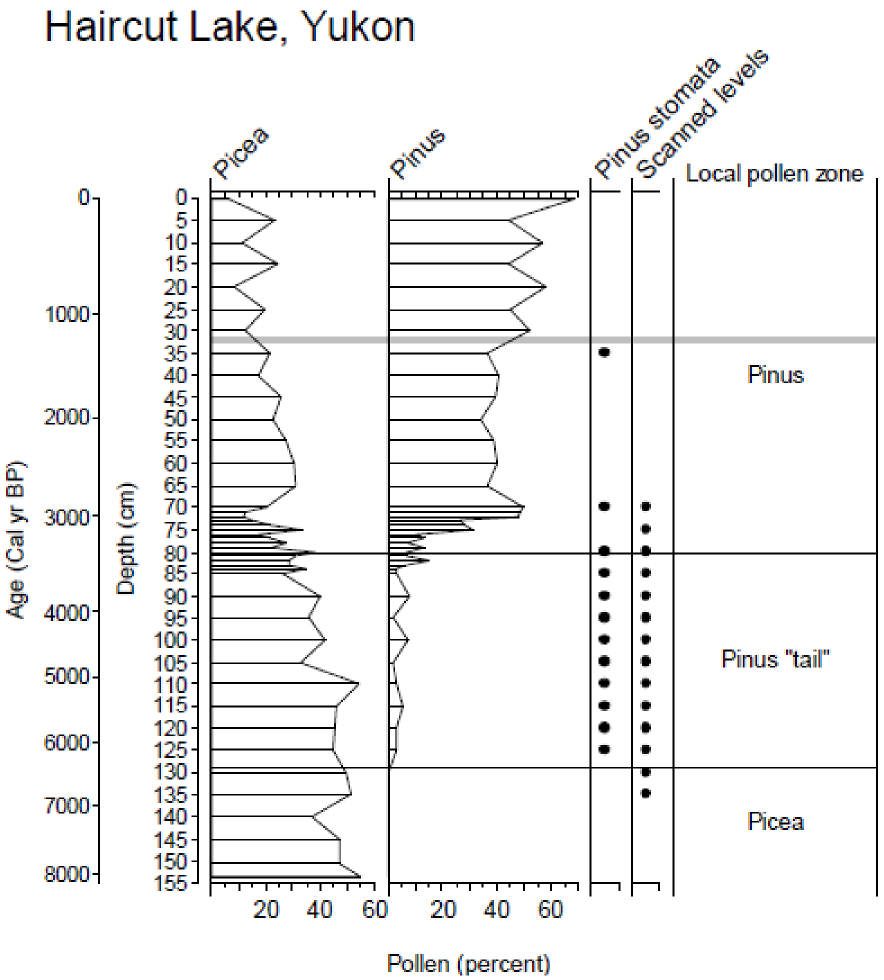

Salmo Lake
Haircut Lake
Marcella Lake
Dragonfly Lake
Depth (cm)
Cal yr BP
0
50
100
150
200
250
300
2000
4000
6000
8000
10000
12000
14000
400

Figure 3


Salmo Lake, Yukon
Picea undiff
Pinus
Betula
Alnus
Salix
Populus
Cyperaceae
Poaceae
Artemisia
Pinus stomata
Picea stomata
Screened levels
Local pollen zone
Pinus
Pinus "tail"
Picea
deciduous
Depth (cm)
0
50
100
150
200
250
Age Cal yr BP
0
1000
2000
3000
4000
5000
6000
7000
8000
9000
10000
11000
12000
Pollen percent
20
40
60
80

1027



1028
1029
1030 Figure 4b
1031

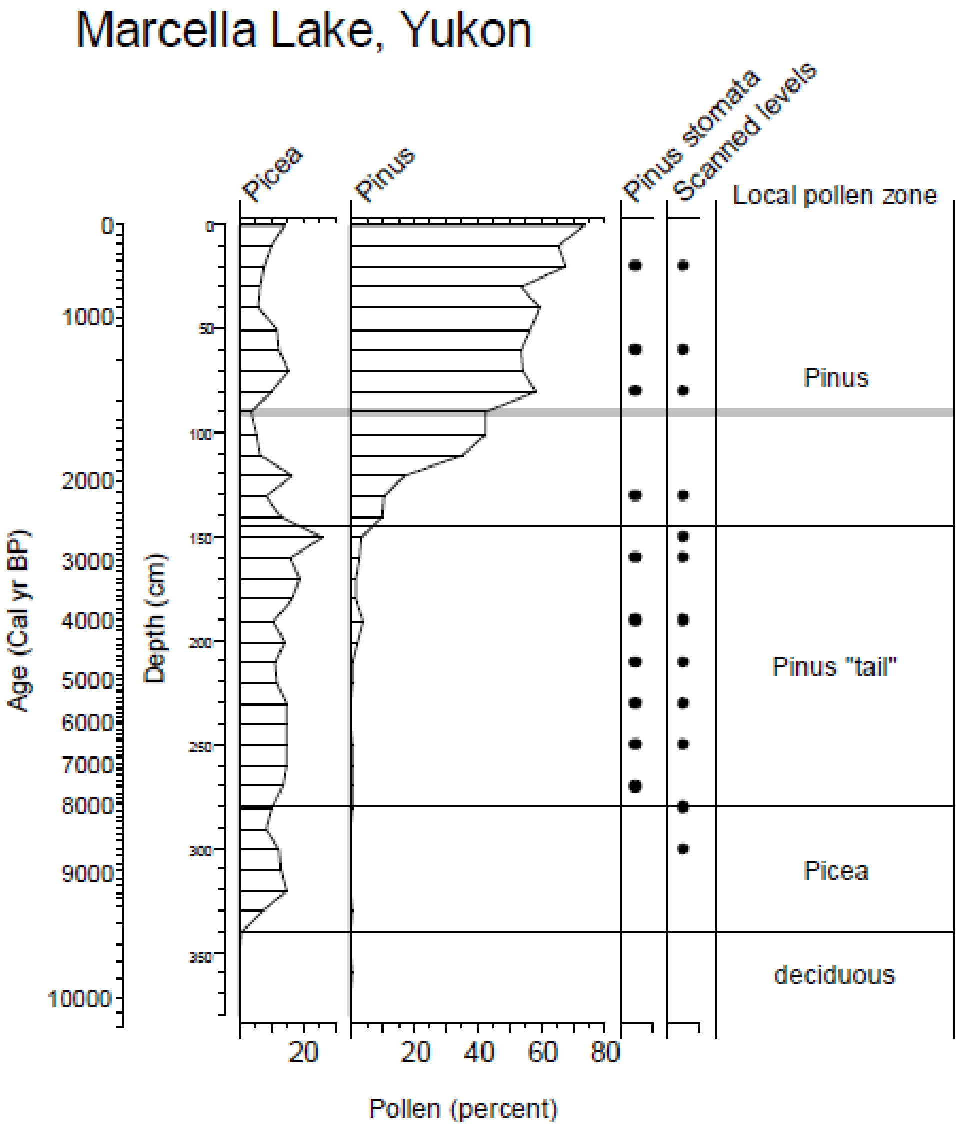

Marcella Lake, Yukon
Picea
Pinus
Pinus stomata
Scanned levels
Local pollen zone
Age (Cal yr BP)
0
1000
2000
3000
4000
5000
6000
7000
8000
9000
10000
Depth (cm)
0
50
100
150
200
250
300
350
Pinus
Pinus "tail"
Picea
deciduous
20
20
40
60
80
Pollen (percent)

Figure 4c

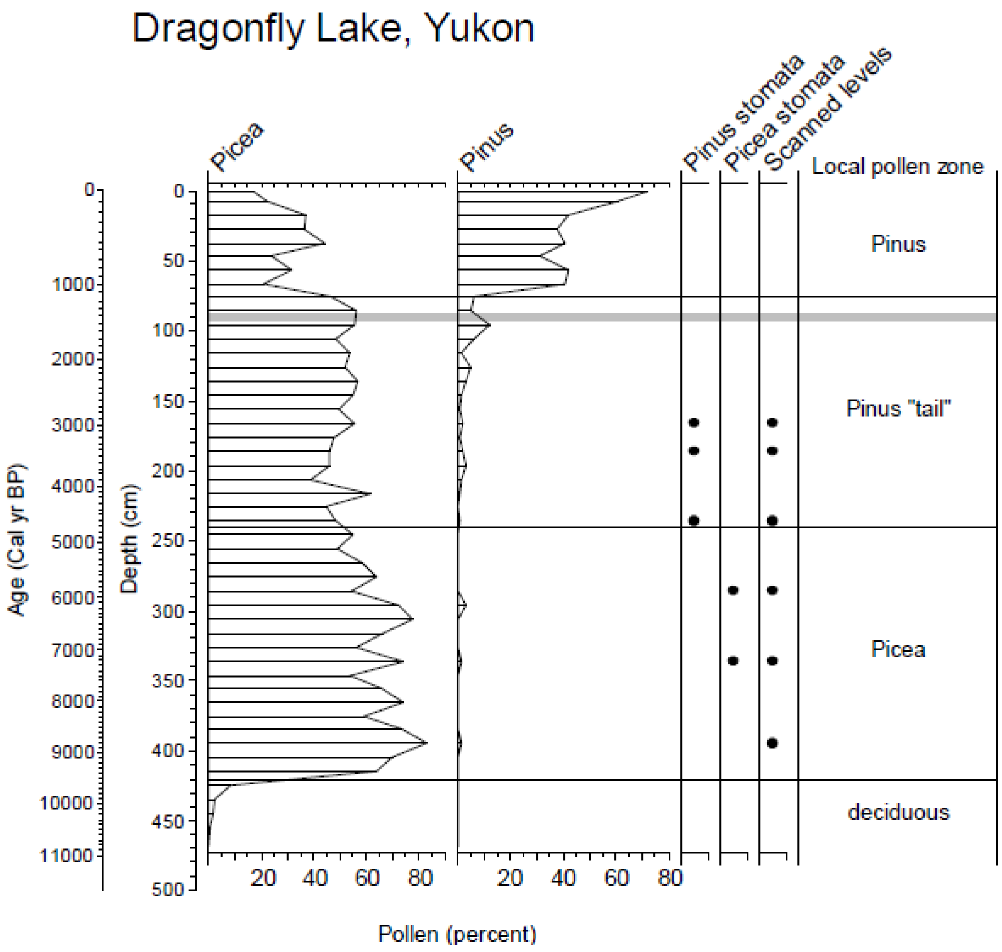

Dragonfly Lake, Yukon
Picea
Pinus
Pinus stomata
Picea stomata
Scanned levels
Local pollen zone
Pinus
Pinus "tail"
Picea
deciduous
Age (Cal yr BP)
0
1000
2000
3000
4000
5000
6000
7000
8000
9000
10000
11000
Depth (cm)
0
50
100
150
200
250
300
350
400
450
500
20
40
60
80
20
40
60
80
Pollen (percent)

Figure 5a

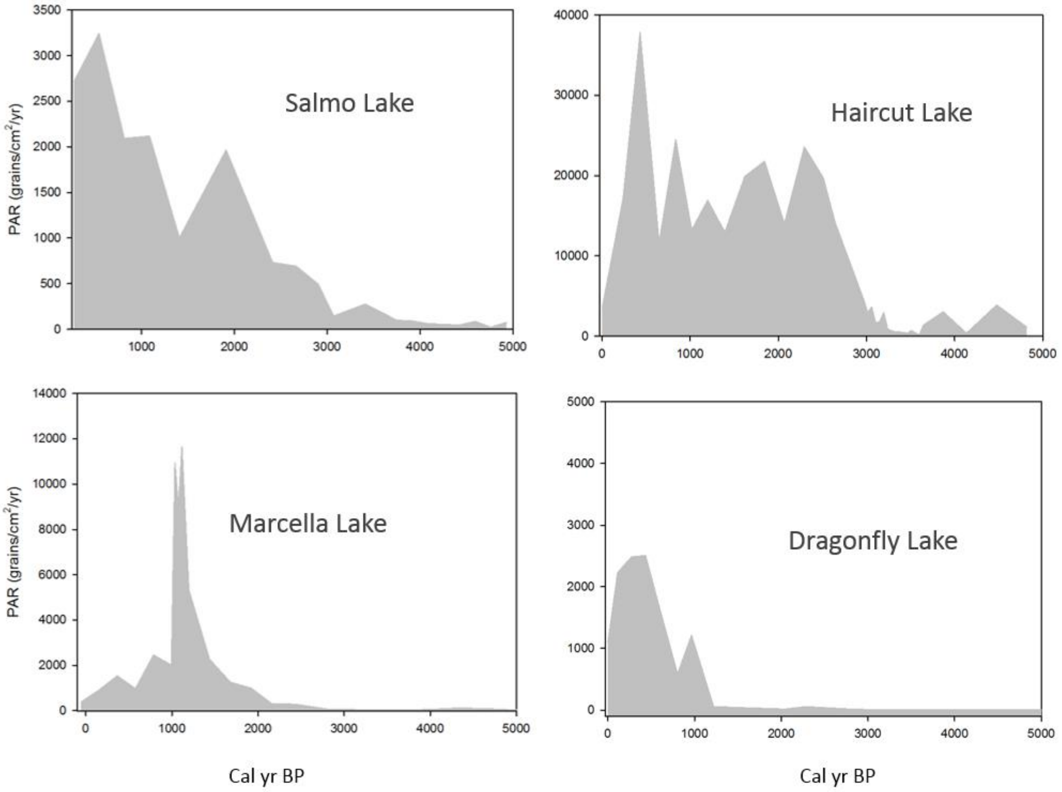

Salmo Lake
Haircut Lake
Marcella Lake
Dragonfly Lake
PAR (grains/cm^2/yr)
PAR (grains/cm^2/yr)
Cal yr BP
Cal yr BP
0
500
1000
1500
2000
2500
3000
3500
0
10000
20000
30000
40000
0
2000
4000
6000
8000
10000
12000
14000
0
1000
2000
3000
4000
5000

Figure 5b

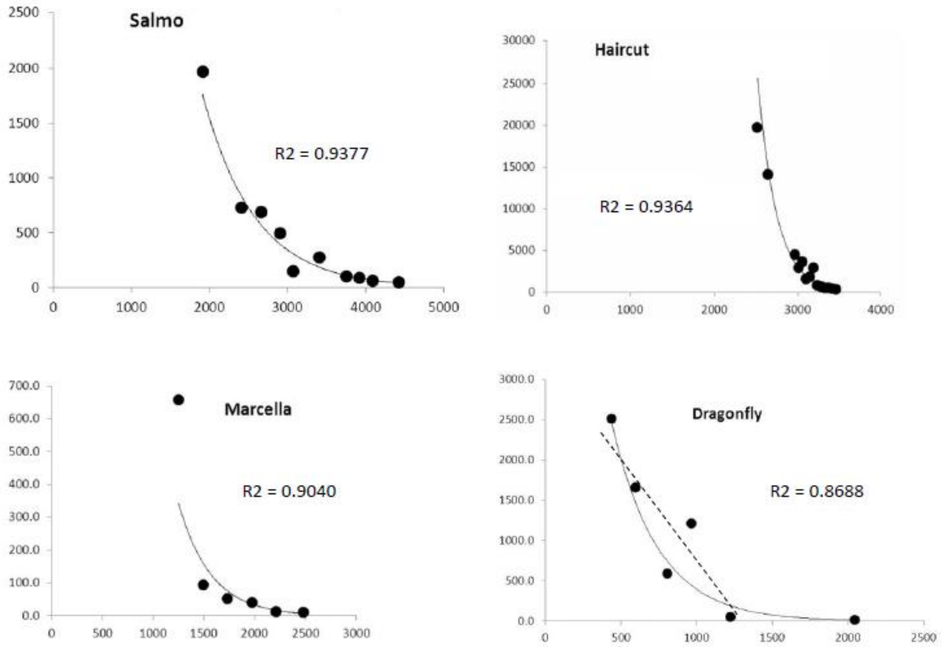
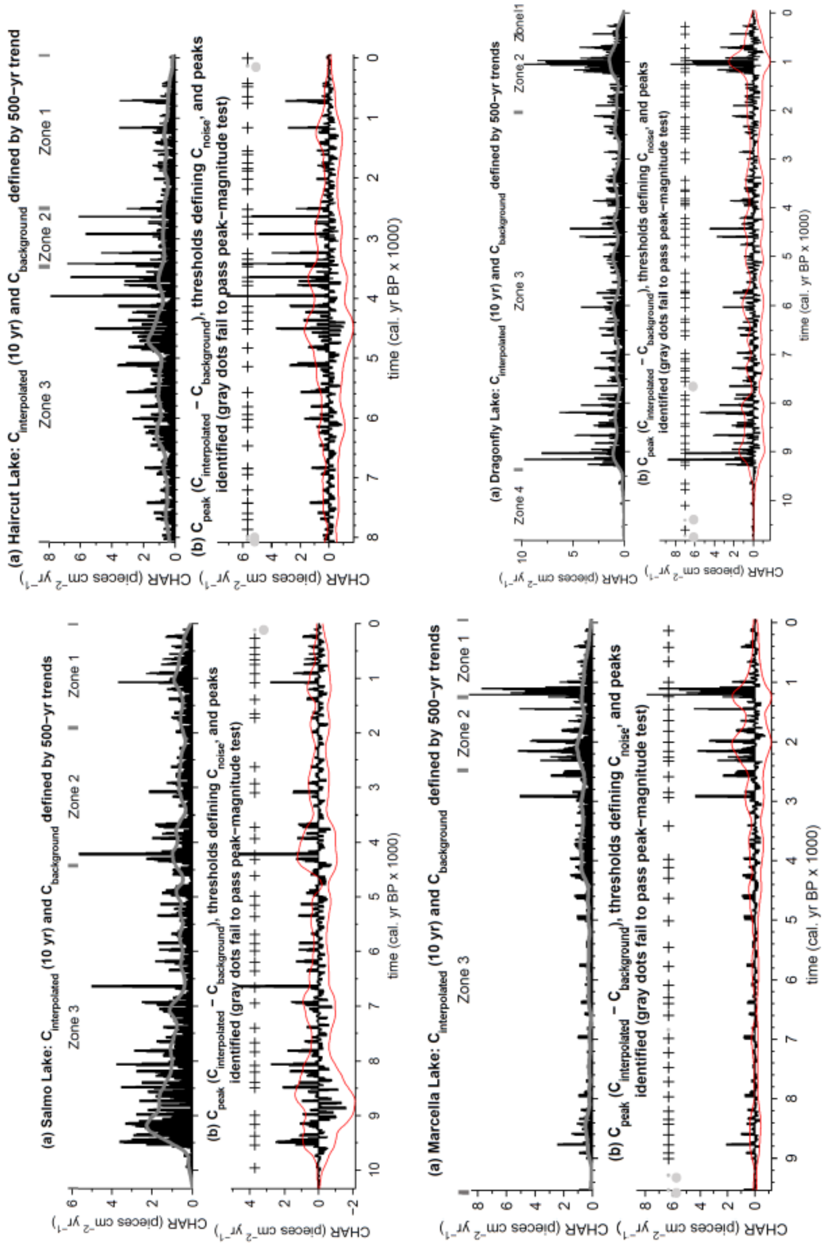

Salmo
R2 = 0.9377
2500
2000
1500
1000
500
0
0
1000
2000
3000
4000
5000
Haircut
R2 = 0.9364
30000
25000
20000
15000
10000
5000
0
0
1000
2000
3000
4000
Marcella
R2 = 0.9040
700.0
600.0
500.0
400.0
300.0
200.0
100.0
0.0
0
500
1000
1500
2000
2500
3000
Dragonfly
R2 = 0.8688
3000.0
2500.0
2000.0
1500.0
1000.0
500.0
0.0
0
500
1000
1500
2000
2500

Figure 6



(a) Haircut Lake: $C_{interpolated}$ (10 yr) and $C_{background}$ defined by 500−yr trend
(b) C_{peak} ($C_{interpolated}$ − $C_{background}$), thresholds defining C_{noise}, and peaks identified (gray dots fail to pass peak−magnitude test)
(a) Dragonfly Lake: $C_{interpolated}$ (10 yr) and $C_{background}$ defined by 500−yr trends
(b) C_{peak} ($C_{interpolated}$ − $C_{background}$), thresholds defining C_{noise}, and peaks identified (gray dots fail to pass peak−magnitude test)
(a) Salmo Lake: $C_{interpolated}$ (10 yr) and $C_{background}$ defined by 500−yr trends
(b) C_{peak} ($C_{interpolated}$ − $C_{background}$), thresholds defining C_{noise}, and peaks identified (gray dots fail to pass peak−magnitude test)
(a) Marcella Lake: $C_{interpolated}$ (10 yr) and $C_{background}$ defined by 500−yr trends
(b) C_{peak} ($C_{interpolated}$ − $C_{background}$), thresholds defining C_{noise}, and peaks identified (gray dots fail to pass peak−magnitude test)
Zone 1
Zone 2
Zone 3
Zone 4
CHAR (pieces cm^{-2} yr^{-1})
time (cal. yr BP x 1000)

Figure 7a

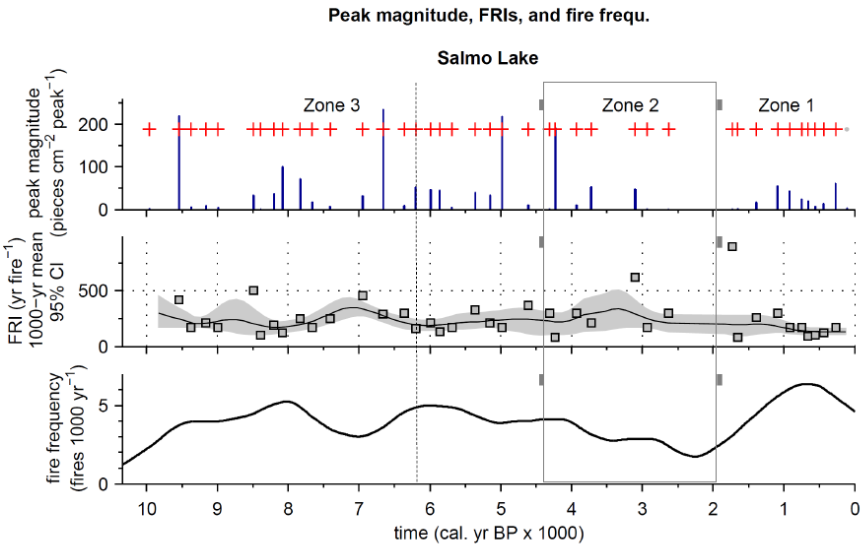


Figure 7b

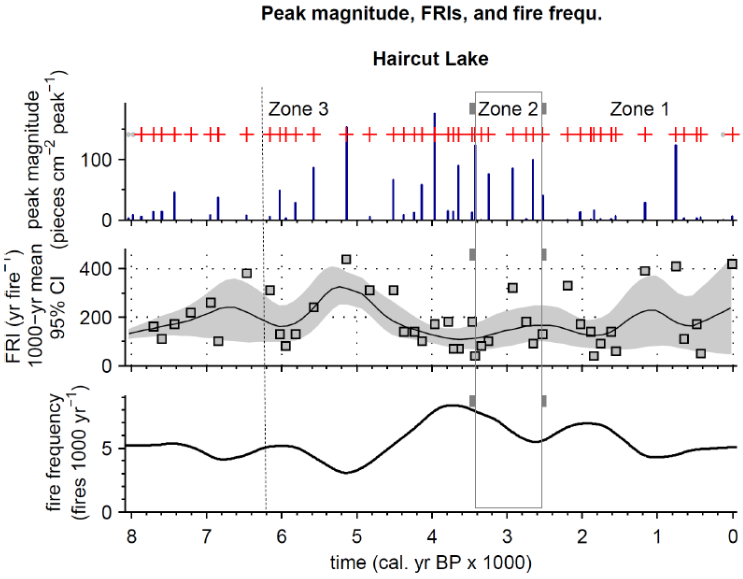


Figure 7c

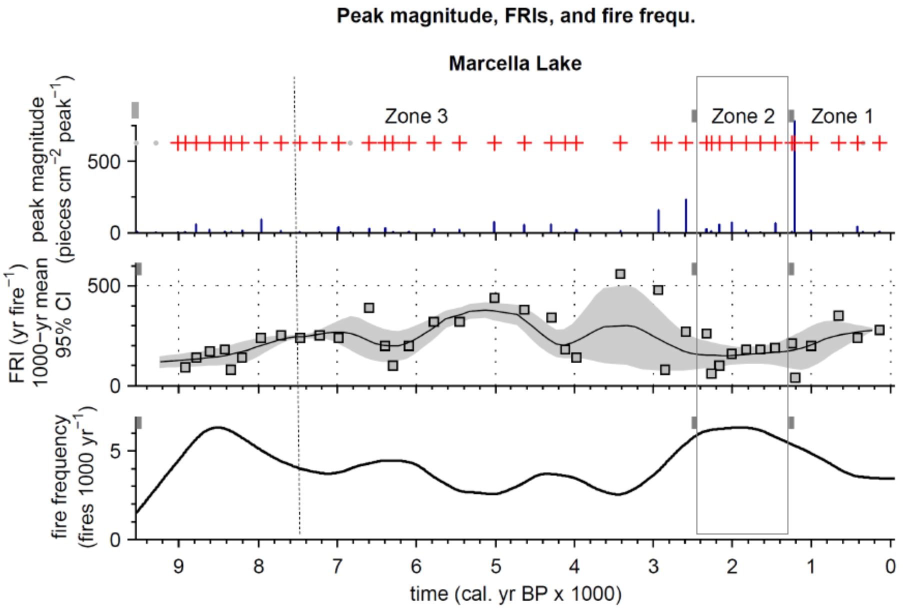


Figure 7d

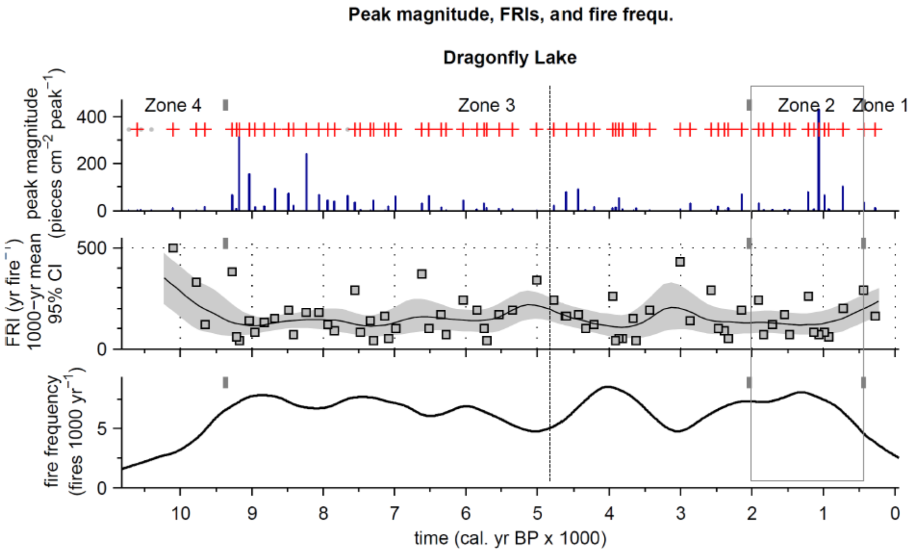


Figure S1

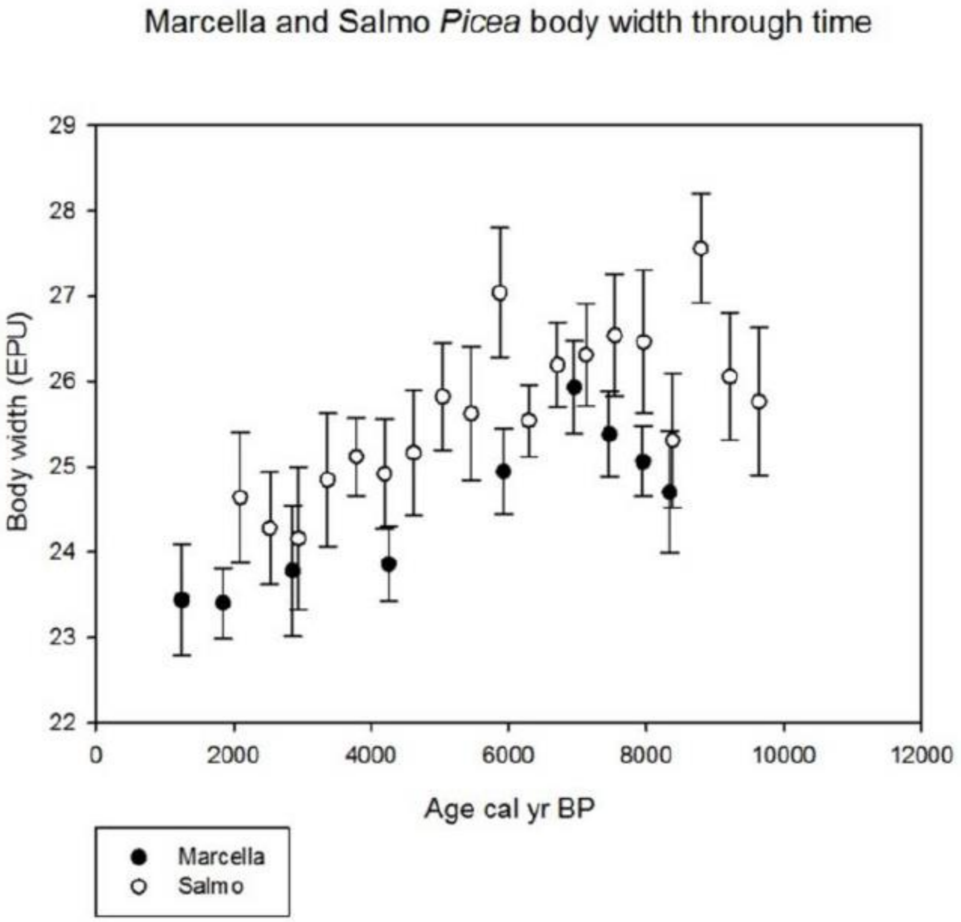
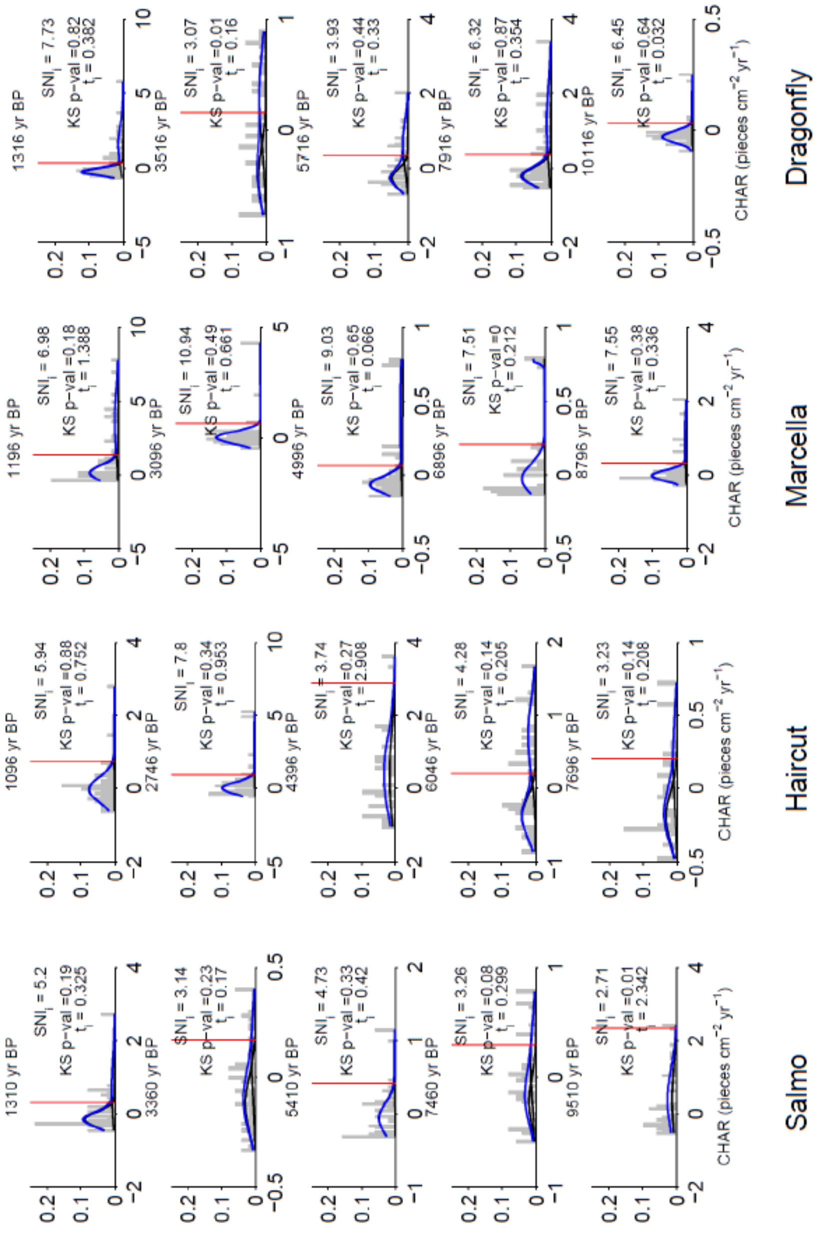

Marcella and Salmo *Picea* body width through time
Body width (EPU)
29
28
27
26
25
24
23
22
0
2000
4000
6000
8000
10000
12000
Age cal yr BP
● Marcella
○ Salmo

Figure S2


Salmo
1310 yr BP
SNI_i = 5.2
KS p−val =0.19
t_i = 0.325
3360 yr BP
SNI_i = 3.14
KS p−val =0.23
t_i = 0.17
5410 yr BP
SNI_i = 4.73
KS p−val =0.33
t_i = 0.42
7460 yr BP
SNI_i = 3.26
KS p−val =0.08
t_i = 0.299
9510 yr BP
SNI_i = 2.71
KS p−val =0.01
t_i = 2.342
Haircut
1096 yr BP
SNI_i = 5.94
KS p−val =0.88
t_i = 0.752
2746 yr BP
SNI_i = 7.8
KS p−val =0.34
t_i = 0.953
4396 yr BP
SNI_i = 3.74
KS p−val =0.27
t_i = 2.908
6046 yr BP
SNI_i = 4.28
KS p−val =0.14
t_i = 0.205
7696 yr BP
SNI_i = 3.23
KS p−val =0.14
t_i = 0.208
Marcella
1196 yr BP
SNI_i = 6.98
KS p−val =0.18
t_i = 1.388
3096 yr BP
SNI_i = 10.94
KS p−val =0.49
t_i = 0.661
4996 yr BP
SNI_i = 9.03
KS p−val =0.65
t_i = 0.066
6896 yr BP
SNI_i = 7.51
KS p−val =0
t_i = 0.212
8796 yr BP
SNI_i = 7.55
KS p−val =0.38
t_i = 0.336
Dragonfly
1316 yr BP
SNI_i = 7.73
KS p−val =0.82
t_i = 0.382
3516 yr BP
SNI_i = 3.07
KS p−val =0.01
t_i = 0.16
5716 yr BP
SNI_i = 3.93
KS p−val =0.44
t_i = 0.33
7916 yr BP
SNI_i = 6.32
KS p−val =0.87
t_i = 0.354
10116 yr BP
SNI_i = 6.45
KS p−val =0.64
t_i = 0.032
CHAR (pieces cm^-2 yr^-1)
0.2
0.1
0