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New Aspects of High-Mountain Palaeobiogeography: A Synthesis of Data from Forefields of Receding Glaciers and Ice Patches in the Tärna and Kebnekaise Mountains, Swedish Lapland

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ABSTRACT. Recent recession of high-mountain glacier ice and perennial snow and ice patches has exposed megafossil and macrofossil tree remnants and peat, offering a new source of Holocene high alpine vegetation history in the Scandes. Radiocarbon dates of 90 tree megafossils from Swedish Lapland, 29 of which had not previously been published, range from 11 980 to 1950 cal yr BP. During the interval 9500–8500 cal yr BP, mountain birch (*Betula pubescens* ssp. *czerepanovii*) and Scots pine (*Pinus sylvestris*) grew 600–700 m higher upslope than they do today, which is a new and remarkable discovery. Subsequently, tree density gradually declined at higher elevations, and as the tree line moved downslope, the ratio of *Betula* to *Pinus* increased. Tree growth ceased around 4500 cal yr BP, presumably in response to the return of perennial ice and snow. A short episode of resumed tree growth of *Betula* indicates conditions warmer than present around 2000 years ago. Between c. 8500 and 7300 cal yr BP, *Picea abies*, *Larix sibirica*, *Populus tremula*, *Sorbus aucuparia* and *Alnus incana* were subordinate species on a forest floor dominated by plant species characteristic of prealpine or subalpine woodlands. Growth of trees as much as 700 m higher upslope than today around 9500 cal yr BP implies that summer temperatures at that time may have been 3.0˚C warmer than today's temperatures (corrected for land uplift). This inferred temperature difference between the early Holocene and the present concurs with changes in the Earth's orbital parameters.

Key words: glaciers; tree growth; megafossils; macrofossils; Holocene; radiocarbon dating; climate change; Swedish Scandes

RÉSUMÉ. Le recul récent de la glace de glacier, de la neige pérenne et des bancs de glace en haute montagne a permis de découvrir des mégafossiles et des macrofossiles de restes d'arbres et de tourbe, ce qui offre une nouvelle source d'histoire de la végétation alpine des Scandes en haute altitude pendant l'Holocène. La datation au carbone 14 de 90 mégafossiles d'arbres en provenance de la Laponie suédoise, dont 29 n'avaient jamais fait l'objet d'une publication, donne des résultats variant de 11 980 à 1 950 années cal. BP. Au cours de l'intervalle allant de 9 500 à 8 500 années cal. BP, le bouleau de montagne (*Betula pubescens* ssp. *czerepanovii*) et le pin sylvestre (*Pinus sylvestris*) poussaient à une hauteur de 600 à 700 m plus élevée qu'aujourd'hui, ce qui représente une découverte à la fois nouvelle et remarquable. Subséquemment, la densité des arbres a diminué graduellement en haute altitude, et au fur et à mesure que la limite forestière s'est mise à descendre, le rapport entre *Betula* et *Pinus* s'est accru. La croissance des arbres a cessé vers 4 500 années cal. BP, probablement en raison du retour de la glace et de la neige pérennes. Un bref épisode de reprise de la croissance des arbres de *Betula* indique la présence de conditions plus chaudes qu'à présent il y a environ 2 000 ans. Entre 8 500 et 7 300 années cal. BP environ, *Picea abies*, *Larix sibirica*, *Populus tremula*, *Sorbus aucuparia* et *Alnus incana* étaient des espèces subordonnées sur une couverture morte dominée par des espèces végétales caractéristiques de terrains boisés préalpins ou subalpins. La croissance des arbres à une hauteur de 700 m plus élevée qu'aujourd'hui il y a environ 9 500 années cal. BP implique qu'à cette époque, les températures estivales pouvaient être plus chaudes dans une mesure de 3,0 ˚C que les températures actuelles (donnée redressée en fonction du soulèvement de la terre). Cette différence inférée de température entre l'Holocène précoce et le présent converge avec les changements caractérisant les paramètres orbitaux de la Terre.

Mots clés : glaciers; croissance des arbres; mégafossiles; macrofossiles; Holocène; datation par le carbone 14; changement climatique; Scandes suédoises

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INTRODUCTION

Megafossil tree remains preserved in low alpine peats and lake sediments have for some decades been successfully used for paleo tree line reconstruction (Karlén, 1976; Aas and Faarlund, 1988; Dahl and Nesje, 1996; Kullman, 1999, 2008, 2013; Paus, 2010). However, the virtual lack of these archives at very high elevations in the alpine zone has precluded accurate reconstruction of the highest postglacial elevation of tree growth, which hampers detailed understanding of past vegetation and climate evolution.

In many parts of the world, recent glacier recession has opened an entirely new window on the palaeoecology, vegetation history, and archaeology of sites at high elevations (Dyurgerov and Meier, 2000; Farnell et al., 2004; Dove et al., 2005; Nesje, 2009; Menounos et al., 2009; Nesje et al., 2011; Andrews and MacKay, 2012; Callanan, 2012). In forefields of mountain glaciers and perennial snow and ice patches, in most cases quite close to the tree line, exposure of megafossil tree remnants of different species spanning major parts of the Holocene is quite common (e.g., Nicolussi and Patzelt, 2000; Hormes et al., 2001; Schlüchter and Jörin, 2004; Koch et al., 2007; Benedict et al., 2008; Joerin et al., 2008; Wiles et al., 2008; Scapozza et al., 2010; Koehler and Smith, 2011; Nicolussi and Schlüchter, 2012). In the Swedish Scandes, reconnaissance surveys of these newly emerging habitats have highlighted a surprising plethora of debris wood currently being released from beneath receding perennial ice and snow bodies at unprecedented elevations high above the tree line (Kullman, 2004a; Öberg and Kullman, 2011a; Kullman and Öberg, 2012).

Here we report and analyze the results of an intensified search for recently exposed debris wood and peat from forefields of glaciers and icefields and snow patches in different parts of Swedish Lapland and at very high elevations above the tree line, presenting a comprehensive synthesis of new and previously published data (Öberg and Kullman, 2011a; Kullman and Öberg, 2012). The present extended sampling effort adds to the understanding of the upper limit, general structure, species composition of tree growth, and palaeoclimate during earlier parts of the Holocene.

FIG. 1. Location of the study areas in Swedish Lapland: 1) Tärna, and 2) Abisko/Kebnekaise.

STUDY AREA

The study area includes two main areas in the province of Lapland in the northern part of the Swedish Scandes: Tärna in the south and Abisko-Kebnekaise in the north (Fig. 1). Geographical names are given in Swedish according to official topographic maps.

The highest peaks range between 1400 and 2100 m above sea level (a.s.l.), while the valley floors are at 500 to 700 m a.s.l. The bedrock is of Cambro-Silurian origin (amphibolite, greenschist, and calcareous phyllite) and the Quaternary deposits consist of peat, till, glacifluvial, and loessic accumulations. The climate is weakly suboceanic. More detailed site descriptions and accounts of the physiography, local climate, and Holocene glacier histories are provided elsewhere (Gavelin, 1910; Svenonius, 1910; Ahlmann and Lindblad, 1940; Schytt, 1959; Karlén, 1973; Holmlund et al., 1996; Lindgren and Strömgren, 2001).

The general character of the forefields fringing the glaciers we focus on in this study is displayed in Figure 2. Representative views of the investigated snow and ice patch sites are presented by Öberg and Kullman (2011a) and Kullman and Öberg (2012).

The valleys and mountainsides are clad with an upper forest rim of mountain birch (*Betula pubescens* ssp. *czerepanovii*), with scattered specimens of Scots pine (*Pinus sylvestris*) and Norway spruce (*Picea abies*). The present-day (2010–13) local tree lines, set by *Betula*, *Picea*, and *Pinus* trees more than 2 m tall (Fig. 3), are used as modern references when calculating the magnitude of past changes in tree-line elevation throughout the Holocene (Appendix 1).

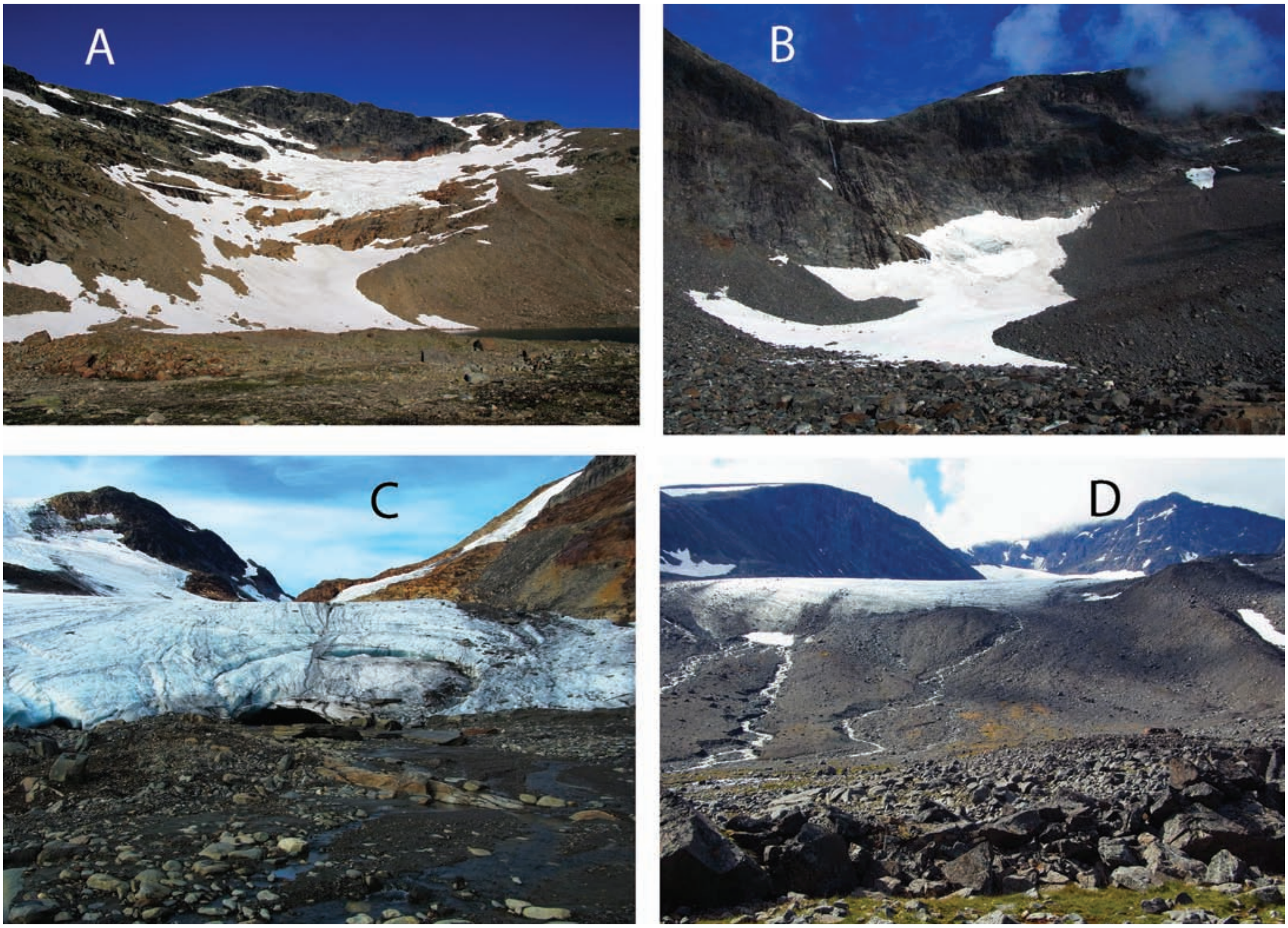

FIG. 2. Lower margins and forefields of the glaciers concerned in this study. A) Tärnaglaciären, B) Kittelglaciären, C) Kårsajökeln, and D) Storglaciären.

METHODS

The surfaces of glacier forefields were systematically searched for megafossil tree and peat remains during the late summer and early autumn of 2012 and 2013. Recovered specimens were instantly wrapped in aluminum foil and stored frozen until delivery to the dating laboratory. Only complete and spatially well separated wood pieces were dated. Thus, the risk of dating wood belonging to different specimens is negligible. This kind of sampling cannot guarantee achievement of a perfectly true representation of tree dates for each time; however, a large sample size may substantially reduce the uncertainty. This improved accuracy is most relevant for the balance between pine and birch, since birch decomposes more rapidly than pine.

Radiocarbon dating was performed by Beta Analytic Inc., Miami (USA). Radiocarbon ages are calibrated to calendar years before present (cal yr BP), with "present" = AD 1950. Dating was carried out after pretreatment with standard laboratory procedures. Calibration was conducted by use of the INTCAL09 database (Reimer et al., 2009). In cases when simplicity is needed (running text and Fig. 6), the calibrated ages are quoted as the values of points where radiocarbon ages intercept the calibration curve. We recognize that these estimates are not ideal. For the present purpose, however, they are considered to be adequate, particularly since they provide data compatible with data from previous studies (Öberg and Kullman, 2011a; Kullman and Öberg, 2012). The discussion is based on the radiocarbon time scale.

Outwashed peat cakes recovered on the forefields were dated on the basis of 2 cm slices of bulk peat samples. Some of these were coarsely analyzed for the presence of macroscopic tree remains, which were dated by accelerator mass spectrometry (AMS). In some cases, macroremains of *Picea abies* and understory species were dated indirectly by the radiocarbon age of the thin peat slice in which they were imbedded. In other cases, approximate ages of representatives of the last-mentioned group were estimated from dated wood samples contained in the same peat slices.

Great effort was devoted to searching alpine tundra (lakes, soils, and mires) slightly below and above the forefields here concerned for the presence of megafossils.

In most cases, the recovered megafossils had remaining bark fragments or cone and leaf characteristics that made species identification unambiguous. Some ambiguous

FIG. 3. The current tree line of mountain birch (*Betula pubescens* ssp. *czerepanovii*) on the south-facing slope of Mt. Kebnetjåkka, 3.5 km southeast of Kittelglaciären, is marked by this individual tree, growing at 910 m a.s.l. Over the past century, the tree line has shifted 170 m upslope. Photo: 2013-08-12.

specimens were identified by wood anatomy analysis (Erik Danielsson/Vedlab Inc.). Altitudes (m a.s.l.) and geographical coordinates of all retrieved tree remains were obtained by a GPS navigator (Garmin 60CS) that was repeatedly calibrated against distinct points on the topographical map. Reported altitudes are rounded off to the nearest 5 m. The nomenclature of vascular plants follows Mossberg and Stenberg (2003).

RESULTS

General Character of Samples and Sites

The representative overview of the general character of tree remains, peat samples, and their discovery sites provided by Öberg and Kullman (2011a) and Kullman and Öberg (2012) is complemented here by a few examples (Fig. 4).

Characteristically, detrital wood and peat cakes occurred in close association with main glacier outwash streams, originating from beneath glacier ice within a few hundred meters of the ice fronts. Obviously, original growing sites are still hidden by permanent ice upstream and at higher elevations. Thus, the sampling sites represent minimum elevations of the original growing sites. Some of the snow and ice patches occur in relatively flat terrain, indicating that recovered megafossils are nearly in situ.

Most of the sampled wood remains were short sections of logs, 0.2–0.5 m in length and 5–15 cm in diameter. As a rule, they appeared to have been recently broken, often displaying soft, rapidly disintegrating, and strongly compressed wood indicative of subglacial burial and transport. Usually, only fragments of the bark remained. In some cases, macroremains of various tree species were found as cones, bark, needles and leaf fragments embedded in peat cakes with a size of 10–20 cm (Fig. 5). Their rounded, somewhat compressed, and compact forms suggest that they had been dislocated by streaming water from their original growth positions, which were still covered by ice. It is reasonable to suppose that many pieces of tree remains were preserved in peat for some millennia prior to the glacier inception, which further contributed to their conservation.

In addition to wood fragments, peat cakes are regularly recovered along the outwash streams. The small fraction of these that have been dated range in age from 3900 to 8400 cal yr BP. As a rule, the peat contains plant macrofossils easily identifiable as common understory forest species and tree species such as *Picea abies* (8450, 8380, and 8180 cal yr BP), *Larix sibirica* (7320 cal yr BP), *Sorbus aucuparia* (8640 cal yr BP), *Alnus incana* (8000 cal yr BP), and *Populus tremula* (8590 cal yr BP) (Kullman and Öberg, 2012; Appendix 1).

Chronology and Elevational Structure

In total, 90 tree remains, distributed among the seven sampling sites, were radiocarbon-dated; ages ranged from 1950 to 11 980 cal yr BP (Appendix 1). Of these 90, 29 are here reported for the first time. *Betula* is the dominant species (53), followed in order of abundance by *Pinus sylvestris* (30), *Picea abies* (4), *Larix sibirica* (1), *Populus tremula* (1), *Alnus incana* (1), and *Sorbus aucuparia* (1).

Figure 6 displays the calibrated radiocarbon ages of all recovered birch and pine megafossils relative to their present-day tree-line elevations in the study area. Except for a pine remnant dated to 11 760 cal yr BP (i.e., right at the Late Glacial/Holocene transition), no tree records originate from the first 2000 years of the Holocene. Around 9500 cal yr BP, a distinct surge of pine and birch dates emerges in the record at elevations 600 to 700 m higher than the present-day tree lines of these species. Records from these high relative elevations remained for about 1000 years. Shortly after 8500 cal yr BP, an abrupt elevational dip of approximately 200 m occurred. Thereafter, a more linear descent of *Pinus* and *Betula* proceeded until about 4500 cal yr BP, after which the records of pine and birch are virtually absent. During this later interval, birch appears to have gained in dominance relative to pine. Notably, a single birch log is dated to 1950 cal yr BP (Appendix 1, Fig. 6).

FIG. 4. Megafossil tree remains sampled at different sites. A) Storglaciären, *Betula pubescens* 8490 cal yr BP, B) Kittelglaciären, *Pinus sylvestris* 9010 cal yr BP.

DISCUSSION AND INTERPRETATION

High-Elevation Tree Growth and Landscape History

The virtual absence of megafossil tree records for the first 2000 years of the Holocene differs from the pattern of other high-mountain parts of the Scandes, where scattered trees grew during this period but exclusively at much lower elevations relative to the present-day tree line (Kullman, 2002, 2013; Öberg and Kullman, 2011b). Apart from sampling stochasticity, this feature may relate to the particular high-altitude habitats concerned here, where snow and ice may build up quite rapidly as a consequence of episodes with modest cooling (cf. Jansson et al., 1999), making tree growth virtually impossible. In fact, short-term glacier advances are inferred from this period in the Norwegian Scandes (Nesje, 2009). Subsequently and until the mid-Holocene, a diverse tree flora characterized glacier and snow cirques without perennial ice and currently situated several hundred meters above modern tree lines. These results parallel the situation in the southern Swedish Scandes (Öberg and Kullman, 2011a), suggesting a more generic pattern, with a richer tree flora and wider amplitude of Holocene tree-line and landscape change, than is usually assumed when focusing on more traditional palaeoarchives, such as peat bogs, soils, and lakes (e.g., Berglund et al., 1996; Karlén and Kuylenstierna, 1996;

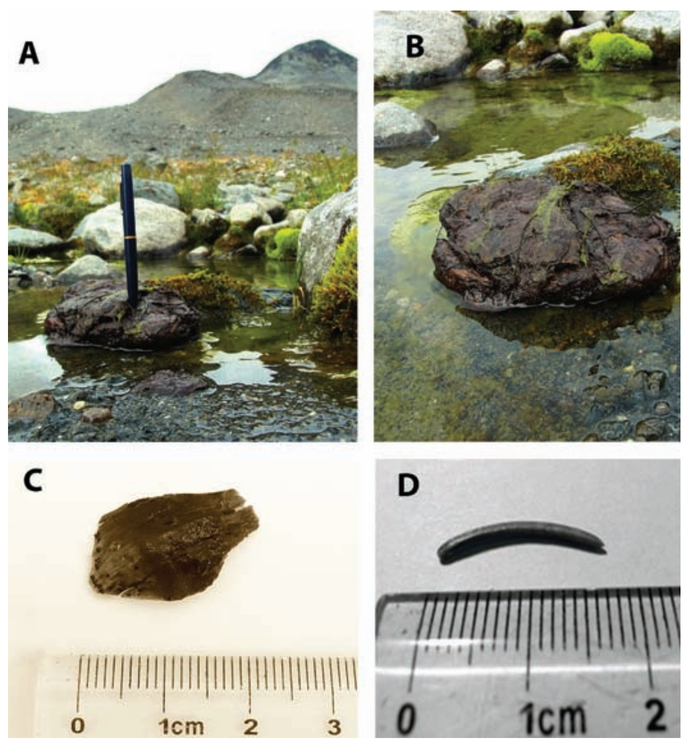

FIG. 5. A and B) Peat cake outwashed from Storglaciären, containing plant macrofossils, C) Cone shell of *Picea abies* 8380 cal yr BP, D) *Picea abies* needle 8380 cal yr BP.

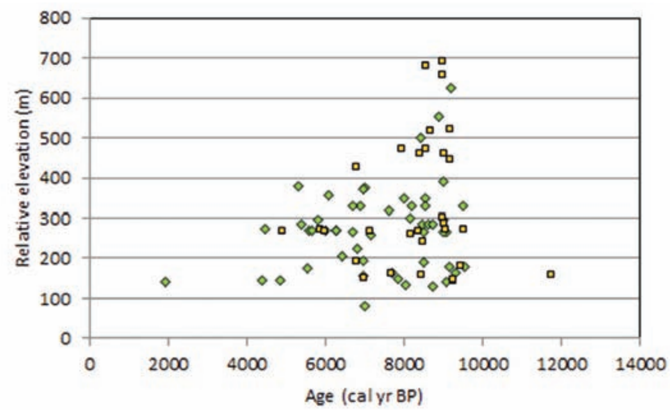

FIG. 6. Radiocarbon dates (intercept values) and corresponding elevations of all birch (green) and pine (yellow) remnants, relative to their present-day tree-line positions.

Barnekow, 1999; Seppä and Birks, 2001; Bergman et al., 2005; Mahaney and Kalm, 2012).

Tree growth 600–700 m above the modern tree lines in 9500–8500 cal yr BP, as evidenced here for a particular type of habitat, is several hundred meters higher than estimated for the same time interval in previous studies that focused on low alpine terrain (e.g., Berglund et al., 1996; Karlén and Kuylenstierna, 1996; Barnekow, 1999; Seppä et al., 2004). Within an elevational zone 200–300 m below the glacier cirques, no megafossil or macrofossil evidence for tree growth could be found either in our study area or in other parts of the Scandes (Kullman, 1995, 2013; Paus, 2010; Öberg and Kullman, 2011a). Thus, it appears that between 9500 and 8500 cal yr BP, present-day glacier and ice patch sites stood out as more or less isolated "wood islands" in a virtually treeless landscape matrix. Thereafter, these islands gradually contracted in size and began to occur at lower elevations. In parallel, birch seems to have gained in relative dominance, after a period when pine was more prominent than previously presumed (e.g., Barnekow, 1999; Seppä et al., 2004).

Isolated multi-species tree islands, restricted to these specific outlier habitats (glacier cirques) high above present-day tree lines, may seem counterintuitive today. They could be understood, however, primarily in light of their particular concave (parabolic) local topography and associated climate, as suggestively illustrated by Öberg and Kullman (2011a). During warmer periods with less ice and snow, sites of this character are likely to provide higher temperatures, better wind shelter, and more stable soil moisture than much of the surrounding and more exposed high mountain landscape (cf. Elven, 1978; Anderson et al., 2009; Scherrer and Körner, 2011). Some further support for the latter contention is provided by frequent observations that these habitats have been particularly targeted by upward expansion of "forest species" in connection with the current warm phase of the climate (Kullman, 2004b, 2010; Öberg and Kullman, 2011a). With their propensity for snow accumulation, these sites offer ideal preconditions for accumulation of wind-driven seeds (Kullman, 1984, 2004b).

Today, tree growth of *Betula* reaches tree-line positions about 200 higher than that of *Pinus* in the study region. The present record provides no clear indication of whether such a situation also prevailed during the early Holocene within the habitats concerned here. It may appear that pine extended somewhat higher relative to its present-day position than did birch, i.e., the vertical separation between birch and pine may have been smaller than it is today. However, it should be kept in mind that the present record is somewhat fortuitous and incomplete, being composed of wood remains that have been dislocated downslope from their original growing sites. Thus, these samples (Fig. 6) at best provide only a subdued view of the tree species zonation pattern and the positional tree-line evolution throughout the Holocene.

A virtually new discovery emerging from this and analogous earlier studies (Öberg and Kullman, 2011a; Kullman and Öberg, 2012) is that during the early Holocene, high alpine forest islands composed predominantly of birch and pine were intermixed with scattered specimens of *Picea abies*, *Larix sibirica*, *Populus tremula*, *Sorbus aucuparia*, and *Alnus incana*. This relatively rich arboreal high mountain flora is paralleled at lower elevations in the mountain region with several warmth-demanding tree species that currently are not growing in the region (Kullman, 2008; Öberg and Kullman, 2011b).

The presence of *Picea abies* and *Larix sibirica* within the interval 8500–7300 cal yr BP contributes to a growing recognition and insight that these species were regular components of the high-mountain flora within the entire extent of the Scandes, from south to north, during the early Holocene and late Weichselian (Kullman, 2002, 2008; Paus, 2010, 2013; Öberg and Kullman, 2011b; Paus et al., 2011; Carcaillet et al., 2012). These features were previously entirely undetected by traditional pollen analysis (cf. Elven et al., 2013). Obviously, a much higher non-analogue biodiversity prevailed during the early Holocene than has ever been supposed for high-mountain regions.

Given the rich tree flora in isolated high alpine habitats during the early Holocene, when lower reaches of the mountain valleys were still ice-covered (e.g., Kullman, 1995; Barnekow, 1999), it is reasonable to assume that such populations have functioned as dispersal nodes for downslope afforestation of the high-mountain landscape (cf. Allen and Huntley, 1999; Kullman, 2002; Kullman and Kjällgren, 2006; Carcaillet et al., 2012). This aspect adds to the current discourse concerning the role of small outlier populations for understanding past, present, and future arboreal biogeography (e.g., Feurdean et al., 2013).

Aspects on Glacier and Climate History

The striking and rapid surge of warming-induced growth of *Pinus* and *Betula* at their highest Holocene levels during 9500–8500 cal yr BP appears to be a common pattern for the entire Scandes (Aas and Faarlund, 1988; Bjune et al., 2005; Eide et al., 2006; Paus, 2010). Apparently, this widespread phenomenon represents a release from the so-called Erdalen 2 Event (10 100 to 9700 cal yr BP), which was characterized by distinct cooling and major glacier advance (Nesje et al., 1991; Dahl and Nesje, 1996).

The tight clustering of our dated tree remains suggests that at the end of this period of rapid tree growth, the glaciers and ice patches we are concerned with here did not exist, or were much smaller than they are today, in response to warmer-than-present summers. This situation prevailed throughout most (or all) of the period 9530 – 4480 cal yr BP, as inferred also in other studies in Scandinavia (e.g., Rosqvist and Østrem, 1989; Bakke et al., 2005; Nesje et al., 2008; Öberg and Kullman, 2011a). It is reasonable to conclude that this circumstance reflects a hemispheric climatic situation related to higher-than-present insolation levels, forced largely by the Earth's orbital variations (Ekholm, 1901; Berger and Loutre, 1991). Obviously, this mechanism has been the ultimate driver of a climate progressively more amenable to glacier expansion throughout the Holocene. Little support remains for repeated major glacier advances and retreats during this period (e.g., Karlén and Kuylenstierna, 1996), as concluded in several other studies (e.g., Berglund et al., 1996; Nesje, 2009).

The youngest peat date (3890 cal yr BP) constrains the continuous "tree period" and approximates the inception of perennial snow and glacier ice, which buried the last living trees and further sealed with ice those peat repositories that contained megafossils from earlier parts of the Holocene. This inference agrees with several studies indicating a distinct shift to cooler and more snow rich conditions (Neoglaciation) around that time (e.g., Karlén, 1976; Caseldine and Matthews, 1987; Snowball and Sandgren, 1996; Bergman et al., 2005; Paus, 2010; Kullman, 2013).

Notably, a single medium-sized birch log was recovered close to the lower, present-day front of the Kårsajökel and 140 m above the modern birch tree line (Fig. 4). Its date of 1950 cal yr BP indicates that, at that time, the glacier was more contracted upslope than at present and by inference, that this log may tentatively point to a period warmer than the present. In fact, this contention is supported by a reported finding near a glacier in SW Norway of a subfossil birch log, also located 140 m above the present tree line, and dating to about 2000 cal yr BP (Nesje et al., 1991). Futhermore, an Icelandic glacier has released a birch log originating from virtually the same time (Ives, 1991). In line with these findings, several other climate proxies from northern Europe indicate warmer-than-present conditions in the first decades of the Roman Empire (e.g., Hormes et al., 2004; Ljungqvist, 2009; Humlum et al., 2011; Esper et al., 2012; Kullman, 2013; Luetscher et al., 2013). Moreover, the discovery of this birch log adds to the insight that present-day glacier recession and associated warming are not unique phenomena during the past 4500 years (cf. Kullman, 2013).

If we assume that the tree line and tree-line change relate primarily to summer temperature (e.g., Körner and Paulsen, 2004; Holtmeier and Broll, 2005), former tree-line positions may be used as proxy indicators of paleoclimate history (cf. Karlén 1976; Tinner and Kaltenrieder, 2005; Kirdyanov et al., 2012; Kullman, 2013), drawing on a conventional temperature lapse rate of 0.6°C per 100 m in elevation (Laaksonen, 1976). Given these assumptions, the Holocene tree-line peaks, at 9500 cal yr BP and about 700 m higher than present, may imply summer temperatures 4.2°C warmer than the first decade of the present century. This is a minimum difference, since most megafossils are downwashed from elevations higher than their sampling sites. As a consequence, the temporal record of dated megafossil tree remains provides only a weak impression of long-term summer temperature variations.

To some extent, the emerging evidence of multi-species early Holocene tree growth at unprecedented high elevations relates to substantial glacio-isostatic uplift throughout the Holocene. Since about 9500 cal yr BP, the land surface in western Lapland has been lifted by at least 200 m (e.g., Möller, 1987; Svensson, 1991; Påsse and Andersson, 2005). Thus, the total tree-line lowering attributable to general climate forcing should be reduced to 500 m (700 minus 200), which reduces the inferred change in summer temperature from 9500 cal yr BP to the present to 3.0°C. This lower estimate matches theoretical calculations based on insolation variations in response to the Earth's orbital changes (cf. Berger and Loutre, 1991; Esper et al., 2012) and compares well with multi-proxy reconstructions from adjacent parts of northern Lapland (Shemesh et al., 2001; Bigler et al., 2003).

Despite the reservations and uncertainties outlined above, there is little doubt that the Holocene thermal optimum for the Scandes occurred in the earliest part of the Holocene, which concurs with multi-proxy inferences from other parts of Europe and Greenland (e.g., Paus, 2013; Luoto et al., 2014). Other studies suggest a substantially later thermal optimum (e.g., Berglund et al., 1996; Seppä and Birks, 2001). However, these reconstructions are based on pollen analysis, an approach that is considered to provide less reliable temperature estimates (Paus, 2013; Elven et al., 2013).

The present study has provided a new and virtually unexpected view of the general structure and species composition of the high-mountain landscape in northern Sweden during the Holocene. The methodological approach depends entirely on rapid melting of perennial ice and snow bodies, which makes them sensitive to annual weather anomalies. Continued research and extensive field inventories urgently need to be implemented in order to gain even more information from these rich sources concerning the structure and species composition of the living mountain landscape in the past.

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APPENDIX 1. Radiocarbon dates of tree remains. Lab. codes marked with an asterisk (*) denote AMS dates. "Relative elevation" refers to the difference in altitude between the sampling site and the nearest tree line of the concerned species. Source: 1 – Öberg and Kullman, 2011a; 2 – Kullman and Öberg, 2013; 3 – this study.

Locality	°N lat.	°E long.	Relative elevation	Altitude (m a.s.l.)	Species	Lab. code	Radio-carbon age	Calibrated 1δ range (^{14}C yr BP)	Intercept (cal yr BP)	Sample size (cm)	Source
Tärnaglaciären	6550945	1516728	270	1070	*Betula pubescens*	Beta-284450	5430 ± 60	6290–6190	6280	18 × 7	1
Tärnaglaciären	6558916	1516681	270	1070	*Betula pubescens*	Beta-284449	4850 ± 50	5610–5580	5590	20 × 8	1
Tärnaglaciären	6550945	1516661	270	1070	*Betula pubescens*	Beta-284455	5240 ± 50	6100–5930	5990	5 × 4	1
Tärnaglaciären	6550910	1516734	265	1065	*Betula pubescens*	Beta-268653	5880 ± 60	6750–6650	6680	17 × 7	1
Tärnaglaciären	6550913	1516724	260	1060	*Betula pubescens*	Beta-268654	6220 ± 60	7240–7020	7160	19 × 8	1
Tärnaglaciären	6550875	1517653	225	1025	*Betula pubescens*	Beta-264395	5990 ± 70	6920–6740	6820	13 × 6	1
Tärnaglaciären	6550927	1516654	275	1075	*Betula pubescens*	Beta-284467	4020 ± 50	4530–4420	4480	15 × 7	1
Tärnaglaciären	6550896	1516761	270	1070	*Betula pubescens*	Beta-284447	4950 ± 50	5730–5610	5660	30 × 11	1
Tärnaglaciären	6550824	1516843	285	1085	*Pinus sylvestris*	Beta-284448	8110 ± 40	9030–9010	9020	50 × 12	1
Tärnaglaciären	6550937	1516648	270	1070	*Pinus sylvestris*	Beta-284453	5110 ± 50	5920–5760	5900	10 × 3	1
Tärnaglaciären	6550950	1516700	260	1060	*Pinus sylvestris*	Beta-284454	7330 ± 60	8190–8040	8170	45 × 14	1
Tärnaglaciären	6550947	1516834	270	1070	*Pinus sylvestris*	Beta-264394	8520 ± 70	9540–9480	9530	35 × 10	1
Tärnaglaciären	6550913	1516724	265	1065	*Pinus sylvestris*	Beta-268655	7600 ± 60	8420–8370	8400	40 × 11	1
Tärnaglaciären	6550942	1516650	270	1070	*Betula pubescens*	Beta-362589	5440 ± 40	6290–6210	6280	12 × 7	3
Tärnaglaciären	6550913	1516658	265	1065	*Betula pubescens*	Beta-362590	7710 ± 40	8540–8430	8485	10 × 5	3
Tärnaglaciären	6550936	1516672	265	1065	*Betula pubescens*	Beta-362591	8160 ± 40	9130–9020	9060	8 × 4	3
Tärnaglaciären	6550927	1516680	265	1065	*Betula pubescens*	Beta-362592	8070 ± 40	9020–9000	9010	22 × 5	3
Tärnaglaciären	6550910	1516677	270	1070	*Pinus sylvestris*	Beta-362585	8170 ± 40	9130–9030	9090	42 × 11	3
Tärnaglaciären	6550951	1516654	265	1065	*Pinus sylvestris*	Beta-358468	4370 ± 30	4970–4870	4915	43 × 6	3
Tärnaglaciären	6550918	1516659	265	1065	*Pinus sylvestris*	Beta-362587	5260 ± 40	6170–5940	5990	20 × 5	3
Tärnaglaciären	6550923	1516656	265	1065	*Pinus sylvestris*	Beta-362588	6190 ± 30	7160–7020	7160	12 × 8	3
Östra Syterglaciären	6553748	1516984	390	1190	*Betula pubescens*	Beta-284469	8080 ± 70	9030–8990	9010	29 × 6	1
Murtserglaciären	6550654	1514291	555	1355	*Betula pubescens*	Beta-332297	7980 ± 40	8990–8770	8885	35 × 8	2
Murtserglaciären	6550779	1514605	625	1425	*Betula pubescens*	Beta-332288	8230 ± 40	9280–9130	9195	30 × 8	2
Murtserglaciären	6550727	1515561	500	1300	*Betula pubescens*	Beta-332283	7660 ± 40	8450–8410	8420	11 × 5	2
Murtserglaciären	6550576	1514882	520	1210	*Pinus sylvestris*	Beta-332287	8220 ± 40	9270–9120	9190	40 × 10	2

Locality	°N lat.	°E long.	Relative elevation	Altitude (m a.s.l.)	Species	Lab. code	Radio-carbon age	Calibrated 1δ range (^{14}C yr BP)	Intercept (cal yr BP)	Sample size (cm)	Source
Murtserglaciären	6550527	1514787	515	1205	*Pinus sylvestris*	Beta-332286	7910 ± 40	8770–8630	8675	13 × 5	2
Murtsernjuone	6550546	1513613	350	1150	*Betula pubescens*	Beta-332290	7200 ± 40	8020–7970	8010	20 × 5	2
Murtsernjuone	6550387	1513589	285	1085	*Betula pubescens*	Beta-322281	4640 ± 30	5450–5320	5380	12 × 5	2
Murtsernjuone	6550563	1513588	470	1160	*Pinus sylvestris*	Beta-332280	7140 ± 40	8000–7940	7960	18 × 7	2
Murtsergure	6549623	1516427	355	1155	*Betula pubescens*	Beta-332298	5300 ± 40	6180–6990	6095	30 × 7	2
Murtsergure	6549626	1516493	350	1150	*Betula pubescens*	Beta-332295	7770 ± 40	8590–8520	8550	40 × 8	2
Murtsergure	6549606	1516568	330	1130	*Betula pubescens*	Beta-332294	7740 ± 40	8580–8570	8540	15 × 13	2
Murtsergure	6549675	1516180	375	1175	*Betula pubescens*	Beta-332292	6130 ± 40	7150–6950	7000	50 × 9	2
Murtsergure	6549590	1516568	330	1130	*Betula pubescens*	Beta-332285	7340 ± 30	8180–8160	8170	30 × 6	2
Murtsergure	6549622	1516430	460	1150	*Pinus sylvestris*	Beta-332296	8110 ± 40	9070–9010	9020	50 × 8	2
Murtsergure	6549605	1516672	425	1115	*Pinus sylvestris*	Beta-332293	5980 ± 30	6860–6760	6800	45 × 8	2
Murtsergure	6549590	1516400	460	1150	*Pinus sylvestris*	Beta-332282	7670 ± 40	8510–8410	8430	40 × 8	2
Kårsajökeln	6821610	1821096	80	930	*Betula pubescens*	Beta- 250909	6130 ± 60	7160–6940	7000	40 × 7	1
Kårsajökeln	6821726	1820156	130	980	*Betula pubescens*	Beta-250917	7920 ± 50	8960–8630	8710	60 × 9	1
Kårsajökeln	6821744	1819853	140	990	*Betula pubescens*	Beta-264383	8160 ± 90	9260–9010	9060	30 × 12	1
Kårsajökeln	6821731	1820152	135	985	*Betula pubescens*	Beta-264385	7250 ± 60	8160–8000	8030	18 × 7	1
Kårsajökeln	6821628	1820292	165	965	*Betula pubescens*	Beta-264386	8290 ± 70	9420–9140	9290	20 × 8	1
Kårsajökeln	6821744	1819885	155	955	*Pinus sylvestris*	Beta-250906	10130 ± 60	11980–11680	11760	30 × 8	1
Kårsajökeln	6821771	1819969	140	940	*Pinus sylvestris*	Beta-250914	8270 ± 60	9400–9130	9280	30 × 12	1
Kårsajökeln	6821735	1819882	190	990	*Pinus sylvestris*	Beta-264384	5980 ± 50	6890–6740	6790	40 × 15	1
Kårsajökeln	6821629	1820316	150	950	*Pinus sylvestris*	Beta-264387	6130 ± 60	7160–6940	7000	7 × 4	1
Kårsajökeln	6821657	1820531	145	945	*Pinus sylvestris*	Beta-264388	8250 ± 60	9380–9120	9260	15 × 5	1
Kårsajökeln	6821728	1819883	140	990	*Betula pubescens*	Beta-362594	2020 ± 30	1990–1900	1950	15 × 6	3
Kårsajökeln	6821794	1819797	150	1000	*Betula pubescens*	Beta-362596	7000 ± 40	7940–7730	7840	8 × 4	3
Kårsajökeln	6821680	1820065	445	965	*Pinus sylvestris*	Beta-362593	8240 ± 40	9250–9150	9200	9 × 4	3
Kårsajökeln	6821714	1819868	470	990	*Pinus sylvestris*	Beta-362595	7800 ± 40	8600–8550	8590	11 × 7	3
Slåttatjåkka	6821886	1841110	175	1025	*Betula pubescens*	Beta-284457	4760 ± 50	5590–5460	5530	45 × 7	1
Slåttatjåkka	6821930	1841297	165	1015	*Betula pubescens*	Beta-284458	6900 ± 60	7790–7670	7700	13 × 6	1
Slåttatjåkka	6821891	1841131	180	1030	*Betula pubescens*	Beta-264392	8210 ± 70	9290–9030	9130	30 × 8	1
Slåttatjåkka	6821888	1841128	180	1030	*Betula pubescens*	Beta-264391	8510 ± 70	9540–9480	9520	31 × 5	1
Slåttatjåkka	6821887	1841126	180	1030	*Pinus sylvestris*	Beta-264390	8380 ± 80	9480–9300	9440	14 × 7	1
Slåttatjåkka	6821861	1841293	155	1005	*Pinus sylvestris*	Beta-284456	7690 ± 50	8540–8420	8450	53 × 10	1
Slåttatjåkka	6821474	1841305	240	1090	*Pinus sylvestris*	Beta-284461	7710 ± 70	8570–8420	8490	40 × 10	1
Kärkerieppe	6823189	1818025	370	1050	*Betula pubescens*	Beta-284459	6090 ± 60	7140–6890	6950	18 × 7	1
Kärkerieppe	6823099	1817956	380	1060	*Betula pubescens*	Beta-284460	4600 ± 50	5440–5300	5310	17 × 6	1
Kåppasglaciären	6821807	1834763	155	1025	*Betula pubescens*	Beta-284462	6100 ± 60	7150–6900	6980	50 × 12	1
Kåppasglaciären	6821833	1834819	145	1015	*Betula pubescens*	Beta-284463	3900 ± 60	4420–4240	4400	12 × 5	1
Kåppasglaciären	6821841	1834883	145	1015	*Betula pubescens*	Beta-284465	4270 ± 50	4860–4830	4840	13 × 6	1
Kåppasglaciären	6821808	1824764	160	1030	*Pinus sylvestris*	Beta-284464	6870 ± 60	7750–7660	7680	30 × 10	1
Låktatjåkka	6824603	1832415	295	975	*Betula pubescens*	Beta-284472	5040 ± 60	5900–5710	5800	18 × 8	1
Låktatjåkka	6824590	1832372	300	980	*Pinus sylvestris*	Beta-284471	8020 ± 70	9010–8770	8990	36 × 10	1
Kittelglaciären	6752996	1831010	320	1230	*Betula pubescens*	Beta-358470	6760 ± 30	7620–7580	7610	30 × 9	3
Kittelglaciären	6753058	1830952	330	1240	*Betula pubescens*	Beta-358475	8470 ± 40	9520–9470	9490	14 × 7	3
Kittelglaciären	6752971	1831002	300	1210	*Betula pubescens*	Beta-358477	7310 ± 40	8180–8040	8160	13 × 8	3
Kittelglaciären	6752885	1831099	285	1195	*Betula pubescens*	Beta-358478	7690 ± 40	8540–8420	8450	10 × 7	3
Kittelglaciären	6752885	1831099	285	1195	*Betula pubescens*	Beta358684	7830 ± 40	8630–8590	8600	18 × 9	3
Kittelglaciären	6752885	1831099	285	1195	*Betula pubescens*	Beta-358479	7920 ± 40	8930–8640	8720	21 × 7	3
Kittelglaciären	6753063	1830944	295	1205	*Betula pubescens*	Beta-362592	8070 ± 40	9020–9000	9010	16 × 6	3
Kittelglaciären	6753038	1831019	330	1240	*Betula pubescens*	Beta-358472	6040 ± 30	6940–6810	6890	14 × 8	3
Kittelglaciären	6753065	1830974	330	1240	*Betula pubescens*	Beta-358473	5880 ± 30	6740–6670	6695	19 × 7	3
Kittelglaciären	6753066	1830945	655	1205	*Pinus sylvestris*	Beta-358469	8050 ± 40	9010–8990	9000	23 × 8	3
Kittelglaciären	6753002	1831012	680	1230	*Pinus sylvestris*	Beta-358471	7800 ± 40	8600–8550	8590	18 × 8	3
Kittelglaciären	6753066	1830945	655	1205	*Pinus sylvestris*	Beta-358469	8050 ± 40	9010–8990	9000	12 × 5	3
Kittelglaciären	6753046	1831268	690	1240	*Pinus sylvestris*	Beta-358474	8080 ± 40	9020–9000	9010	13 × 5	3
Storglaciären	6754189	1836540	205	1115	*Betula pubescens*	Beta-358480	5650 ± 30	6430–6410	6420	15 × 7	3
Storglaciären	6754285	1836708	190	1100	*Betula pubescens*	Beta-358690	7720 ± 40	8550–8430	8490	14 × 6	3
Storglaciären	6754205	1836701	195	1105	*Betula pubescens*	Beta-358483	6110 ± 30	7000–6940	6980	19 × 8	3
Murtserglaciären	6550585	1514774	515	1225	*Picea abies*	Beta-332275*	7360 ± 40	8190–8170	8180	Cone	2
Murtsernjuone	6550563	1513588	515	1160	*Picea abies*	Beta-332274*	7690 ± 40	8540–8420	8450	Cone	2
Storglaciären	6754287	183670	555	1105	*Picea abies*	Beta-366360*	7650 ± 40	8420–8340	8380	Cone shell	3
Murtsergure	6549599	1516574	510	1125	*Larix sibirica*	Beta-332277*	6410 ± 30	7420–7310	7320	Cone	2
Murtsergure	6549599	1516574	1125	395	*Alnus incana*	Beta-332278*	7280 ± 40	8170–8020	8000	Leaf	2
Murtsergure	6549625	1516669	1115	465	*Populus tremula*	Beta 332276*	7790 ± 40	8600–8540	8590	Leaf	2
Murtsergure	6549599	1516574	1125	345	*Sorbus aucuparia*	Beta-332279*	7890 ± 40	8750–8600	8640	Leaf	2
Tärnaglaciären	6550927	1516654	1075		Peat	Beta-268652*	3590 ± 50	3970–3840	3890	13 × 11	1
Murtsergure	6549565	1516591	1115		Peat	Beta-322289*	4500 ± 40	5300–5050	5175	15 × 15	2
Kittelglaciären	6757899	1830978	1230		Peat	Beta-366365*	4650 ± 30	5340–5310	5380	14 × 14	3
Storglaciären	6754287	1836700	1105		Peat	Beta-366360*	7650 ± 40	8420–8340	8380	17 × 12	3
Kårsajökeln	6821644	1820126	982		Peat	Beta-366362*	6980 ± 40	7880–7700	7830	12 × 10	3