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Ecological tree line history and palaeoclimate – review of megafossil evidence from the Swedish Scandes

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The postglacial tree line and climate history in the Swedish Scandes have been inferred from megafossil tree remains. Investigated species are mountain birch (*Betula pubescens* ssp. *czerepanovii*), Scots pine (*Pinus sylvestris*) and grey alder (*Alnus incana*). *Betula* and *Pinus* first appeared on early deglaciated nunataks during the Lateglacial. Their tree lines peaked between 9600 and 9000 cal. a BP, almost 600 m higher than present-day elevations. This implies (adjusted for land uplift) that early Holocene summer temperatures may have been 2.3°C above modern ones. Elevational tree line retreat characterized the Holocene tree line evolution. For short periods, excursions from this trend have occurred. Between *c*. 12 000 and 10 000 cal. a BP, a pine-dominated subalpine belt prevailed. A first major episode of descent occurred *c*. 8200 cal. a BP, possibly forced by cooling and an associated shift to a deeper and more persistent snow pack. Thereafter, the subalpine birch forest belt gradually evolved at the expense of the prior pine-dominated tree line ecotone. A second episode of pine descent took place *c*. 4800 cal. a BP. Historical tree line positions are viewed in relation to early 21st century equivalents, and indicate that tree line elevations attained during the past century and in association with modern climate warming are highly unusual, but not unique, phenomena from the perspective of the past 4800 years. Prior to that, the pine tree line (and summer temperatures) was consistently higher than present, as it was also during the Roman and Medieval periods, *c*. 1900 and 1000 cal. a BP, respectively.

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On long and short temporal scales, alpine tree lines, generally constrained by heat deficiency, may perform as sensitive indicators of climate change and variability (Kullman 1998a, 2010; Lloyd & Fastie 2002; Holtmeier 2003; Shiyatov 2003; Tinner & Kaltenrieder 2005; Kullman & Öberg 2009; Kirdyanov *et al*. 2012; Körner 2012). Moreover, tree line dynamics are paralleled by concurrent trajectories of alpine/subalpine plant species richness and certain vegetation patterns (Kullman 2007a, 2012). Thus, tree line history appears to be an efficient proxy for palaeoclimate and associated broad-scale vegetation transformation in high mountain areas.

In central and northern Scandinavia, our understanding of the Holocene tree line history has been progressively refined over the past 50 years or so by the use of radiocarbon-dated megafossil tree remains, preserved above the modern tree line elevation in peat and lakes and under glacier ice (G. Lundqvist 1959; J. Lundqvist 1969; Karlén 1976; Eronen 1979; Aas & Faarlund 1988, 1999; Nesje *et al*. 1991; Moe & Odland 1992; Kullman 1995, 2000; Selsing 1998; Kullman & Kjällgren 2000, 2006; Helama *et al*. 2004; Paus 2010; Öberg & Kullman 2011a, b). The megafossil approach provides *prima facie* evidence with a minimum of subjective interpretation. Fundamental aspects of glacial, Lateglacial and early Holocene plant cover and landscapes in northern Scandinavia, as inferred by this approach (Kullman 2006, 2008), are consistent with independent fossil, genetic and palaeogeographical data (Paus 2010; Paus *et al*. 2011; Carcaillet *et al*. 2012; Parducci *et al*. 2012). Thus, it has become increasingly recognized that extensive samples of well-investigated megafossils can provide a direct and accurate interpretation (space, time and species composition) of past tree cover evolution in high mountain regions (cf. Helama *et al*. 2004). Despite some shortcomings (see below), megafossil analysis is the only methodology that can accurately document the existence of a certain tree species at a certain spot and at a certain point of time in the past.

The most comprehensive tree line histories from the Scandes draw on an extensive Holocene sample of megafossil-based pine tree line elevations (m a.s.l.) in the south and central Swedish Scandes (Kullman & Kjällgren 2000, 2006). In these studies, the main conclusion was that the tree line and the summer temperature declined consistently and in covariance from the earliest part of the Holocene until an all-time low about a century ago. In addition, a maximum recorded tree line rise by about 200 m during the past century was tentatively inferred to have taken the pine tree line to a level that was virtually unprecedented during the late Holocene. Here, these issues are revisited and further developed as a synthesis of all previously published and some new megafossils representing principal tree species in the south and central Swedish Scandes. These analyses may contribute towards an improved understanding of palaeoclimate as well as of the structural and compositional dynamics of the tree line ecotone

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and upper mountain forest belt throughout the Holocene. The new and increased set of dated megafossils implies that some prior inferences, for example in Kullman & Kjällgren (2006), need to be slightly modified. The novelty of the present study is that the difference in elevation between each dated megafossil and the present-day tree line can be more accurately quantified than before. This has been made possible by extensive recent regional investigations documenting tree line levels about a century ago and their displacements up to the present-day (Kullman & Öberg 2009). We thus now have a firm basis for a nuanced evaluation of the significance of modern tree line rise and concurrent climate warming in the context of the entire Holocene. No other study provides this perspective with comparable accuracy.

Study area

Megafossil tree remains have been sampled in three separate areas in the south and central Swedish Scandes (66 to 61°N and 15 to 12°E), comprising the provinces of Dalarna, Jämtland/Härjedalen and Lapland, respectively (Fig. 1). Further details are given by Kullman & Kjällgren (2006).

In addition to the extensive megafossil record, the study area is uniquely well researched with respect to modern tree line dynamics, which have been surveyed by direct observation at a multitude of sites since the early 20th century (Kullman & Öberg 2009). Thus, past and present tree lines can be very accurately compared in this area, which is a prerequisite for relevant palaeoclimatic inferences.

The tree line, much in focus in this study, is by convention defined as the maximum elevation (m a.s.l.) at a given site of upright trees taller than 2 m (cf. Miehe & Miehe 2000). Typically, mountain birch (*Betula pubescens* ssp. *czerepanovii*) forms a subalpine birch forest belt and the highest tree line. Norway spruce (*Picea abies*) and Scots pine (*Pinus sylvestris*) display their tree lines, ~50 and 100 m, respectively, below the tree line of birch. Grey alder (*Alnus incana*) is a subordinate element in the low and mid-reaches of the subalpine birch belt, with the tree line somewhere between those of pine and birch (Kullman 2002). The general features of the tree line ecotone and its environmental correlates are provided by Kullman (1992b). More detailed accounts of the physiography, geology, climate, plant cover and human impacts are given by Kjällgren & Kullman (1998).

Materials and methods

The general structure of the tree line ecotone and its recent dynamics are much the same in all three areas

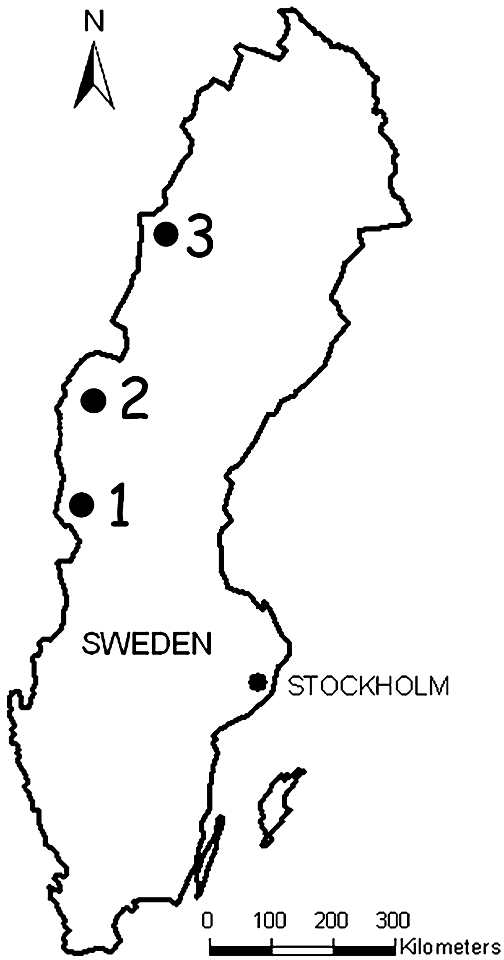

Fig. 1. Location map showing the three sampling areas in the Swedish Scandes. 1 = Province of Dalarna; 2 = Province of Jämtland/Härjedalen; 3 = Province of Lapland.

(cf. Öberg & Kullman 2011b), which provides the motivation for analysing composite megafossil records for birch, pine, alder. The samples derive from previous studies, which also contain metadata, including exact positions, concerning each dated megafossil (Lundqvist 1969; Kullman 1992a, 1995, 2004a; Kullman & Kjällgren 2000, 2006; Öberg & Kullman 2011a, b, and literature cited therein). A number of unpublished megafossil dates of pine and birch are also added.

The megafossil records embrace tree remains (trunks, branches, bark and roots) of a size and weight that excludes dislocation from the growing site by wind, although some down-slope transport caused by gravitational forces may have occurred. A general description of these records and the circumstances of their appearance, preservation and interpretation are given in Kullman (1994).

As with most other proxies, tree line and temperature reconstructions by megafossil trees are in principle beset with various uncertainties (see Aas & Faarlund

1988). Aside from temporally shifting preservation conditions (see Dubois & Fergusson 1985), a potential caveat is the seemingly fortuitous procedure of finding the highest preserved megafossil of each time period. However, extensive fieldwork (large sample size) may largely overcome this obstacle. It should be noted also that the highest record for any point of time represents a minimum elevation for the contemporary tree line, as ideal conditions for long-term conservation of wood, for example peat deposits, do not necessarily provide optimal growth conditions (Aas & Faarlund 1988; Hammarlund *et al.* 2004). Possibly, tree lines may be relictual and temporary not synchronous with climate cooling. However, this appears to be a minor problem, as tree line pines are rarely older than 200–300 years and observations during recent decades have shown that even short-term (years to decades) cooling episodes may exterminate well-established mature tree line pines (Kullman 1991, 2011; Karlén 1998).

It is generally accepted that, at larger spatial and temporal scales, growing season temperature is the key factor defining the tree line position (Holtmeier 2003; Körner 2012). At shorter and more local scales, tree line responses to climate change may be modulated by factors such as wind, precipitation, snow cover, geomorphology, soil development and biotic interactions, sometimes operating in a non-linear manner (Körner & Paulsen 2004; Kullman 2007b; Kullman & Öberg 2009; Elliott & Kipfmueller 2010; Holtmeier & Broll 2010; Paus 2010; Malanson *et al.* 2011; Mathisen & Hofgaard 2011; Kirdyanov *et al.* 2012; Sutinen *et al.* 2012; Takahashi *et al.* 2012). In addition, it is impossible to rule out the possibility that climatic requirements and tolerances have changed during the postglacial period (cf. Davis & Shaw 2001; Rehfeldt *et al.* 2002).

As the main focus of the present study is on consistent long-term (low-frequency) and regional change, the impact of locally unique modulators is reasonably minimal. Moreover, the use of the 'tree line' (i.e. solitary trees in relatively open landscapes) reduces the impact of biotic interactions (cf. Körner 2007; Kullman 2010).

Megafossil tree remains were searched for by extensive screening of large expanses of the treeless alpine landscape and slightly below the current tree line. In particular, erosion scars in peat deposits and surficial lake sediments were targeted. During the past decade, a new source of high-elevation megafossils has been discovered, as melting glaciers and perennial snow/ice patches have exposed tree remains that have been preserved by ice for several millennia (Fig. 2A). This latter source has substantially improved knowledge of the maximum tree line positions during the early Holocene and opens a new window for alpine palaeoecology (Kullman 2004b; Nesje *et al.* 2011; Öberg & Kullman 2011b).

In most cases, identification to species was unambiguous, thanks to characteristic bark and branching. Some enigmatic samples were determined from their wood anatomy by Dr Thomas Bartholin, Copenhagen. Each sample originated from a single piece of wood, which precludes the dating of mixed samples of different ages. Samples were taken as close to the centre of each trunk as possible.

Radiocarbon dating was conducted at the Radiocarbon Dating Laboratory in Stockholm and at Beta Analytic Inc., Miami (USA). Ages are given as calibrated years before present (cal. a BP), with 'present'=AD 1950. Calibration was conducted using CALIB 5.0.2 software (Stuiver *et al.* 2005) and IntCal04. This calibration set was chosen in order to comply with the earlier published part of the megafossil record. For simplicity, the intercepts with the calibration curve are used in the text and figures to represent the age of each sample.

For the purpose of palaeoclimatic reconstruction, the elevation of each sample site (pine and birch) is related to the nearest position (m a.s.l), with the same aspect, of the present-day (2005–2007) tree line. These data originate from Kullman & Öberg (2009), with some recent updates. Since the early 20th century, the tree lines have advanced by a maximum of about 200 m. At several localities, however, local factors (e.g. wind, snow distribution, geomorphology) have constrained the rise to lower magnitudes. This implies that points on the current tree line, and probably on historical tree lines too, are not all entirely compatible in climatic terms (Kullman & Öberg 2009), which should be considered in connection with palaeoclimatic inferences based on the present material.

Results

This study involves a sample of 455 radiocarbon-dated megafossils (258 *Pinus*, 172 *Betula*, 25 *Alnus*), originating from the present-day tree line ecotone and above. Thirteen of these have not been previously published (Table 1). In most cases, the megafossils represent tree-sized specimens (Fig. 2B), although entire stems are rarely found at the uppermost localities.

Together with *Picea abies*, *Betula* and *Pinus* appeared (megafossils) episodically during the Lateglacial on early-deglaciated nunataks in the region considered here (Kullman 2002, 2008). Although important from a biogeographical point of view, these are not included in the present review. Obviously, these specimens represent sparsely distributed individuals of unknown size, growing in particularly favourable local climates, which complicates inferences of general climatic conditions and comparisons with the Holocene record of megafossils.

The total sample of megafossils declines in density with increasing elevation, and the dated megafossils

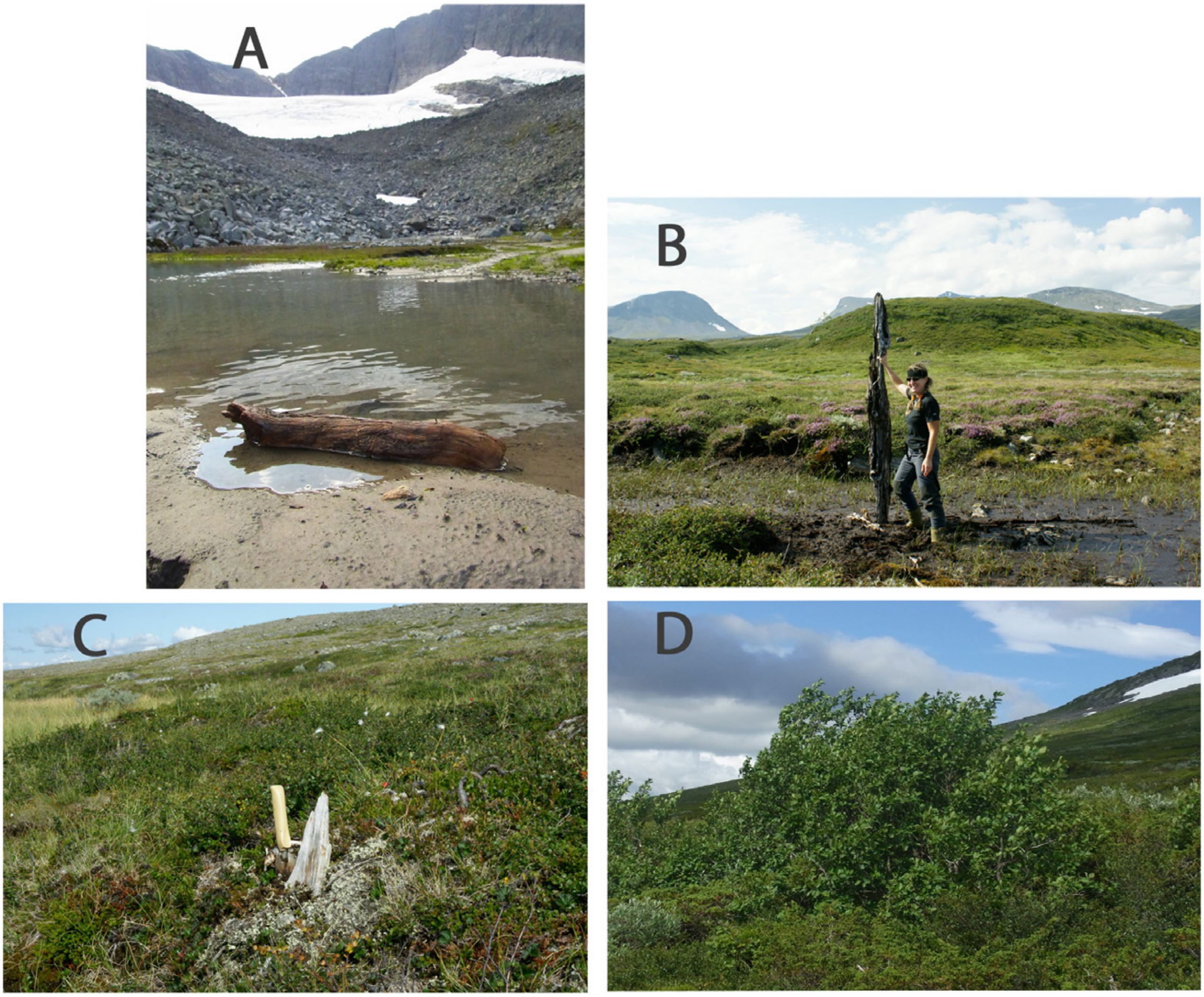

Fig. 2. A. Subfossil birch recently exposed in the forefield of the glacier Helagsglaciären, 1345 m a.s.l. This remnant was found 390 m above the local tree line and dated to 7670 cal. a BP (Beta-284470). From: Öberg & Kullman (2011b). B. Megafossil pine log, uncovered from an eroding peat bog, 130 m higher than today's pine tree line. Radiocarbon-dating yielded 7000 cal. a BP (Beta-268161). Mt Mieskentjakke, 900 m a.s.l. C. Megafossil pine stump, dated to 1940 cal. a BP (Beta-268651), protruding from a peat mound in open and windswept terrain, 110 m above today's local tree line. Mt Hårdeggen, 900 m a.s.l. D. Clonal grey alder (*Alnus incana*), currently forming the local alder tree line, which has advanced 100 m altitudinally since the early 1950s (Kullman 2007a). A decidedly ancient origin of this individual is indicated by megafossil remains retrieved from the soil underneath the canopy. Four radiocarbon-dated wood pieces, apparently not from tree-sized stems, range between *c.* 4400 and 1300 cal. a BP.

become bound to a narrow range of habitats towards the uppermost finding localities (cf. Öberg & Kullman 2011b). This may suggest that the megafossil record quite accurately captures the tree line, rather than the upper limit of continuous forest. Thus, the present-day *tree line* (defined below) appears as the most adequate analogue to the 'fossil' situation.

The earliest Holocene record of mountain birch is for *c.* 9900 cal. a BP, and the highest position was attained *c.* 9600 cal. a BP, at an elevation 575 m higher than the modern tree line position (Figs 3, 4). The upper 200–250 m of this range was characterized by widely scattered birches interspersed with some pines (in the lower reaches). In addition, sparsely distributed spruces belonging to the Late Weichselian and early Holocene tree flora reached as high as the uppermost birches (Kullman 2002). This zone was actually a patchwork of dominant alpine tundra, with small tree stands growing in sheltered habitats. There is no indication, whatsoever, that this landscape had any characteristic of a continuous birch forest belt, as we know it today (Öberg & Kullman 2011b).

A minor and transient elevational dip of the birch tree line may have taken place within the interval 8500–8000 cal. a BP (Fig. 3). About 7000 cal. a BP, a more persistent descent was initiated, which progressed

Table 1. New radiocarbon dates of subfossil tree remains and their altitudes relative to the present-day tree line (2010). All four dates of *Alnus* belong to the same individual.

Species	Lab. code	Age (^{14}C BP)	Age (cal. a BP)	Sample altitude (m a.s.l.)	Tree line 2010 (m a.s.l.)	Relative altitude (m)	Locality	Coordinates N lat., E long.
Pinus	Beta-268163	850±60	740	770	760	10	Täljstensvalen	63°14.568′N, 12°27.562′E
Pinus	Beta-284466	990±50	920	745	760	–15	Täljstensvalen	63°14.543′N, 12°27.187′E
Pinus	Beta-268161	6130±50	7000	900	770	130	Mieskentjakke	62°58.153′N, 12°21.869′E
Pinus	Beta-268164	1990±70	1940	920	810	110	Hårdeggen	63°11.804′N, 12°28.052′E
Pinus	Beta-268651	1380±50	1300	950	875	75	Falkvålen	62°45.872′N, 12°45.729′E
Pinus	Beta-268162	1910±50	1870	875	800	75	Storsnasen	63°13.281′N, 12°22.860′E
Betula	Beta-264397	4120±60	4755	905	975	–70	Getryggen	63°10.181′N, 12°19.785′E
Betula	Beta-99208	6210±60	7160	1100	975	125	Storsnasen	63°13.161′N, 12°21.855′E
Betula	Beta-79712	7025±70	8975	1080	930	150	Storsnasen	63°13.003′N, 12°21.733′E
Alnus	Beta-108778	1620±70	1520	885	885	±0	Getryggen	63°10.201′N, 12°20.108′E
Alnus	Beta-268650	1300±50	1270	885	885	±0	Getryggen	63°10.201′N, 12°20.108′E
Alnus	Beta-268165	1760±40	1700	885	885	±0	Getryggen	63°10.201′N, 12°20.108′E
Alnus	Beta-250910	3950±50	4420	885	885	±0	Getryggen	63°10.201′N. 12°20.108′E

steadily until about 3200 cal. a BP. Lack of data precludes a detailed analysis of birch performance thereafter.

Pine was present at high elevations by the early Holocene, *c.* 11 200 cal. a BP. The tree line reached its all-time peak elevation *c.* 9000 cal. a BP, at 580 m above its current position (Figs 3, 5). However, a paucity of data from this early period means that the exact time for the culmination of the tree line is somewhat uncertain. During the first 1500–2000 years of the Holocene, pine appears to have been the dominant tree species in the high mountain landscape. However, scattered birches may have occurred equally as high as the pine, judging from their presence at similar elevations during the Lateglacial (see above).

The overall view of the Holocene pine tree line dynamics during the Holocene is one of progressive elevational retraction (Fig. 5). In greater detail, this process accelerated *c.* 8200 cal. a BP, when a drastic descent by ~200 m was initiated and completed within 200 years or so. It is possible that a few tiny trees (judging from the diameters of the preserved stems) survived for a shorter period above the general tree line of the time. Thereafter, the tree line never transgressed this new and markedly lower elevation, although it was consistently higher than modern until *c.* 4800 cal. a BP, when it dipped by 200 m or so. During the period 8200 to 4800 cal. a BP, the proportion of pine megafossils in the tree line ecotone declined substantially, to the favour of mountain birch. For most of the past 4800–4500 years, the descending elevational pine tree line trend has been relatively insignificant, and the tree line has lingered slightly below its present-day elevation (Fig. 5). Adjusted for a glacio-isostatic land uplift by 50 m (Påsse & Andersson 2005; Eronen 2005), the latter pattern is even more marked. However, distinct and temporary reversals took place around 1900 and 1300–900 cal. a BP (Fig. 5). The pine megafossils, which rep-

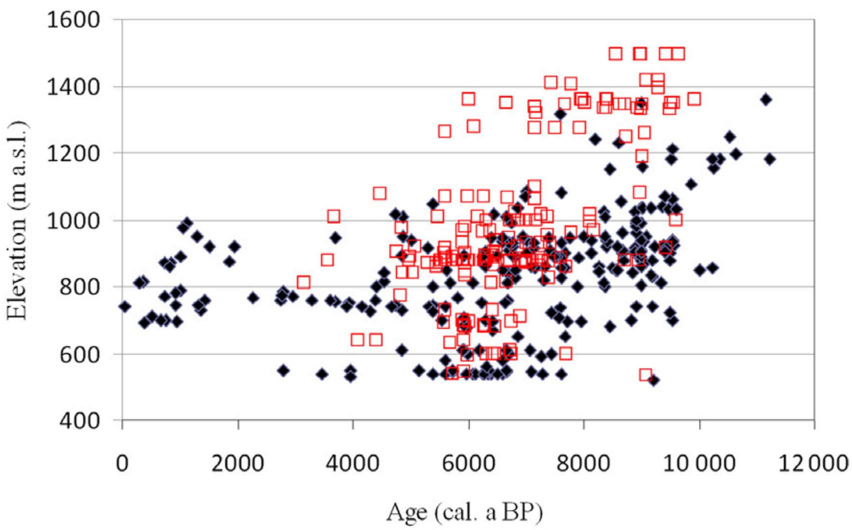

Fig. 3. Composite of all radiocarbon-dated birches (transparent) and pines (filled), relative to the elevation of each finding site.

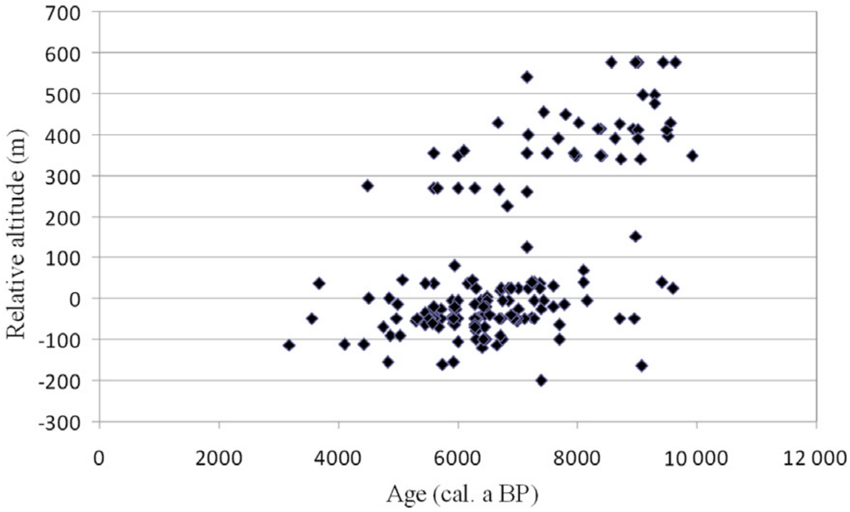

Fig. 4. Composite of all radiocarbon dates (old and new) of mountain birch, relative to the altitude of the present birch tree line (2010). This figure is available in colour at http://www.boreas.dk.

resent these two episodes, are encountered in extremely wind-exposed habitats, where not even the hardier mountain birch manages to grow today. This clearly stresses that these trees grew in a much more favourable period (warmer and less windy) than today (Fig. 2C). The dating resolution, in combination with the sampling strategy, precludes a more detailed view of the past millennium, although descent may be gleaned as the prevailing tendency.

Megafossil data narrating the tree line history of the grey alder (*Alnus incana*) are too sparse to admit any firm conclusions about elevational shifts and trends over time (Fig. 6). It is clear, however, that during the period 9100–4400 cal. a BP, alder occurred and persisted a few hundred metres above its present-day position, but apparently never as high as the maximum elevations of birch and pine. A transient gap in the record is centred *c.* 8200 cal. a BP. If not a sampling artefact, this feature may indicate some elevational and/or population thinning. Interestingly, clonally propagating *Alnus* copses, currently growing in the tree line ecotone, may be relicts from the mid-Holocene, as evident from radiocarbon-dated megafossils unearthed beneath the canopy of a living specimen (Fig. 2D).

Discussion and interpretations

Postglacial tree line shifts and palaeoclimate

The discontinuous nature of the megafossil record means that only the major tree line trends and the largest deviations from these can be discussed with any confidence. Because tree species with such different ecologies as *Betula*, *Pinus* and *Alnus* have displayed similar large-scale trends it is reasonable to assume that general climate change, rather than local modulators, has been the main driver. Thus, the present study highlights a greater treeline difference and climate change between

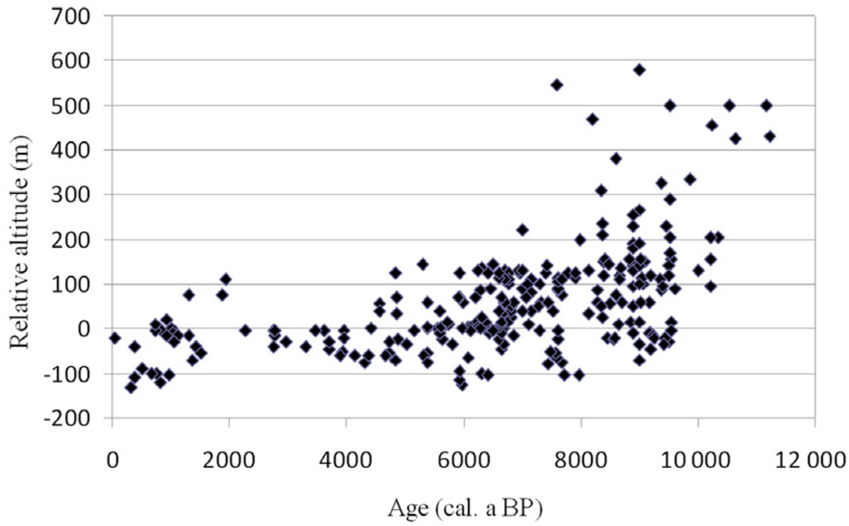

Fig. 5. Composite of all radiocarbon dates (old and new) of pine, relative to the altitude of the present pine tree line (2010). This figure is available in colour at http://www.boreas.dk.

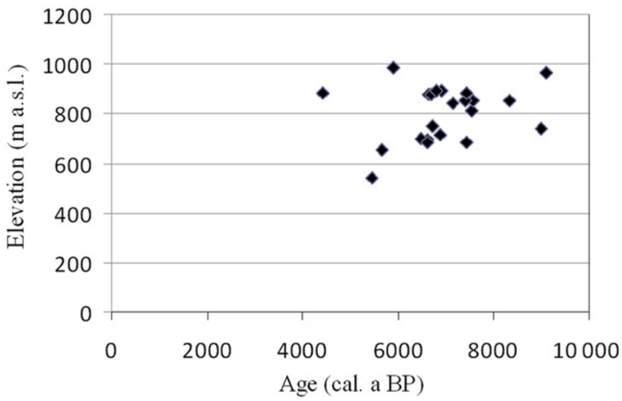

Fig. 6. Composite of all radiocarbon dates (old and new) of tree-sized grey alder, relative to the altitude of the present alder tree line (2010). This figure is available in colour at http://www.boreas.dk.

the early Holocene and the present than often assumed. In fact, a major part of the present-day treeless alpine tundra ecosystem in the mid- and southern Swedish Scandes has evolved as a consequence of climatically forced tree cover demise throughout the Holocene. Thus, the alpine tundra, delimited by the tree line, reached its largest Holocene extension about a century ago.

Most boreal tree species may have survived the last glacial period (Weichselian) much closer to Scandinavia than traditionally believed. On the basis of firm megafossil evidence, the first presence of tree-*Betula* has been documented on the Arctic coast of northern Norway by the Late Glacial Maximum, *c*. 20 000 cal. a BP (Kullman 2006, 2008). Drawing on multiple recoveries of Late Weichselian and early Holocene megafossils exclusively along the Scandes, glacial tree refugia (*Picea abies* in particular) were hypothesized to have existed W or SW of the Scandes (Kullman 2000; Öberg & Kullman 2011a). Using different lines of independent palaeobiological evidence, Parducci *et al*. (2012) failed to falsify this hypothesis.

During the Late Weichselian and earliest part of the Holocene, tree growth in the form of single individuals and small clusters of birch and pine were confined to elevations high above their respective modern tree lines (Kullman 2008). Scattered spruces, some still living to date, grew at the same elevations in this landscape (Kullman 2000, 2002; Öberg & Kullman 2011a). Analogously, macrofossil analyses in high-alpine lakes (central Norway) sustain the view of a sparsely treed landscape during the Late Weichselian (Paus *et al*. 2011). The contemporary lack of tree megafossils of any species at relatively lower elevations indicates that these landscapes were still occupied by active glaciers and dead-ice bodies.

Spatial patterns of megafossil tree remains indicate that early Holocene tree pioneers were strictly bound to wind-sheltered and well-moistened sites with locally benign environmental conditions in an otherwise inhospitable regional climate. Ideal conditions in this generally dry and windy landscape (cf. Hafsten 1987; Paus 2010) were provided by ice-free glacier cirques and nivation hollows high above the current tree line (Öberg & Kullman 2011b). The particularly favourable local thermal climate characterizing these early postglacial tree enclaves is indicated by the fact that during the past few decades birch and other tree saplings have selectively colonized these habitats (Öberg & Kullman 2011b).

The time of the highest tree line positions for both birch and pine, namely 9600–9000 cal. a BP, should reasonably approximate the Holocene thermal optimum in the region considered (Figs 3–5). In addition, a similar view is emerging from various firm terrestrial and marine proxies in the Scandinavian/Greenland region (see review by Paus 2012). Until about 8200 cal. a BP, only the highest mountain peaks (>1500 m a.s.l.) were entirely treeless. Below the widely spread high-altitude birches, the tree line ecotone and the upper closed forest were characterized by predominant pine and scattered birches. This belt of unknown density extended from the valley floors to at least 500 m higher than the present-day pine tree line (Fig. 3). In general, the maximum forest density (pine and mountain birch) above the modern tree lines appears to have occurred about 7500–5000 cal. a BP; that is, substantially delayed relative to the Holocene tree line and thermal peaks. This may reflect that the formation of closed forest communities, in comparison to tree line dynamics, is a more complex and non-linear process, relating to climate change in subdued form. Soil and geomorphic development as well as species and individual interactions (facilitation and competition) stand out as potentially important ingredients in this context (e.g. Lloyd & Fastie 2003; Dullinger *et al*. 2004; Bekker 2005; Smith *et al*. 2009).

The early culmination of postglacial warmth, as inferred above, is supported by high-elevation macro- and megafossil occurrences of thermophilic broad-leaved trees, *Quercus robur*, *Corylus avellana*, *Tilia cordata*, *Ulmus glabra*, *Alnus glutinosa* and *Betula pendula*, confined to a relatively narrow interval, 9500–7700 cal. a BP (Kullman 1998b, c). However, as these species co-existed in open stands with decidedly cold-adapted genera, such as *Picea*, *Larix* and *Alnus incana* (Kullman 1998d, 2000; Paus 2010; Carcaillet *et al*. 2012), the climate at that time may have involved unknown nuances with respect to temperature distribution over the year.

The more or less coherent pine and birch tree line descent by 580–575 m since the Holocene optimum corresponds to an average retreat of 6 m per 100 years and is partially a result of incomplete glacio-isostatic land uplift. This implies that the land surface has been lifted, possibly by as much as 200 m since about 9000 cal. a

BP, more rapidly in the beginning and more slowly towards the present (Mörner 1980; Björck & Svensson 1994; Eronen 2005; Påsse & Andersson 2005). In congruence with this decelerating model, the local climate has become cooler (see Eronen *et al.* 1999), which is reflected in the general course of the pine tree line chronology. It should be considered, however, that the uplift data are based on extrapolations from coastal regions far east and west of the concerned mountain region, which makes them quantitatively somewhat uncertain (see Lundqvist 1969).

An estimate of the regional summer thermal decline (adjusted for land uplift) between the early Holocene peak (9600–9000 cal. a BP) and the present emanates from an elevational tree line difference of 380 m, namely 580 minus 200 m, with the latter figure representing the total land uplift. Based on this figure and a lapse rate of 0.6°C/100 m (Laaksonen 1976), summer temperatures during the early Holocene thermal optimum may have been 2.3°C higher than present. This difference corresponds to a general cooling trend of 0.024°C/century, which matches the Milankovitch model of orbitally driven climate forcing (cf. Berger 1988; Esper *et al.* 2012) and indicates that this mechanism has operated as the ultimate driver of climate change throughout the Holocene. As outlined in more detail above, palaeotemperature reconstruction of the above kind is uncertain for various reasons. For example, it may be an oversimplification to base palaeotemperature records on the assumption that the lapse rate is constant in space and time (cf. Mook & Vorren 1996). Nevertheless, the inferred cooling by 2.3°C throughout the Holocene concurs roughly with other quantitative estimates for northern Fennoscandia and adjacent regions (e.g. Nesje & Kvamme 1991; Shemesh *et al.* 2001; Bigler *et al.* 2003; Väliranta *et al.* 2003; Hammarlund *et al.* 2004; Bjune *et al.* 2005; Heikkilä 2010; Paus *et al.* 2011). Other studies infer a more modest temperature amplitude and a Holocene thermal optimum some millennia later (Barnekow 1999; Rosén *et al.* 2001; Velle *et al.* 2005; Seppä *et al.* 2009). On the other hand, some chironomid-based studies place the optimum prior to 10 000 cal. a BP (e.g. Hammarlund *et al.* 2004; Velle *et al.* 2005; Paus *et al.* 2006). Anyhow, the vast majority of prior studies agree with the present one with respect to a long-term gradual thermal decline since an early or mid-Holocene thermal optimum and up to about a century ago (e.g. Lilleøren *et al.* 2012).

In addition to the progressive Holocene tree line and temperature trends, ultimately driven in conjunction with reduced summer solar insolation (Milankovitch model) and land uplift, the present data indicate some emergent discontinuities, probably related to other mechanisms, judging from their abrupt character. The coarse nature of the megafossil records makes detailed causal understanding of these sudden shifts highly speculative.

One of the clearest episodes of this nature is the abrupt and deep pine tree line dip centred *c.* 8200 cal. a BP, which is possibly reflected in weakened form also in the birch and alder records. Stratigraphic macrofossil studies in the same area provide a similar picture (Bergman *et al.* 2005). This event also corresponds to a widely recognized temperature decrease in various parts of the world, the cause of which is debated (Karlén 1976; Alley *et al.* 1997; Barnett *et al.* 2001; Nesje & Dahl 2001; Paus 2010; Kobashi *et al.* 2011; Paus *et al.* 2011). The drastic nature of this irreversible pine tree line downshift marks the termination of the Holocene thermal optimum in this region (cf. Fronval & Jansen 1996). Hypothetically, it may have resulted from the combined effects of a short-term cooling mechanism and rapid land uplift, superimposed on the long-term orbitally forced cooling trend. Another striking and persistent downshift of 200 m or so appears to have taken place *c.* 4800 cal. a BP, as deduced from a long period virtually without finds of pine megafossils at high elevations. Independent climate proxies support the contention that this was actually a relatively cool period, signalling the definitive start of the Neoglacial period (cf. Karlén 1976, 1998; Caseldine & Matthews 1987; Dahl & Nesje 1994; Eronen *et al.* 1999; Hammarlund *et al.* 2004; Bergman *et al.* 2005; Bakke *et al.* 2008; Paus 2010). In addition to lower temperatures, the driving force behind this episode without megafossil finds may include components such as increased humidity, expansion of ombrogenous peat, delayed snowmelt and enhanced climatic instability in general (Kullman 1995; Hammarlund *et al.* 2004). As a consequence of these environmental changes, the plant cover in the high mountain regions of the Scandes experienced a perceivable process of 'alpinization', which progressed until about a century ago (Kullman 2012 and literature cited therein).

The lack of a major birch response of the same dimension as recorded for pine *c.* 8200 cal. a BP should possibly be considered in the light of the widely different ecologies of these two species. It is tempting to contemplate that the pine demise at this time was enhanced by increased and prolonged snow cover, which strengthened the effect of a relatively modest cooling as a critical threshold of decreased ratio between wet and solid precipitation was passed (cf. Barnett *et al.* 2001; Bergman *et al.* 2005). It is well known that pine is less adapted and less tolerant than the mountain birch to such a situation (Aas & Faarlund 2000; Kullman 2010). Notably, there are some indications that snow activity (e.g. avalanches) increased substantially some millennia after the thermal optimum (Blikra & Selvik 1998).

Hypothetically, the lack of birch megafossils for the past 3200 calendar years relates to insignificant individual mortality, rather than to absence from elevations corresponding to the present-day tree line ecotone. To a large extent, birches may have survived up to the modern-day by a change of growth mode from upright to krummholz, leaving a scant megafossil record. Thereby, birch tree line descent during the predominantly cooling late Holocene may be interpreted as mainly an effect of phenotypic regression. This is not an unreasonable option in the light of the documented longevity, at least 4770 calendar years, of still-living tree line birches by Öberg & Kullman (2012), based on phenotypic plasticity and clonal reproduction. In fact, much of the rapid birch tree line rise in the studied region during the first warming pulse of the past century was achieved by phenotypic transformation of old-established individuals, originating prior to the 20th century (Kullman 1979, 2010). Analogous conservative situations, based on phenotypic plasticity, have been reconstructed for spruce (Kullman 2000; Öberg & Kullman 2011a) and grey alder (this study) growing in the tree line ecotone. In general, phenotypic plasticity may have a stabilizing effect on tree line performance (cf. De Witte & Stöcklin 2010; Hampe & Jump 2011). This resilience at the individual level complicates the usefulness of these species as climate change proxies over the long term. In this respect, the pine tree line is more interpretable and appears to have prevailed, with some replace shorter with short deviations, below the present-day level during most of the past 4800 calendar years, although the resolution of the record precludes a detailed analysis and a definitive opinion.

For both birch and pine, a few particularly distinct tree line reversals (upshifts) are discernible during the past 2000 calendar years. The pine tree line was about 100 m higher than today (i.e. early 21st century) *c.* 1940 and 1300–930 cal. a BP, and the same applies to birch by c. 1700 and 1300 a BP. Apparently, these clusters represent the Medieval and Roman times. Megafossil and tree-ring studies in the northernmost part of the Scandes and adjacent regions display broadly the same features (Karlén & Kuylenstierna 1996; Karlén 1998; Hiller *et al.* 2001; Shiyatov 2003; Kremenetski *et al.* 2004; Moberg *et al.* 2005; Esper *et al.* 2012). Presumably, these episodes were characterized by climates that were relatively favourable for high-altitude tree growth in the wide geographical perspective of the Northern Hemisphere (e.g. Esper & Frank 2009; Ljungqvist 2009). These temperature anomalies were succeeded by a distinct tree line/temperature dip, broadly corresponding to the Little Ice Age (cf. Grove 2004). Detailed population-level tree line studies have documented profound and still prevailing landscape-scale impacts of the Little Ice Age in various parts of the world (e.g. Kullman 1987, 2005, 2010; Payette 2007; MacDonald *et al.* 2008). Overall, a clear trend of tree line lowering characterizes the last two millennia, which matches independent inferences of a cooling trend (Esper *et al.* 2012).

During the past 100 years (post-Little Ice Age), tree lines and temperatures have advanced to levels that are unusual, although not entirely unique, in the perspective of the past 4800 years or so (Kullman & Öberg 2009). With respect to temperature evolution, this anomaly is supported by various proxies elsewhere in the Scandes and in different parts of the world (Haeberli & Beniston 1998; Hantemirov & Shiyatov 2002; Velle *et al.* 2005; Grosjean *et al.* 2007; Bakke *et al.* 2008; Buffen *et al.* 2009; Carrara 2011; Ljungqvist *et al.* 2012).

The emergence during the past two millennia of at least two short-term tree line and thermal excursions to higher than present levels (i.e. early 21st century) indicates that the current performance of the ecological and climatic systems is well within the envelope of the natural variability of the late Holocene (cf. Karlén 2008; Akasofu 2010; Curry & Webster 2011; Humlum *et al.* 2011; Kobashi *et al.* 2011; Ljungqvist *et al.* 2012).

History of the subalpine birch belt

All megafossil dates of birch and pine and corresponding site elevations (m a.s.l.) have been amalgamated in Fig. 3, as a basis for discussion and inferences concerning the broad framework for the evolution of the tree line ecotone, that is, for compositional and structural changes over time. In particular, the much debated issue on continuity or not throughout the Holocene of a distinct subalpine birch belt above the coniferous forest can be highlighted by analysis of these data (Hafsten 1965; Aas & Faarlund 1988, 2000; Kullman 1995, 2001; Gunnarsdottir 1996; Barnett *et al.* 2001; Eide *et al.* 2006; Paus 2010; Öberg & Kullman 2011b).

The obtained data confirm that mountain birch has constituted the upper tree line since about 10 000 cal. yr BP, which complies with pollen data obtained in the Scandes of central Norway (Eide *et al.* 2006; Paus 2010). Prior to that, during the first *c.* 1500–2000 years of the Holocene, the tree line ecotone appears to have been dominated by pine, although possibly interspersed with scattered birches. Judging from the increasing numbers of megafossil birch records, a distinct upper belt of predominantly subalpine birch forest above the closed coniferous forest (like today) seems to have emerged in association with the drastic pine decline and deforestation *c.* 8200 cal. a BP. Based on general experiences of analogous events, extensive soil erosion and exposure of bare mineral soil may have taken place in the wake of extensive forest demise (cf. Kauppila & Salonen 1997; Hammarlund *et al.* 2004; Velle *et al.* 2005; Hede *et al.* 2010). Disturbance of this kind is known to be conducive for extensive seed regeneration by birch (Kinnard 1974; Atkinson 1992) and may have facilitated penetration of birch into habitats evacuated by pine. A possible seed source could have been the high-elevation founder enclaves, which, as mentioned above, were established during the Lateglacial and prevailed by the early Holocene (cf. Öberg & Kullman 2011b). Thus, as deduced by Smith (1920), it may be inferred from the present data set that a subalpine birch belt of any note has not existed above the coniferous forest since the earliest part of the Holocene. Gradually until about 4800 cal. a BP, *Betula* increased its relative importance at the expense of *Pinus* and *Alnus*. The demise of *Alnus incana*, previously an important member of the subalpine tree flora (Kullman 1995), was possibly more a reflection of peat expansion than a direct effect of climate cooling, as solitary alders may still grow at high elevations, given that the organic layer is thin or lacking (Tallantire 1974; Kullman 1992b; Fig. 2D). These circumstances would favour the evolution of a gradually broader and monospecific subalpine birch belt. Concurrently, the birch tree line declined in elevation. Following a peak density at 7500–4800 cal. a BP, the upper birch tree cover appears to have become increasingly sparse and disintegrated towards the present. Gradually it approached the modern, often fragmented, structure by growing patches of windswept treeless alpine heath and snow bed plant communities (cf. Gunnarsdottir 1996; Eide *et al.* 2006). Birch became effectively excluded from the lower part of the local-scale snow-patch/wind-ridge topography, being confined to intermediate snow-cover conditions between windy alpine heath and more sheltered snow beds (Kullman 2003). The prevalent ecotonal mosaic of birch ribbons/islands, alpine heath and snow beds, characteristic of the upper part of the present-day birch belt (Kullman 2010), has obviously emerged in this way, forced predominantly by a deeper and more persistent snow cover and increasing wind strengths. This process culminated with the Little Ice Age, which also saw extensive mortality of solitary, old and reproductively silent pines, trailing in the lower birch belt (Kullman 1987, 2005). At lower elevations, spruce replaced prior pre-alpine pine stands to a large degree (cf. Segerström & von Stedingk 2003; Bergman *et al.* 2005; Giesecke 2005).

During the past century, tendencies for a major reversal of the Neoglacial tree cover trajectories have been discernible. Birch has re-occupied swales in response to earlier seasonal snow melt, while scattered pines have established in higher and less snow-rich parts of the local topography (Kullman 2003; Kullman & Öberg 2009). From the perspective of uncertain climate projections it appears too early to judge if these recent trajectories represent a transient episode or the initiation of a more persistent trend.

Conclusions

- Radiocarbon-dated megafossils from the Swedish Scandes reveal a gross tree line descent by nearly 600 m between the early Holocene (9600–9000 cal. a BP) and the present. Adjusted for land uplift, this could imply a summer cooling by ~2.3°C, although with reservations owing to some uncertain assumptions.
- Distinct centennial-scale deviations are superimposed on the long-term and gradual tree line lowering throughout the Holocene.
- The most striking excursions from the long-term trend occurred about 8200 and 4800 cal. a BP, when the pine tree line irreversibly dipped by about 200 m.
- The 8200 cal. event may have initiated the emergence of the subalpine birch belt, as prior pine-dominated stands thereafter became increasingly fragmented and intermixed with birch.
- The upper tree line was formed by mountain birch throughout the Holocene, after about 10 000 cal. a BP. Prior to that, pine dominated the tree line ecotone.
- During the past 4800 cal. a BP, tree lines (pine in particular) were predominantly lower than at present, except *c.* 1900 and 1000 cal. a BP, when clearly higher positions prevailed.
- Tree line position during the past 100 years has reached a level that is unusual, although not entirely unique, for these past 5000 years or so.

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