



RESEARCH ARTICLE

MELTING GLACIERS IN THE SWEDISH SCANDES PROVIDE NEW INSIGHTS INTO  
PALAEO TREELINE PERFORMANCE

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ABSTRACT

Climate warming and associated post-Little Ice Age recession of glacier ice and permanent snow in high mountains of the Swedish Scandes have opened a new view for alpine palaeoecology. Receding glaciers and snow/ice patches, high above current tree-lines of all boreal tree species, have exposed forefields with a plethora of megafossil tree remnants, representing discrete multi-species tree groves. Radiocarbon-dating of associated wood debris offers new insight into the early Holocene structure and species composition of the tree-line ecotone. The emerging pattern deviates substantially from the conventional view, deduced from the pollen stratigraphical approach, which needs to be questioned in general, both with respect to tree-line reconstruction and in the context of more general biogeographic evolution. Boreal tree species were present in the concerned settings from late-glacial, 16 800 cal. yr BP to the late Holocene, about 4000 cal. yr BP. The frequency of megafossil tree remains peaked 9600-9000 cal. yr BP, maximum 600-700 m above modern tree-lines. This implies (corrected for land uplift) that the summer temperatures may have been 3 °C warmer than current standards. The postglacial immigration history of *Picea abies* to the Scandes, a stumbling stock in Scandinavian palaeobiogeography, is at least 8000 years prior to traditional pollen-based text book narrative. Discrete tree groves, embracing most present-day boreal tree species, were strictly confined to empty glacier cirques and snow hollows. These populations may have played an important role as dispersal nodes for the postglacial afforestation of the mountain landscape. In addition, the results add to the increasingly recognized view that *Larix sibirica*, an eastern species, currently not native to Scandinavia, prevailed quite frequently at high elevations during the early Holocene. Further shortcomings of traditional methods of vegetation reconstruction are highlighted when viewed in perspective of megafossil analyses, which support a relatively firm framework on which the detailed vegetation history can be built.

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INTRODUCTION

The current discourse concerning proposed future climate change and the balance of natural versus anthropogenic drivers in that context would benefit from increased concern and improved understanding of palaeoclimate and its impacts on biota. By tradition, palaeovegetation and palaeoclimate information have to a large extent been inferred from pollen stratigraphical analyses (e.g. Hafsten 1992). This approach has provided important ideas concerning the broad outlines of postglacial vegetation development and biogeographic dynamics (e.g. Huntley & Birks 1983; Segerström & von Stedingk 2003; Giesecke 2005). A main and particularly critical aspect of this approach is the interpretation of trace amounts of pollen. Do these represent local presence or long-

distance transport and can they pin-point the first arrival of a species to a specific site or region? (cf. Ali *et al.* 2003; Froyd 2005; Brubaker *et al.* 2005; Hicks 2006). Despite recent methodological improvements (e.g. Barnekow *et al.* 2008), the outcome from pollen analyses is inferential and biased by the imaginativeness and general vegetation know-how possessed by the interpreter, leaving room for a certain amount of subjectivity (e.g. Rubiales *et al.* 2012; Elven *et al.* 2013). At best, pollen analytical results are hypothetical, in need for robust, testing against available independent data, ideally provided by megafossil analyses (Aas & Faarlund 1999; Kullman 2008). Support for that contention is that traditional pollen analyses have failed to decide the postglacial thermal optimum and the reinstatement patterns of the main tree species in northern Scandinavia as well as the general structure and elevational

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differentiation of the early postglacial mountain landscape (e.g. Berglund *et al.* 1996; Seppä *et al.* 2002; Birks *et al.* 2005). Indeed, there are substantial incongruencies between results achieved by pollen analysis and more robust and objective methods (Kullman 2002, 2008; Parducci *et al.* 2012a, b).

The tree-line, a concept much focused on in this study, is defined as the altitude (m a.s.l.) of the uppermost specimen of each tree species, taller than 2 m. The position and structure of the alpine (upper) tree-line is generally considered to be a consequence of thermal deficiency (Körner 2007) and a good climate indicator (Fagre *et al.* 2003; Holtmeier 2003; Nagy 2006; Kullman 2010a, in press). Treeline history may be used for reconstructing past climates and high-mountain vegetation trajectories (Karlén & Kuylenskierna 1996; Kullman 1995, 2008, 2013). This contention is supported by documented tree-line responses to climate variability over the past 100 years (Kullman & Öberg 2009), which almost perfectly matches the instrumentally recorded temperature trend. Accordingly, and viewed in more long-term retrospect, it appears that maximum 225 m pine tree-line upshift, recorded for this period has brought it to a higher position than any time during the past 7000 years (Kullman & Kjällgren 2006; Kullman 2013, in press). This circumstance attests to the unusual climate favorability for high-elevation tree growth of the past 100 years or so, which marks a fundamental break in the Neoglacial cooling trend since the mid Holocene. These prior studies are based on radiocarbon-dated megafossils, i.e. tree remains (trunks, twigs, roots) and macrofossils (cones, leaves, needles, bark, stomatae, etc.), recovered in peat deposits, lake sediments and raw humus layers above the current tree-line. Notably, these purported past tree-line positions are of minimum character (cf. Aas & Faarlund 2000; Barnett *et al.* 2001), since effective preservation media, foremost peat, have an upper limit some hundred meters above the current tree-line. In addition, megafossils may have been displaced downslope from their original growth places by gravitational forces. This “minimum aspect” is particularly critical in the case of birch, the wood of which decays relatively rapidly.

During recent years, however, a new avenue of high-alpine palaeoecology has appeared, as a special application of megafossil analysis, with potential to reveal tree-lines closer to their highest postglacial growth positions. The importance of this new source for historical biogeography and palaeoclimatology cannot be overstated. In addition, an opportunity offers to calibrate and test the accuracy of the palynological method of vegetation reconstruction.

This novel methodology, little used by Scandinavian palaeoecologists, draws on fortuitous melt out of alpine glaciers and large snow/ice fields since the 1930s or so (Holmlund 2012) and the exposure of debris wood on forefields of increasingly ice-free glacier cirques. Outside Scandinavia, this source of palaeoenvironmental information has received much attention and provided important new insights (Hormes *et al.* 2001; Schlichter & Jörin 2004; Koch *et al.* 2007, 2014; Joerin *et al.* 2008; Wiles *et al.* 2008; Ivy-Ochs *et al.* 2009; Scapozza *et al.* 2010; Nicolussi & Schlichter 2012). In the Swedish Scandes analogous palaeoecological studies are quite few and relatively recent (Kullman 2002, 2004b,c; Öberg & Kullman 2011a; Kullman & Öberg 2013,

2015). However, this archive has become much used by archaeologists, coining term “ice patch archaeoecology” providing a plethora of interesting findings concerning human life at high elevations during earlier parts of the Holocene (e.g. Spindler 1995; Farbregd 2009; Nesje *et al.* 2011; Reckin 2013; Rogers *et al.* 2014).

There is little doubt that recent and ongoing glacier recession has opened a new view to the understanding of high-alpine vegetation history. The main objective with this paper is to review the Swedish recoveries, showing their potential to uncover past tree-line positions. In this way recent tree-line and climate change can be evaluated in a proper perspective. A secondary intention is to highlight the incongruencies between the views and interpretations provided by megafossil and pollen analyses, which may open historical biogeography for new views and questions.

### Study Areas

Data are gathered at three extensive high-mountain regions from south to north along the entire Swedish Scandes (Fig. 1). Characteristic features of focused glaciers in their cirques are depicted in Fig. 2. All concerned glaciers (G) and ice patches (IP) have thinned and receded substantially at the lower front during the past 100 years (Lundqvist 1969; Holmlund 2012). Detailed meta-data (geomorphology, climate and vegetation) concerning the individual glaciers, adjacent fore-fields and their performance during the past 100 years or so are provided below (point 1-3) and by Öberg & Kullman (2011a), Kullman & Öberg 2013, 2015. All focused objects are situated well above the uppermost tree-line, which is formed by mountain birch (*Betula pubescens* ssp. *czerepanovii*). A more detailed description of the current tree-line ecotone is provided by Kullman (2010a). Geographical names are given in Swedish and refer to official topographical maps.

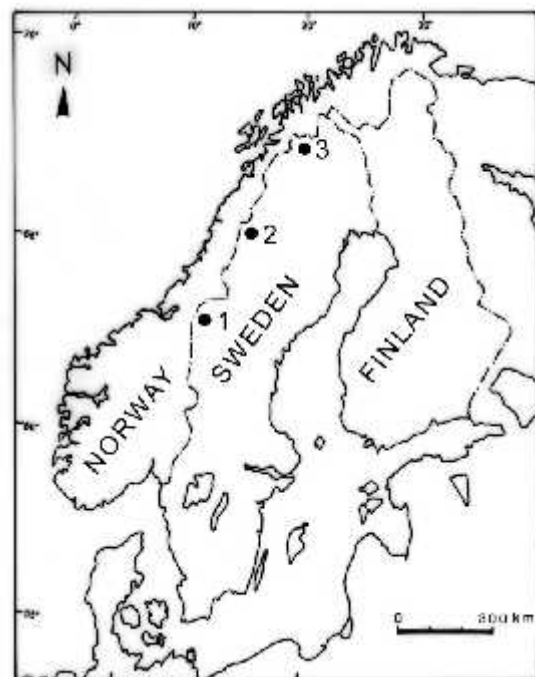


Fig. 1 Location map, showing the three study regions. 1. Helags-Sylarna Mts. 2. Tärna Mts. 3. Abisko-Kebnekaise Mts.

1. Helags-Sylarna area in the southern part of the Swedish Scandes, provinces of Jämtland and Härjedalen (Fig. 2A). Forefields of the following glaciers (G) and ice patches (IP) were investigated (names in Swedish): Helagsglaciären (G), 62°54' N; 12°27' E. Ekorrglaciären (G), 62°59' N; 12°13' E. Tempelglaciären (G), 63°00' N; 12°14' E. Storsylglaciären (G), 63°01' N; 12°13' E. Lillsylen (IP), 63°02' N; 12°12' E.
2. Tärna Mountains in the middle part of the Swedish Scandes, province of Lapland (Fig. 2B). Forefields of the following glaciers and ice patches were investigated: Tärnaglaciären (G), 65°51' N; 15°16' E. Östra Syterglaciären (G), 65°54; 15°17' E. Murtserglaciären (G), 65°51' N; 15°14' E. Murtsernjuone (IP), 65°50' N; 15°13' E. Lake Murtsergure (IP). 65°49' N; 15°16' E.
3. Abisko-Kebnekaise Mountains in the northern part of the Swedish Scandes, province of Lapland (Fig. 2C). Forefields of the following glaciers and ice patches were investigated: Kårsaglaciären (G), 68°18' N; 18°20' E, Slättatjåkka (IP), 68°21' N; 18°42' E Njulla (IP), Kärkerieppeglaciären (G). 68°23' N; 18°18' E, Kåppasglaciären (G/IP), 68°22' N; 18°35' E. Låktatjåkka (IP), 68°23' N; 18°32' E. Kittelglaciären (G), 67°53' N; 18°31' E. Storglaciären (G), 67°54' N; 18°37' E.



Fig. 2. **A.** Ekorrglaciären in region 1 (Fig. 1), with its lower margin 1380 m a.s.l., representing withdrawal of 180 m over the past 100 years. 2009-09-10. **B.** Tärnaglaciären in region 2 (Fig. 1). The glacier has retreated 160 m from its maximum position in the mid of the lake. Currently, a large ice patch prevails between the lake and the glacier terminus. 2010-08-19. **C.** Kårsaglaciären in region 3 (Fig. 1) has its lower margin at 965 m a.s.l., which is 155 m above its position by the early 20th century. 2013-09-12.

## METHODS

Detrital wood and outwash peat cakes have been systematically searched for on recently exposed forefields of alpine glaciers (Fig. 2) and snow/ice patches (Fig. 3) along the entire Swedish Scandes (Fig. 1). Recovered specimens were instantly wrapped in aluminium foil and stored frozen until delivery to the radiocarbon dating laboratory.

Radiocarbon dating was performed by Beta Analytic Inc., (USA). The obtained ages were calibrated to calendar years (cal. yr BP), with “present” = AD 1950. Calibration was conducted by use of the INTCAL09 database (Reimer *et al.* 2009). For consistency and ease of comparison, intercept values are quoted in the running text and figure captions.

In addition to glaciers, large perennial snow/ice patches may provide preconditions for long-term wood preservation. These archives has the advantage of being kinetically stable and ideal for conservation of the tree remnants (Nesje *et al.* 2011; Reckin *et al.* 2013). Accordingly, some of the largest megafossils are found under such circumstances (Figs. 3 & 10)

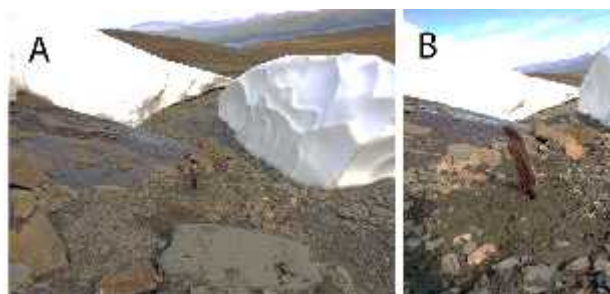


Fig. 3 **A.** Overview of Låktatjåkka snow/ice patch, 980 m a.s.l. **B.** Close-up view of a pine megafossil (up-raised), which dated 8990 cal.yr BP. Owing to the flat topography, this site should be quite close to the original growing position. 2010-08-30.



Fig. 4 Outwash peat cake, containing wood fragments, rowan (8640 cal. yr BP), grey alder (8000 cal. yr BP) and macrofossils of various forest floor plant species. Murtserglaciären 1125 m a.s.l. 2012-08-28. Source: Kullman & Öberg (2013).



Outwash peat cakes (Fig. 4), deposited on forefields of glaciers and snow/ice patches were analyzed for the presence of tree remains, which were dated by accelerator mass spectrometry (AMS). In some cases macroremains of *Picea abies*, some other tree species and ground floor plant species were dated indirectly by the radiocarbon age of the thin (2 cm) peat slice in which they were embedded (Kullman & Öberg 2013, 2015).

In most cases recovered specimens were identified to species by bark fragments or specific leaf or cone characteristics. Some ambiguous samples were determined by wood anatomy analysis (Erik Danielson/Vedlab Inc.) Altitudes and geographical coordinates were obtained by a GPS navigator (Garmin 60CS), calibrated against the topographical map. Reported altitudes are rounded off to the nearest 5 m. The nomenclature of vascular plants follows Mossberg and Stenberg (2003).

## RESULTS AND DISCUSSION

The present study draws on the following papers: Kullman 2002, 2004c; Öberg & Kullman 2011a; Kullman & Öberg 2013, 2015. These account for characteristics of the study areas, methodology and provide geographical coordinates for all individual finds of radiocarbon-dated mega- and macrofossil tree remains. Only records from forefields of glaciers or snow/ice patches above the current tree-line are considered. Most specimens, in general shorter than 1 m, have been outwashed by melt-water streams from positions underneath the glacier ice. The lower margin of the concerned glaciers have retreated by average 165 m during the past 100 years (Fig. 2), a figure which corresponds to the contemporary upshift of the birch tree-line (Kullman & Öberg 2009). This coincidence argues for the a causal operation of a common driver, i.e. temperature change.

Within the tree main study regions, the number of recovered specimens are as follows: 84 *Betula pubescens*, 38 *Pinus sylvestris*, 5 *Picea abies*, 1 *Populus tremula*, 1 *Alnus incana*, 1 *Sorbus aucuparia*, 1 *Larix sibirica*. Except for *Larix*, they all belong to the present-day native arboreal flora of northern Sweden. The dated megafossil recoveries span the period 16 815 cal. yr BP (Fig. 5 & 6) to 1950 cal. yr BP. Notably, these quantitative figures do not represent the relative proportions of tree species in the landscape, since they have been selected quite subjectively on the basis of preservation, to allow species identification.

### *Late-glacial and early-Holocene tree instatement to high elevations*

The oldest birch, pine and spruce dates, obtained on glacier forefields, are unprecedentedly old (Fig. 3) and imply that these species were present at high elevations (presumably on nunataks) in the Scandes during the Late Glacial (Fig. 5 & 6), some thousand earlier than previously assumed (Huntley & Birks 1983; Barnekow 1999; Berglund *et al.* 1996; Bigler *et al.* 2002; Seppä *et al.* 2004), during a period when the mountains should have been ice-covered according to the conventional wisdom (Lundqvist 1998). Trees at high elevations during the Late Glacial is not a singularity to Mt. Åreskutan (Fig. 5), but recorded also at other sites of the same character in the Swedish Scandes (Fig. 7). Presumably, the early trees

emanated from cryptic ice age refugia, which existed at the coast of northern Norway, e.g. on Andøya, where megafossil evidenced that tree birch prevailed c. 20 000 cal. yr BP (Fig. 8) (Kullman 2006), possibly in coexistence with other boreal tree species (Parducci *et al.* 2012a, b). These inferences have been questioned by Birks *et al.* (2005, 2012), merely on the general deviation from their conventional and pollen-based conception of the world.



**Fig. 5** Megafossils recovered at a site recently released from an extensive snow/ice patch. Mt. Åreskutan in the southern Swedish Scandes, 1360 m a.s.l. **A.** The earliest known mountain birch in the Scandes dated 16 815 cal. yr BP. **B.** Stout megafossil pine trunk recovered at a site which was covered by a snow/ice patch until the early 20th century. Radiocarbon dating yielded 13 010 cal. yr BP. **C.** Part of a spruce stem, which grew here 13 010 cal. yr BP. Source: Kullman (2002).



**Fig. 6** Site for the megafossils exposed in Fig. 5. An extensive snow patch prevailed here during the Little Ice Age and well into the 20th century, as witnessed by old reports from botanical pioneers (cf. Kullman 2014a) and the lichen-free zone on the boulder and rocks in the background. Most megafossils were covered by the moss carpet (*Warnstorfia tundrae* H. Arn.)



**Fig. 7** **A.** Pine megafossil below the lower margin of Helagsglaciären, 1150 m a.s.l., dating 13 150 cal. yr BP. Source: Öberg & Kullman 2011a. **B.** Remnant of pine just outside the lower fringe of Kärsaglaciären, 955 m a.s.l., dated 11 760 cal. yr BP. Source: Öberg & Kullman 2011a.





**Fig. 8** Subfossil birch megafossils recovered in a peat deposit on Andøya at the coast of Northern Norway 63 m a.s.l. Radiocarbon dating yielded 20 130 cal. yr BP. 1999-06-17. Source: Kullman 2006.



**Fig. 9** Lake Pompe (999 m a.s.l.) from the south. Megafossil trees were recovered right at the inlet stream in the western part (left) of the lake. The lake receives its water with megafossils from perennial snow patches upslope (1020-1030 m a.s.l.). 2015-08-07.



**Fig. 10** Megafossil pine trunk upraised from the peaty shore of Lake Pompe, dated back to 8995 cal. yr BP and emphatically showing the inadequacy of the pollen analytical method of vegetation reconstruction. Source: Kullman (1999).

An illustrative case, showing the conflicting results from pollen stratigraphical and megafossil analysis is provided by a case in northern Swedish Lapland, viz. Lake Pompe, near Abisko. This minor lake (Fig. 9) is located 999 m a.s.l., 100 and 470 m above the current tree-lines of *Betula pubescens* ssp. *czerepanovii* and *Pinus sylvestris*, respectively (Kullman

2015b). The lake is fed by melt water and pine megafossils (about 9500 to 8500 cal. yr BP) from a snow and ice patch area higher upslope (Öberg & Kullman 2011a). At the present day, the lake is surrounded by treeless alpine tundra. Megafossil tree remnants were retrieved from peat at the western lake shore (Fig. 10). These species were *Betula pubescens* ssp. *czerepanovii*, *Pinus sylvestris* and *Alnus incana*. The oldest record of each species was, 9485, 9395 and 9205 cal. yr BP, respectively (Kullman 1999). Lake sediments were analyzed for the presence of pollen and macrofossils of tree species (seeds, needles and bark fragments (Barnekow 1999). Macrofossils of birch were found at times analogous to those indicated by megafossils and interpreted as local presence. However, no such indications of early Holocene pine growth at this site could be found, neither from pollen nor from macrofossils. Thus, only megafossil analysis, as outlined above, could broadly reconstruct a landscape with different boreal tree species during the early Holocene. As evident from megafossils emerging from retreating snow patches in the neighbourhood, this landscape extended at least to 1090 m a.s.l., where pine grew 8490 cal. yr BP and birch at 9520 cal. yr BP (Fig. 11). In the case of *Pinus*, the latter record is 465 m higher and about 3500 years earlier than the previous highest estimate (pine needle) of the maximum pine tree-line during the Holocene, 625 m a.s.l. (Barnekow 1999). Taken together, these circumstance indicate that the megafossil approach more truly than pollen and certain macrofossils (stomata, seeds, bark fragments) reflects the early Holocene structure and species composition of the tree-line ecotone, although the highest treeline position may still be hidden, as long as glacier ice remains in the high mountains.



**Fig. 11** Megafossil remnant of *Pinus sylvestris* exposed from beneath a disintegrating snow patch on Mt. Slåttafjället in northern Lapland, 1090 m a.s.l. Radiocarbon dating yielded 8490 cal.yr BP. Source: Öberg &Kullman (2011a).

### Aspects on *Picea abies* performance during the Holocene

In Fennoscandia, *Picea abies* has for long been held as a mid- and late-Holocene immigrant. In great contrast, the oldest spruce date at the Åreskutan site and elsewhere in the Swedish Scandes are about 8000 years earlier (see above) than the palynologically inferred immigration time to this part of Scandinavia (Lundqvist 1969; Sonesson 1974; Moe 1970; Tallantire 1977; Hafsten 1992; Huntley & Birks 1983; Huntley 1996). However, certain early researchers, without <sup>14</sup>C-dating facilities, inferred, on purely stratigraphical grounds, an early Holocene instatement of spruce to Scandinavia (e.g. Lindqvist 1948). In addition, early Holocene frequent presence of spruce in the high mountains at various sites in the Scandes is reported on megafossil evidence, (Kullman 2000, 2002, 2004a; Kullman & Öberg 2013, 2015, 2016).

A particularly interesting find of macrofossil spruce is made on the forefield of Storglaciären in northern Lapland. Here a cone shell, extracted from an outwashed peat ball, was indirectly dated 8380 cal. yr BP (Fig. 12). This is far outside (west off) and much higher than the current distributional limit of spruce in this part of Lapland. In addition, this is substantially earlier than the conventional paradigm of spruce instatement in this northern part of the Scandes, although a stray find of *Picea* pollen have been reported from adjacent regions (Rosén *et al.* 2001).

The early Holocene presence of spruce in the mountain range is sustained also by radiocarbon dates of subfossil wood emanating from still living clonal individuals, with maximum ages of about 9500 cal. yr BP and somewhat younger (Öberg & Kullman 2011b).



**Fig. 12** Cone shell from *Picea abies*, recovered in a peat ball retrieved from the forefield of Storglaciären in northern Lapland, 1105 m a.s.l., which is about 550 m higher than the present spruce tree-line in the region. Source: Kullman & Öberg (2015).

The pattern outlined above, has launched the hypothesis of early postglacial or late glacial spruce instatement to northwestern Scandinavia from cryptic glacial refugia in the west. This concept was originally proposed on the basis of megafossil evidence along the Scandes (Kullman (2000, 2008). Later on it was supported by DNA-analyses of lake sediments and living tree specimens. Taken together, these circumstances prompted speculations that spruce existed on ice-free refugia at

the Norwegian coast or on nunataks during parts of the Weichselian glaciation (Parducci *et al.* 2012a, b; Parducci & Tollefsrud 2016). Influenced by newly available mega- and macrofossil evidence (see above), certain pollen analysts have increasingly tended to support the early postglacial tree immigration option by changing their interpretational paradigm of trace amounts of spruce pollen (e.g. Segerström & van Stedingk 2003; Bergman *et al.* 2004; Giesecke 2005; Hörnberg *et al.* 2006; Paus 2010; Paus *et al.* 2011). Given these quite new results, it is easy to comply with and give credit to early explorers (e.g. Hansen 1929; von Post 1930; Lindqvist 1948), stating that the immigration history of *Picea abies* was an early postglacial phenomenon and more complex than a distinct front moving from east to west in the late Holocene, in contrast to advocates of the traditional paradigm, i.e. step-wise spread from the east (Russia) to western Sweden, only 2000-2500 years ago (Tollefsrud 2008; Seppä *et al.* 2009).

### *Larix sibirica* – a new species in the postglacial arboreal history of Scandinavia

*Larix sibirica*, an eastern species, not currently belonging to the native Scandinavian tree flora, has recently been evidenced by macrofossils (wood and cones) at different sites along the Scandes, between 9145 and 7320 cal. yr BP (Kullman 1998; Kullman 2004a; Öberg & Kullman 2011b; Kullman & Öberg 2013). Its presence at very high elevations is illustrated by a cone extracted from a peat ball at the forefield of an ice patch near Lake Murtsergurein southern Swedish Lapland (Fig. 13). For long, conventional pollen analysis has failed to confirm the presence of *Larix* in Scandinavia during the Holocene (cf. Elven *et al.* 2013). However, recent pollen studies from different parts of the Scandes, performed with a less guarded and conservative attitude, seem to comply with the megafossil record in this respect (Paus 2010; Paus *et al.* 2011; Carcaillet *et al.* 2012).



**Fig. 13** Subfossil cone of *Larix sibirica* contained in an outwash peat ball, retrieved from a snow/ice patch near Lake Murtsergurein, 1125 m a.s.l. Radiocarbon dating yielded 7320 cal. yr BP. Source: Kullman & Öberg (2013).

Apparently, *Larix* had a wider distribution towards the west in Fennoscandia during the early and mid-Holocene. Today, the westernmost and nearest natural stations (relictual?) are on the Kola Peninsula (Kuosmanen *et al.* 2016; Kozhin & Sennikov



2016). Presence of *Larix* near the Russian/Finnish border, as well as documented occurrences at high elevations in the Swedish Scandes during the early Holocene (Kullman 2008, this paper), do suggest a climate more continental than today and refute speculations of westward migration over the mid- and late-Holocene (e.g. Huntley & Birks 1983; Binney *et al.* 2009; Seppä *et al.* 2009).

Currently, young *Larix* saplings, with unknown origin have become established in natural birch-pine forest in Abisko national park, northern Swedish Lapland (Kullman 2015b).

### ***Holocene tree-line, glacier and climate history***

For all three study regions along the Swedish Scandes, the frequency of findings for birch and pine peaked sharply 9600-9000 cal. yr BP, 500-700 m higher than present-day tree-lines (Fig. 14 & 15). A contemporary surge of early tree establishment at high elevations is inferred by studies in other parts of the Scandes (Dahl & Nesje 1996; Aas & Faarlund 2000; Bergman *et al.* 2005; Eide *et al.* 2005; Paus *et al.* 2011).

In northern Lapland, the difference between the previous highest pine tree-line during the Holocene and the present position was interpreted to be 100-150 m, based on pollen analysis (Berglund *et al.* 1996). Drawing on the most recent and adequate estimates in the present study, this figure should be 690 m (Kullman & Öberg 2015). As a rule, pine megafossils attained higher (50 m) relative positions than pine during this early period. The highest position, relative to the present-day tree-line, was a pine megafossil recovered at Kittelglaciären in the Kebnekaise Mts. (Fig. 14). Another "high-flying" megafossil is provided by a birch log at the rim of Murtserglaciären, which dated 9195 cal. yr BP (Fig. 15).



**Fig. 14** Subfossil pine, dated 9010 cal. yr BP, which is emerging from beneath the snow/ice rim, displays the highest recorded position, relative to the present-day tree-line, of all species within the three study regions, viz. 690 m. Kittelglaciären, northern Lapland, 1240 m a.s.l. Source: Kullman & Öberg (2015).



**Fig. 15** Megafossil birch log (9195 cal. yr BP) right at the margin of a snow/ice patch by Murtserglaciären, 1425 m a.s.l., 625 m above the present-day tree-line. Source: Kullman & Öberg 2013.

This relatively high tree-line position during the early Holocene, puts further focus of the inadequacy of the pollen analytical method of vegetation reconstruction. These megafossil results provide an entirely new view on the early postglacial landscape structure in the high mountains, implying e.g. that only the highest peaks were entirely treeless.

Based on the highest records and with a conventional temperature lapse rate of 0.6 °C per 100 m (Laaksonen 1976), it may be tentatively inferred that temperatures were about 4 °C higher than present during the early Holocene. Adjusting for glacio-isostatic land uplift by c. 200 m since 9500-9000 cal. yr BP (e.g. Pässe & Andersson 2005), implies the true tree-line descent throughout the Holocene should be reduced to c. 500 m. This means that the corresponding temperature decline to the present-day may amount to 3.0°C. This is about 1 °C higher than previous estimates, based on megafossils, predominantly recovered outside glacier cirques, in northern Lapland and further south along the Scandes (Kullman 2013). In addition, it appears that this episode represents the Holocene thermal optimum, as inferred also from other recent studies (e.g. Paus 2013; Luoto *et al.* 2014). In contrast, many pollen-based studies suggest a much later thermal optimum in this region (Berglund *et al.* 1996; Seppä & Birks 2002). However, with respect to tree-lines, pollen analysis is considered to yield less accurate results than analyses of megafossils, in particular when tree-lines and palaeoclimate are concerned (Faegri & Iversen 1975; Paus 2013; Elven *et al.* 2013).

These paleotemperatures inferred above, add to a recent trend to place the Holocene thermal optimum to the earliest part of the Holocene (Heikkilä 2010; Paus *et al.* 2011, Paus 2013; Luoto *et al.* 2014; Välranta *et al.* 2015) in likely response to orbital forcing (Milankovitch model) of insolation change as the ultimate temperature driver (Berger 1988). Furthermore, this model predicts a gradual insolation decline and associated broadly consistent summer temperature decline until the late 19th century (cf. Shemesh *et al.* 2001; Marchal *et al.* 2002). The megafossil record reflects this situation by a gradual lowering of the upper limit of progressively younger megafossil tree recoveries throughout the Holocene (Öberg & Kullman 2011a).

Given the tight and overlapping assemblage of tree megafossils around 9600 and about 5000 years onwards, it appears that the studied glaciers/snow patches, did not exist at all or were substantially smaller during this time span (Bakke *et al.* 2005; Nesje *et al.* 2008; Öberg & Kullman 2011; Kullman & Öberg 2013, 2015).

The obtained Holocene temperature decline, manifests a cooling by 0.037°C/century, which matches theoretical estimates (Esper 2012). Consistently for all study regions, the megafossil record is discontinued about 4400-4000 years ago, with birch dominating the last 1000 years or so (Öberg & Kullman 2011a; Kullman & Öberg 2013, 2015). Peat samples, post-dating the final disappearance of trees, indicate that the inception of glaciers took place 3900-3000 cal. yr BP, after a period of absence or minimum extent since at least 9600 cal. yr BP. This late-Holocene break in the tree-line and glacier history, broadly matches the intensification of progressive neoglaciation, as inferred from other studies of processes in the mountain landscape (Karlén & Kuylenskierna 1996; Caseldine & Matthews 1987; Snowball & Sandgren 1996; Bakke *et al.* 2008; Ivy-Ochset *et al.* 2009; Larsson *et al.* 2012; Koch *et al.* 2014). Possibly, however, minor positive excursions of tree-lines and temperature may have occurred during the Holocene (Karlén & Kuylenskierna 1996; Kullman 2013, 2015a), although this is largely beyond the resolution of the present study.

In fact, a solitary pine date, 1950 cal. yr BP, 140 above the present-day tree-line position may indicate a more short-lived and contracted glacier extension during a warmer-than-present interval. An analogous record is reported from Norway (Nesje *et al.* 1991), which further supports an interpretation in terms of a relatively warm episode, as also inferred from other contemporary proxies in various parts of northern Europe (e.g. Ljungqvist 2009; Humlum *et al.* 2011; Esper *et al.* 2012; Luetscher *et al.* 2013).

#### **The vegetation character of the glacier cirques during the early and mid-Holocene**

The forest islands, which during the early and mid-Holocene occupied ice-free glacier cirques, supported mixed tree islands, with predominant *Betula* and *Pinus* and some admixture of *Picea*, *Larix*, *Populus*, *Alnus* and *Sorbus*. Apparently, they had the character of wood islands in a surrounding treeless landscape. The presence of peat, with contained forest floor species, further attests to the character of more or less complete and diverse boreal forest/mire mosaics with some prealpine and subalpine attributes. Characteristic species, found as macrofossils, were *Empetrum hermaphroditum*, *Vaccinium myrtillus*, *Vaccinium vitis-idaea*, *Betula nana*, *Calluna vulgaris*, *Ledum palustre*, *Juniperus communis*, *Rubus chamaemorus*, *Arctostaphylos alpinus*, *Trientalis europaea*, *Pleurozium schreberi*, *Dicranum spp.*, *Sphagnum spp.* (Kullman & Öberg 2013).

It may seem strange that sites which until the late Holocene supported great expanses and accumulations of ice and snow supported early postglacial "oases" of boreal trees and understorey forest plant species. However, in the absence of snow and ice, many high-alpine cirques may offer favourable environmental conditions for plant growth (Elven 1978, 1980;

Anderson *et al.* 2009; Scherrer & Körner 2011). Parabolic and dark back walls may optimize local radiation heating. Wind shelter, ample snow cover/moisture further accentuate the congenial premises. Striking support for this contention is provided by a young, 1.5 m tall rowan (*Sorbus aucuparia*) growing on a cliff ledge, 1600 m a.s.l. in the cirque of Tempelglaciären, 700 above the local tree-line (Öberg & Kullman 2011a). Further testimony for particularly favorable conditions in the steep slopes of some glacier cirques is provided by young saplings of boreal tree species, as evidenced in many studies (Olsson 1967; Elven 1973; Holtmeier 1974; Kullman 2004b, c, 2010b). Accumulation of wind-driven snow, i.e. an integral quality of the concerned habitat, is accompanied by concentration of different propagule, which contribute to the floral enrichment.

The concerned early postglacial tree enclaves at high elevations may have functioned as dispersal nodes in the process of the early Holocene downslope forestation of the alpine landscape (cf. Allen & Huntley 1999; Kullman & Kjällgren 2000; Kullman 2002; Carcaillet *et al.* 2012). It has been argued that these sites, when ice-covered during glacial phases, may have harboured refugial tree populations, growing on debris-covered glacier ice (Richter *et al.* 2004; Fickert *et al.* 2007).

## **CONCLUSIONS**

- Recent melting of alpine glaciers and snow/ice patches (high above current tree-lines) reveals previously hidden deposits of megafossil trees, which grew here when no glaciers existed.
- The species assemblage comprises most currently occurring boreal tree species in the region; *Betula pubescens*, *Pinus sylvestris*, *Picea abies*, *Sorbus aucuparia*, *Populus tremula*, *Alnus incana*. The earliest occurrences of trees were during the Late Glacial, 16 800-13 000 cal. yr BP. Later on, the frequency of megafossils clustered at 9600-9000 cal. yr BP. During this period trees grew almost 700 m higher upslope than today, which could imply summer temperatures 3.0 °C higher than current standards (early 21st century).
- The currently non-native *Larix sibirica* prevailed quite frequently along the Scandes at high elevations during the early Holocene. Previously, pollen analysis had entirely failed to identify presence of *Larix* in Fennoscandia during the Holocene.
- Taken together, the results presented and reviewed in this study, provide a fundamentally new view on the early-Holocene alpine/subalpine vegetation composition and altitudinal differentiation, which cannot be obtained by the traditional interpretational paradigm of pollen stratigraphical studies, many of which need reconsideration. For sure, those days are gone, when pollen analysts could claim interpretative prerogative within the realm of vegetation history.

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