

MEGAFOSSIL TREES REVEAL PAST LANDSCAPES OF THE SWEDISH SCANDES

Maria Sofia Andersson and Olof Erik Johansson

Department of Ecology and Environmental Science, Umeå University, SE 901 87 Umeå, Sweden

Abstract: The structure and plant species composition of Late-glacial and Early-Holocene landscapes in the Swedish Scandes are poorly understood. Traditional pollen analytical inferences, glacier histories, and textbook narratives are beset with inaccuracies and uncertainties, particularly in high-mountain regions. More direct, robust, and reliable mega- and macrofossil records provide unambiguous evidence of the former early local presence of tree species at specific sites and elevations, far beyond modern treelines.

Keywords: Megafossils, Treelines, Holocene, Scandes, Climate, Plant species

Introduction

The structure and plant species composition of Late-glacial and Early-Holocene landscapes in the Swedish Scandes are poorly comprehended. In this respect, traditional pollen analytical inferences, glacier histories and textbook narratives are beset with inaccuracies and uncertainties, particularly in high-mountain regions (e.g. Lundqvist 1969; Huntley & Birks 1983; Berglund et al. 1996; Karlén & Kylenstierna 1996; Barnekow 1999; Johnsen 2010). These methodological shortcomings are evidenced by analyses of more direct, robust and reliable mega- and macrofossil records (cf. Helama et al. 2004; Paus 2013; Paus & Haugland 2017; Kullman 2017a). Unambiguously, these approaches are stating former early local presence of tree species at specific sites and elevations, far beyond modern treelines.

Megafossil¹ tree remains, representing former higher-than-present alpine treelines, mainly preserved in peat and lake mud, have for long been known and discussed in the Scandes. These records have contributed broad outlines of the Holocene history of high mountain landscape and climate evolution (Smith 1920; Lundqvist 1969; Karlén 1976; Kullman 1995; Aas & Faarlund 2000; Kullman & Kjällgren 2000, 2006). However, studies of this kind are constrained by sparsity of peat as an efficient preservation medium at high elevations, which has urged for alternative megafossil archives when searching for the highest positions of tree growth during earlier epochs.

¹Megafossils are large pieces of wood, which are preserved near their growth places and which can be accurately determined to species and dated by the ¹⁴C-method. Ages are reported as calendar years BP (AD 1950), by intercept-values, and derive from sources, cited above.

Megafossil records, originating from different elevations above the modern treeline, have displayed a discernible trend of treeline lowering throughout the Holocene, about 50 m per millennium (Kullman 1995; Kullman & Kjällgren 2000), in broad agreement with orbital forcing of insolation at the top of the atmosphere (Berger & Loutre 1991). Since this mechanism suggested a thermal maximum somewhat prior to the earliest and highest existing records, further search for megafossil wood remnants was extended to even higher elevations.

Particular focus was on the fringes of currently melting glaciers and snow/ice patches along the entire Swedish Scandes (Fig.1). In addition, these efforts were inspired by positive results, based on megafossils, from emerging proglacial sites worldwide, showing that forest trees had prevailed at sites until recently covered by ice, during earlier parts of the Holocene, (Nicolussi & Patzelt 2000; Schlüchter & Jörin 2004; Benedict et al. 2008; Ivy Ochs et

al. 2009; Koch et al.2014). Prior to the studies reviewed in this study, no such discoveries had been reported from the Scandes.

Results of these recent investigations, carried out in different parts of the Swedish Scandes, constitute the main core of this paper. The present review upsets the traditional comprehension of the late-glacial and early postglacial climate as well as the structure and composition of the high-elevation landscape (cf. Paus 2013; Kullman 2013; Luoto et al. 2014; Väiliranta et al. 2015; Schenk et al. 2018). Possibly, the emerging views may serve as proxy analogues of future subalpine landscapes in a potentially warmer world. In fact, the initial phase of such a course of change may be already underway in the Swedish Scandes (Kullman 2010, 2019). However, such projections should be treated cautiously, since future directions of the climate evolution remain uncertain.



Figure 1. Subfossil pine, which inspired search for megafossils at exceptionally high elevations, particularly on the forefields of receding glaciers. The lower fringe of the glacier “Sylglaciären”, 1195 m a.s.l., about 400 m higher than the present treeline. Radiocarbon yielded 10 425 cal. yr BP. Photo: 1997-07-16. Source: Kullman&Kjällgren 2000.

Results Late-Glacial and early-Holocene trees as evidenced by megafossils-the new landscape perspective

All main tree species of the current treeline ecotone were present on what has to be interpreted as ice-free nunataks (Fig. 2-5) already at the Late-Glacial/Early-Holocene transition, 17 000- 13 000 years before the present day (BP) at unprecedented high elevations along the entire Swedish Scandes (Kullman&Kjällgren 2000; Kullman 2002, 2004). These species are mountain birch (*Betula pubescens* ssp. *czerepanovii*), Norway spruce (*Picea abies*) and Scots pine (*Pinus sylvestris*). Henceforth, these will be cited as *Betula*, *Picea* and *Pinus*, respectively.

The core site for discovery of the earliest tree megafossils is Mt. Åreskutan (1420 m a.s.l.) in the southern Swedish Scandes (province of Jämtland), 1360 m a.s.l. and 510 m above the treeline of pine. This mountain has, close to its summit, until quite recently, harboured an ice patch or a small glacier, which has gradually vanished in response to 20th century climate warming and consequently megafossil trees have been exposed (Figs. 2 & 3).

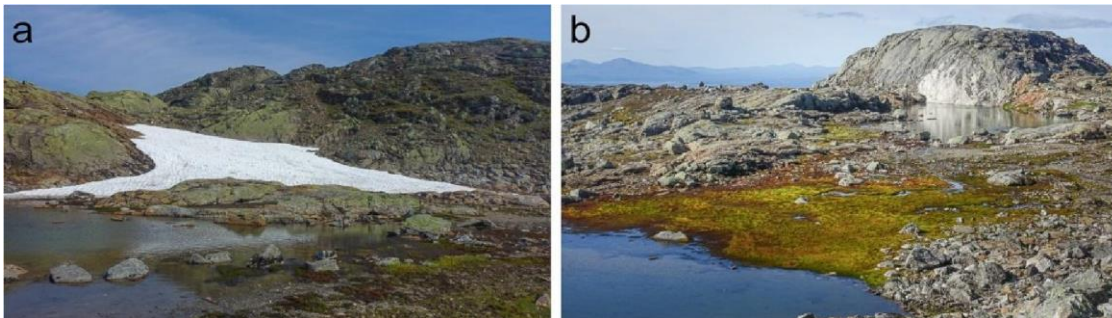


Figure 2. *Locus classicus*, 1360 m a.s.l., the site for the discovery of Late-glacial and Early-Holocene tree presence on early emerging nunataks in the Scandes (Kullman 2002). These findings have changed the conception of the earliest subalpine/alpine landscape-history. **a.** A small glacier/ice patch prevailed here until quite recently. Its former position is indicated by the snow patch and the row of blocks in the foreground. The snow has completely melted by the end of late summer during most years of the past few decades. Photo: 2018-07-18. **b.** The former ice-distribution embraced the green moss-covered area in the center. Here, most of the megafossils have been recovered, reasonably dislocated downslope by snow avalanches from higher upslope positions. Photo: 2018-09-01.



Figure 3. Overview of the earliest megafossils recovered at the Åreskutan-site, 1360 m a.s.l. **a.** *Pinus sylvestris*, 13 810 cal. yr BP. **b.** *Picea abies*, 13 010 cal. yr BP. **c.** *Betula pubescens* lat., 16 810 cal. yr BP. These samples highlight earlier local deglaciation and tree instatement than previously inferred by more traditional approaches. Source: Kullman 2002.



Figure 4. Examples of Late-Glacial megafossil tree recoveries at sites along the entire Swedish Scandes. **a.** The glacier Helagsglaciären (province of Härjedalen), has receded areally by c. 40% during the past 100 years. Photo: 2015-08-13. **b.** Close to its former lower maximum range, 1150 m a.s.l., megafossils of *Pinus* were recovered and dated 13 145 cal. yr BP. Photo: 2008-07-04. Source: Kullman&Kjällgren 2000.**c.** The glacier Tärnaglaciären (province of Lapland). Currently, a large snow-field prevails in the mid-slope below the glacier, which extended down to the mid of the lake (1070 m a.s.l.) about 100 years ago(Lindgren &Strömgren 2001). Photo:2010-08-20. **d.** Preserved in a downwashed peat-cake 630 m a.s.l., a cone of *Picea* was dated 11 200 cal. yr BP. Photo: 2017-09-01. **e.** The glacier Kårsaglaciären, 965 m a.s.l. (province of Lapland). Photo: 2009-08-21. **f.** A megafossil remnant of *Pinus* appeared in the outwash stream from beneath the glacierKårsaglaciären, 955 m a.s.l. It dated 11 760 cal. yr BP. Photo: 2008-09-17. Source: Öberg &Kullman 2011.**g.** Mt. Stådjan (province of Dalarna), 1100 m a.s.l. **h.** Megafossil*Pinus* protruding from a thin soil layer between boulders in the south-facing slope of Mt. Stådjan. Dating yielded 12 425 cal. yr BP. Photo: 2007-07-14.

The firm evidence, presented above, conflicts with traditional glacial geologic and paleobotanical opinions and have been questioned and opposed by proponents and defenders of these approaches, drawing on negative evidence (Birks et al. 2005) and refuted by Kullman (2006).

Holocene megafossils in their settings

Below, a representative sample of megafossils recovered in geomorphic glacial cirques, with currently receding ice cover,is presented. This is a comprehensive and richly illustrated review of previously published data and updates, representing the Swedish Scandes, from south to north (Öberg & Kullman 2011, Kullman & Öberg 2013, 2015; Kullman 2017a,b) (Figs. 5-20). A popular overview is given by Kullman & Öberg (2019). Surprisingly, little research on these issues has been carried out in Scandinavia by palaeoecologists, although archaeologists, particularly in Norway, are making rich findings of human artifacts on the forefields of melting glaciers and ice patches (e.g. Nesje et al. 2011).

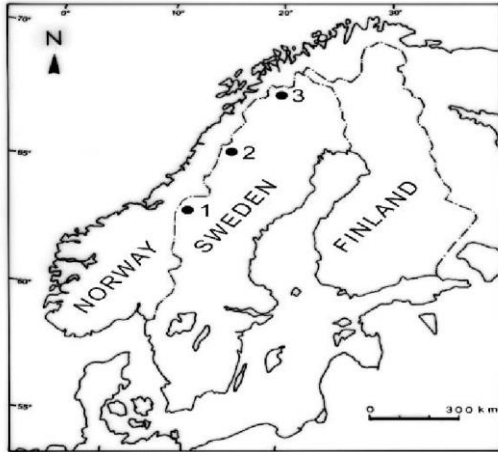


Figure 5. The position of the glacier sites, particularly focused in this review. 1. Helags-Sylarna glaciers. 2. The glacier Tärnaglaciären with adjacent ice patches. 3. Glaciers and snow/ice patches in northern Lapland.

1. Helags-Sylarna glaciers



Figure 6. Downwashed stem of *Betula*, 1345 m a.s.l., which dated 8620 cal. yr BP. Mt. Helagsfjället. Photo: 201008-11.



Figure. 7. Subfossil *Betula*, extracted from eroding moss-cover in a downstream proglacial delta below the glacier, 1350 m a.s.l. Dating yielded 9520 cal. yr BP. Mt. Helagsfjället. Photo: 2006-10-15.

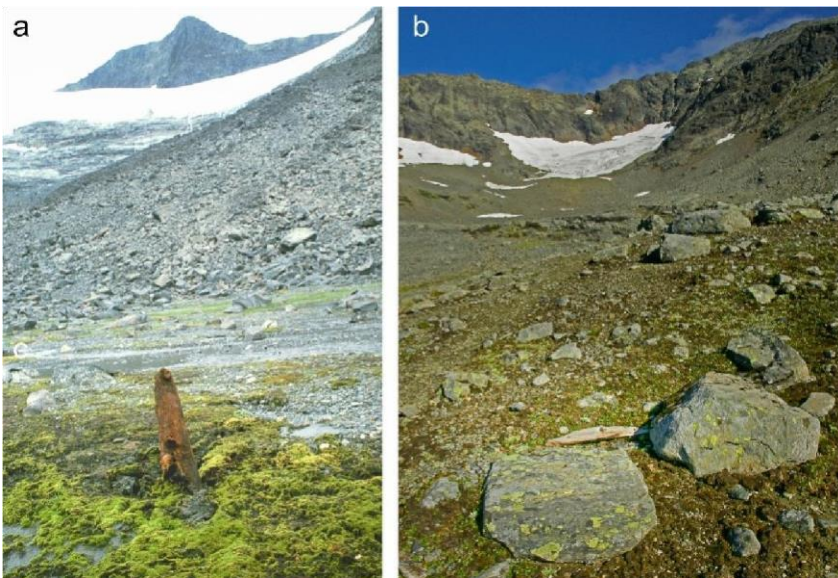


Figure 8.a. Remnant of a fairly stout *Betula*-tree, uplifted from beneath the moss-cover in the delta below Storsylglaciären, 1275 m a.s.l. Presumably, the original growth position was higher upslope. Dating yielded 7170 cal. yr BP. Photo: 2001-08-22. b. A downwashed *Pinus*-remnant, 1210 m a.s.l., recovered well below its assumed original growth position, underneath the background Ekorrglaciären. Radiocarbon-dating gave 9530 cal.yr BP. Photo: 2008-08-24.

2. The glacier Tärnaglaciären with adjacent ice patches



Figure 9. “High-flying” *Betula*-megafossil at the margin of an ice-patch adjacent to Tärnaglaciären, 1425 m a.s.l. This is 635 m higher than the current local treeline. Dating yielded 9195 cal. yrBP. Murtsergure ice patch. Photo: 2012-08-28.



Figure 10. Piece of a *Betula*-stem, recovered 1410 m a.s.l., 700 m higher than the nearest present-day treeline. It is currently being washed downslope from a growth place close to an ice-patch, adjacent to the glacier Tärnaglaciären. It dated 9365 cal. yr BP. Photo: 2017-09-01.



Figure 11. *Betula*-megafossil, protruding from the snow rime at the glacier front, 1395 m a.s.l. This site is 685 m higher than the current local treeline. Dating yielded 9450 cal. yr BP. The glacier Tärnaglaciären. Photo: 2017-0901.



Figure 12. A virtually new source of past high-mountain vegetation composition is provided by outwashed "peatballs" of this kind. Here uplifted from behind a stone in the main melt-water stream. Their content of plant remains represents some of the former plant cover composition where ice prevailed until quite recently (see Fig.13). Ice-patch near the glacier Tärna-glaciären, 1115 m a.s.l. Photo: 2012-09-22.

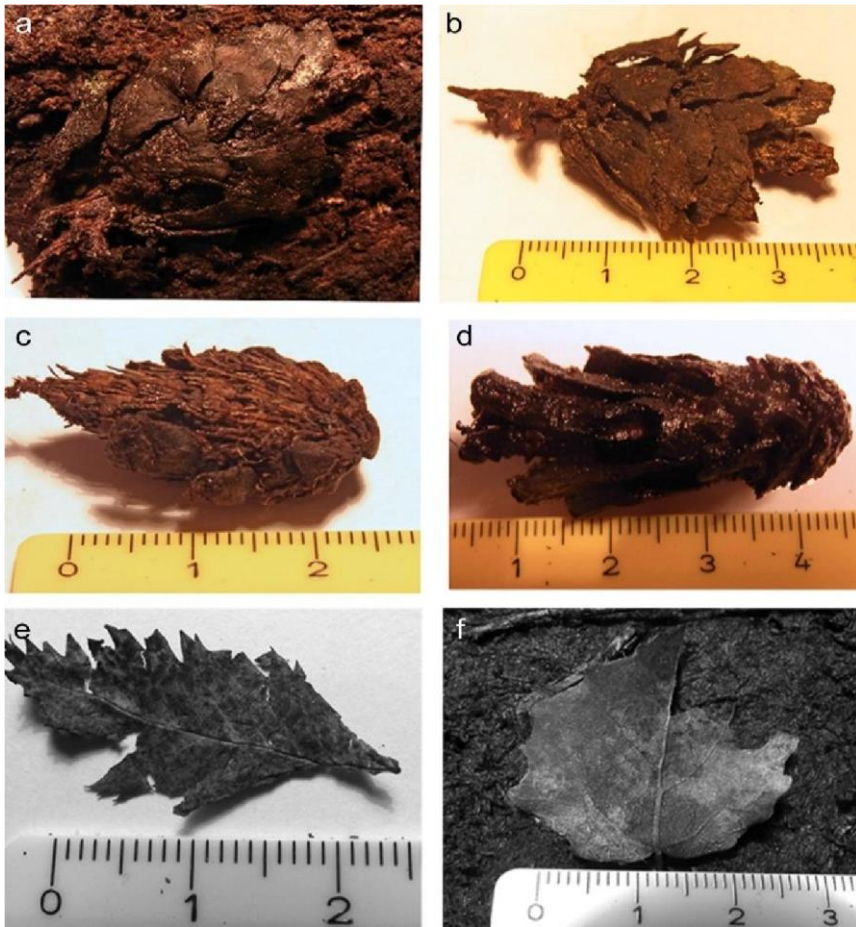


Figure 13. Tree remains of different species contained in “peat balls”, released from beneath glacier ice in the Tärna region (source: Kullman& Öberg 2013). Except for common forest bryophytes and dwarf-shrubs, cones of *Larix sibirica* and *Picea abies* as well as leaves of deciduous boreal tree species, have been extracted and radiocarbon dated; **a. b.** *Larix sibirica*, 7320 cal. yr BP. **c.** *Picea abies*, 8450 cal. yr BP. **d.** *Pinus sylvestris*, 7960 cal. yr BP. **e.** *Sorbus aucuparia*, 8460 cal. yr BP. **f.** *Populus tremula* 8590 cal. yr BP.

3. Glacier and snow/ice patches in northern Lapland



Figure 14. Trunk of *Pinus*, dug out from glacier sediment, 940 m a.s.l. Obviously, it is worked by beaver (*Castor fiber*), indicative of a local forest environment at the dated time; 9280 cal. yr BP. The glacier Kårsaglaciären. Photo: 2008-09-17.



Figure 15. Megafossil remains of *Betula*, exposed just outside the lower glacier margin and much higher than the present local treeline, 990 m ö.h. They date 1950 cal. yr BP and support a general conception of a warmer-than-present time, with a smaller glacier (Kullman 2013). The glacier Kårsaglaciären. Photo: 2013-09-12.



Figure 16. **a.** The glacier Kåppasglaciären, c. 9 km west of Abisko in Swedish Lapland. Today, it should possibly be characterized as an ice-field. It released a megafossil *Pinus* at its lower margin, 1030 m a.s.l. **b.** Dating yielded 7860 cal. yr BP. Photo: 2010-08-28



Figure 17.**a.** An elongated snow/ice patch, located c. 15 km northwest of Abisko, extending 975-980 m a.s.l. At the lower margin, an extensive stone pavement indicates a prior more extensive size of this object. The front is currently disintegrating by “calving”, which exposes new mineral ground with some emerging megafossil tree remans. Photo: 2010-08-30.**b.** Megafossil *Pinus*, dated 8900 cal. yr BP, up-raised from original position. Photo: 2010-08-30.**c.** Basal part of a *Betula*-stem, possibly preserved *in situ*, 975 m a.s.l. Radiocarbon-dating gave 5800 cal. yr BP. Låktatjåkka Ice Field. Photo: 2010-08-30.

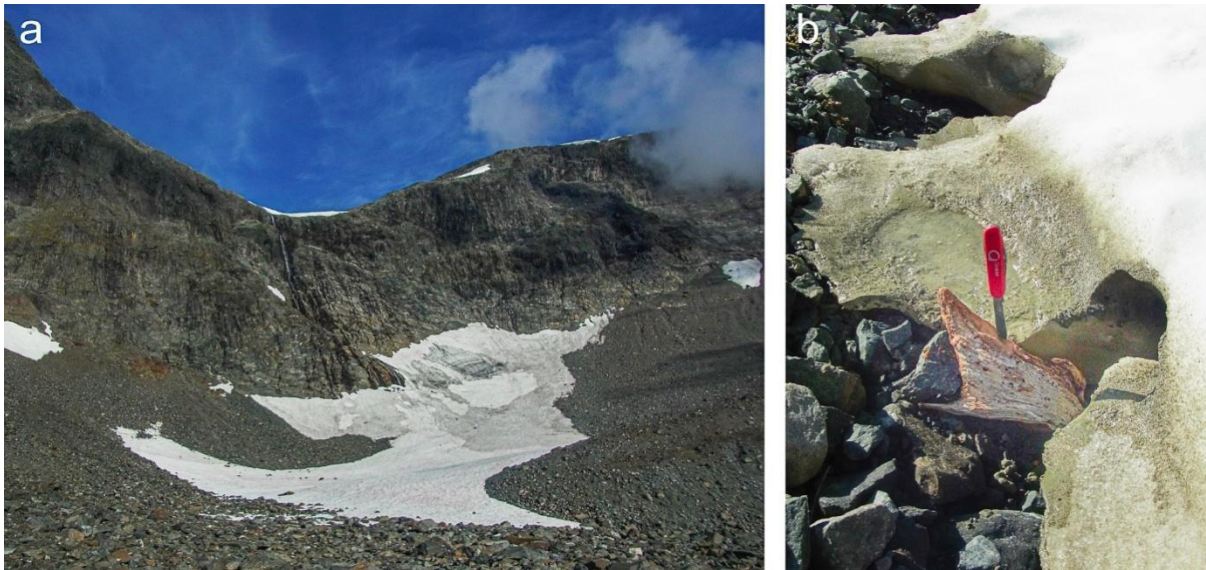


Figure 18.**a.** The glacier Kitteldalsglaciären in the Kebnekaise-massif. The lower front is about 1190 m a.s.l. Megafossils of *Pinus* and *Betula* are recovered along the right-hand (east-facing) margin of the glacier. Photo: 201308-11.**b.** *Pinus*-log melting out from the glacier, 1240 m a.s.l. It dated 9010 cal. yr BP and is located 690 m higher than the local present-day treeline. Photo: 2013-08-11.



Figure 19. The glacier Storglaciären in the Kebnekaise-massif is one of the most thoroughly investigated glaciers in the Swedish Scandes, although mainly with respect to size and mass balance changes. About 100 years ago the lower front was close to the lake, c. 1115 m a.s.l. (cf. Holmlund 2012). Photo: 2013-08-13

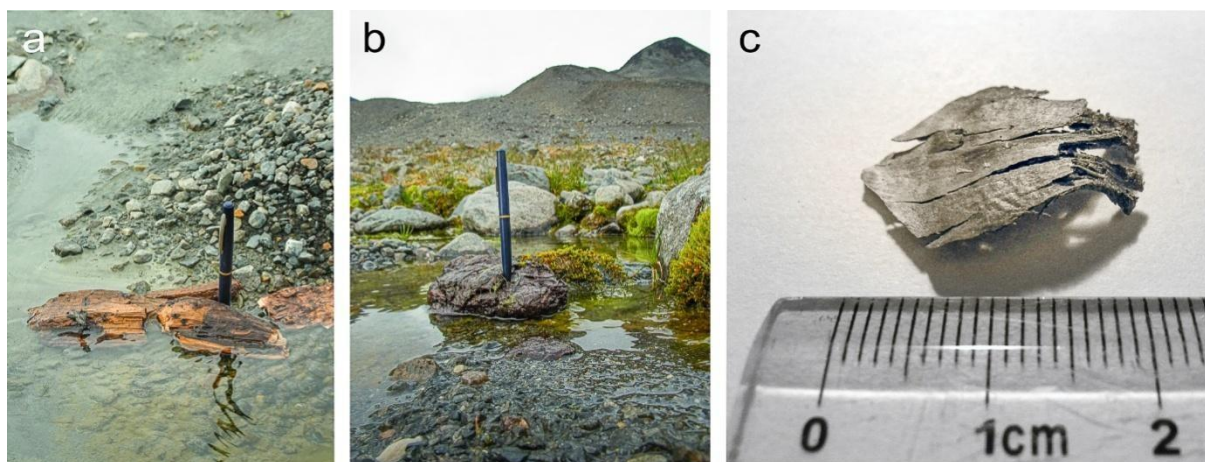


Figure. 20. **a.** Megafossillog of *Betula*, which dated 8490 cal. yr BP, 1100 m a.s.l. Photo: 2013-08-30. **b.** Downwashed peat cake, containing a *Picea* cone shell, 1105 m a.s.l. Photo: 2013-08-13. **c.** A *Picea* cone shell dated 8380 cal. yr BP. The glacier Storglaciären.

Synthesis and discussion

Demonstrably, alpine glaciers along the entire Scandes have been melting over much of the past century (Lundqvist 1969; Holmlund et al. 1996, Bakke et al. 2008). At their lower fronts, mega fossil tree remnants of different species are currently exposed. Radiocarbon-dated, these samples provide a new view of the Late Glacial and Early-Holocene high mountain landscape. It now stands out, that along the entire Swedish Scandes, all of our common tree species grew in small isolated populations, much earlier and at higher positions, than ever evidenced or contemplated. Main features are quantified and summarized in Table 1. The highest relative treeline positions and reasonably, the highest summer temperatures were attained 10 000-9500 cal. yr BP. This inference agrees with temperature reconstructions from other northern regions (e.g. Shenk et al. 2020; Mörner et al. 2020)

The discussion below draws on an “amalgam” of previously published original studies, based on megafossils retrieved from glacier forefields (Kullman 2004; Öberg & Kullman 2011, Kullman & Öberg 2013, 2015; Kullman 2017a,b). These references provide additional detail and documentation to the images, which make up the core of this paper.

Table 1. For each of the study sites (Fig. 5), age range of all megafossils, given as cal. yr BP, and corresponding relative elevation range of sample sites, displayed as altitudinal meters above the current treeline.

Site	Age-range	Relative elevation range
1	16 810-6100	115-585
2	9530-4480	225-700
3	11 760-1950	80-690

A particular noteworthy novelty is that boreal trees grew at sites of present-day glaciers already during the Late-Glacial as early as about 17 000-12 000 years before the present. Analogous inferences are presented from the Norwegian Scandes (Paus et al. 2011). Taken together, these discoveries have a bearing both on glacier and vegetation history. The common wisdom, until present, has been that the high mountains were completely icecovered at this early stage (Lundqvist 1986, 1994), a view questioned (e.g. by Dahl et al. 1997; Follestad 2003; Hörnberg et al. 2006; Goeringa et al. 2008), and certainly not compatible with the presence of trees, if not assuming supraglacial tree growth. In fact, the last-mentioned option is discussed by different authors (Fickert et al. 2007; Zahle et al. 2018).

The ice-free glacier cirques displayed the character of outlying forest enclaves, high above the closed and continuous forest below. Prior to 10 000 BP, the dated samples are too few to form definite opinions about the relative abundance of *Betula*, *Pinus* and *Picea* in the concerned habitats, although all three species were present at high elevations during that period, as evidenced by this review. Possibly, the contemporary sparsity of recoveries related to still incomplete deglaciation and relatively small areas available for tree growth on the nunataks.

Since about 10 000 years BP, *Betula* appears to have formed the upper treeline in these habitats, although *Pinus* is found to have joined *Betula* at the highest elevations, 600-700 m above current treelines, as these appeared during the past 10 years or so (Kullman & Öberg 2009; Kullman 2013). Except for the dominating tree species particularly focused and depicted in this study, the early tree vegetation contained an array of sub-ordinate boreal tree species, which today prevail sparsely in the mountain forest below. These species are *Sorbus aucuparia*, *Alnus incana* and *Populus tremula*, all documented by megafossils (Kullman & Öberg 2013, 2015).

Presumably, the Late-glacial and Early-Holocene nunatak tree groves may have served as dispersal nodes for trees and other plants, enabling their rapid subsequent downslope spread and establishment over the ice-free landscape as it gradually emerged (cf. Väliiranta et al. 2011, 2015).

It is of particular interest to find that, *Picea abies* occurred on a regular basis and at unprecedented high elevations above its current treeline, and so even during the Late-Glacial. This contrasts with the orthodox view (based on pollen analysis) of spruce as a particularly late postglacial immigrant to western and high-elevation Sweden (Moe 1970; Giesecke & Bennett 2004; Seppä et al. 2009). Encouraged by the megafossil evidence presented above, some researchers, drawing on microfossils and DNA-technique, support the option of early Holocene presence of *Picea* in the high-mountains (Segerström & von Stedingk 2003; Hörnberg et al. 2006; Paus 2010; Paus et al. 2011; Parducci et al. 2012; Carcaillet et al. 2012). In addition, during the early Holocene, the concerned tree groves harboured a tree species not growing spontaneously in Sweden today, namely *Larix sibirica* (Kullman 2018), which also occurred outside the present kind of habitats along the entire Scandes, both in Sweden and Norway (Kullman 1998; Bergman et al. 2004; Paus 2010; Carcaillet et al. 2012). Possibly this light-demanding species was outcompeted by advancing denser populations of *Betula* and *Picea* by the mid-Holocene, as these species were favored by the evolving Neoglacial climate, which then turned to a more oceanic and snow-rich character (cf. Kullman 2018). By analogy with the rich tree flora, it is reasonable to assume that plant species richness in general was high in these, obviously sparse high-elevation tree stands. This gains support from analyses of plant remains in peat-cakes released from beneath the glacier ice (cf. Kullman & Öberg 2013, 2015). The presence of tree assemblages is suggested also from the fact that beaver (*Castor fiber*), an obligate forest dweller, utilized trees growing in these sites (Fig. 14).

Tentatively, the maximum difference by 700 m between the early-Holocene treeline position and the present treeline may be translated into summer temperature change decline over this period of time. Based on a general temperature lapse rate of 0.6 °C per 100 m altitude (Laaksonen 1976), it may be inferred that the temperature has lowered by 4.2 °C since 9500 cal. yr ago. However, this figure, has to be adjusted due to the effect of subsequent glacio-isostatic land uplift, which here may be in the order of 200 m (Påsse&Andersson 2005). This reduces the figure on which temperature change may be calculated to 500 m and consequently a temperature 3.0 °C higher than at the present day.

A warmer climate in the future, as commonly alleged, may turn the high mountain landscape into a state envisioned by the findings for the early Holocene, as depicted in this study. Tentatively, this implies a highmountain landscape, virtually without glaciers and large late-lying snow/ice patches. The former sites of these elements are likely to stand out as isolated treed oases high above the continuous forest. The surrounding more wind-exposed and snow-poor terrain remains virtually untreed, by analogy with the reluctance of trees and forests to colonize this type of habitats in response to the warming of the past 100 years (Kullman & Öberg 2009).

References

- Aas, B. &Faarlund, T. 2000. Forest limits and the subalpine birch belt in North Europe with focus on Norway. *AmS-Varia* 37, 103-147.
- Bakke, J., Lie, Ø., Dahl, S.O., Nesje, A. &Bjune, A.E. 2008. Strengths and spatial pattern of the Holocene wintertime westerlies in the NE Atlantic region. *Global and Planetary Change* 60, 28-41.
- Barnekow, L. 1999. Holocene tree-line dynamics and inferred climatic changes in the Abisko area, northern Sweden, based on macrofossil and pollen records. *The Holocene* 9(3), 253-265.
- Benedicht, J.B., Benedicht, R.J., Lee, C.M. & Staley, D.M. 2008. Spruce trees from a melting ice patch: evidence for Holocene climatic change in the Colorado Rocky Mountains, USA. *The Holocene* 18, 1067-1076.
- Berger, A. &Loutre, M.F. 1991. Insolation values for the climate of the last 10 million years. *Quaternary Science Reviews* 10, 297-317.
- Berglund, B., Barnekow, L., Hammarlund, D., Sandgren, P. & Snowball, I.F. 1996. Holocene forest dynamics and climate changes in the Abisko area, northern Sweden – the Sonesson model of vegetation history reconstructed and confirmed. *Ecological Bulletins* 45, 15-30.
- Bergman, I., Olofsson, A., Hörnberg, G., Zackrisson, O. &Hellberg, E. 2004. Deglaciation and colonization; pioneer settlements in northern Fennoscandia. *Journal of World Prehistory* 18, 155-177.
- Birks, H.H., Larsen, E. & Birks, H.J.B. 2005. Did tree-*Betula*, *Pinus* and *Picea* survive the the last glaciation along the west coast of Norway? A review of the evidence in light of Kullman (2002). *Journal of Biogeography* 32, 1461-1471.
- Carcaillet, C., Hörnberg, G. &Zackrisson, O. 2012. Woody vegetation, fuel and fire track the melting of the Scandinavian ice-sheet before 9500 cal.yr BP. *Quaternary Research* 78(3), 540-548.
- Dahl, S.O., Nesje, A. &Øvstedal, J. 1997. Cirque glaciers as morphological evidence for a thin Younger Dryas ice sheet in east-central southern Norway. *Boreas* 26, 161-180.
- Fickert, T., Friend, D., Grüniger, F., Molina, B. & Richter, M. 2007. Did debris-covered glaciers serve as Pleistocene refugia for plants? A new hypothesis derives from observations of recent plant growth on glacier surfaces. *Arctic, Antarctic, and Alpine Research* 39, 245-257.
- Follestad, B. 2003. Development of minor late-glacial ice domes east of Opdal, Central Norway. *NorgesGeologiskeUndersøkelseBulletin* 441, 39-49.

- Goehringa, B.M., Brook, E.J., Linge, H., Raisbeck, G.M. & Yiou, F. 2008. Beryllium-10 exposure ages of erratic boulders in southern Norway and implications for the history of the Fennoscandian Ice Sheet. *Quaternary Science Reviews* 27, 320-336.
- Helama, S., Lindholm, M., Timonen, M. & Eronen, M. 2004. Dendrochronologically dated changes in the limit of pine, northwest Finland during the past 7.5 millennia. *Boreas* 33, 250-259.
- Holmlund, P., Karlén, W. & Grudd, H. 1996. Fifty years of mass balance and glacier front observations at the Tarfala Research Station, *Geografiska Annaler* 78A, 105-114.
- Hörnberg, G., Bohlin, E., Hellberg, E., Bergman, I., Zackrisson, O., Olofsson, A. & Wallin, J.-E. 2006. Effects of Mesolithic hunter-gatherers on local vegetation in a non-uniform glacio-isostatic land uplift area, northern Sweden. *Vegetation History and Archaeobotany* 15, 13-26.
- Huntley, B. & Birks, H.J.B. 1983. An atlas of past and present pollen maps for Europe: 0-13000 years ago. Cambridge University Press, Cambridge.
- Ivy-Ochs, S., Kerschner, H., Maisch, M., Cristl, M., Kuabik, P. W. & Schlüchter, C. 2009. Latest Pleistocene and Holocene glacier variations in the European Alps. *Quaternary Science Reviews* 28, 2137-2149.
- Johnsen, T.F. 2010. Late Quaternary ice sheet history and dynamics in central and southern Scandinavia. PhD thesis, Stockholm University, Sweden.
- Karlén, W. 1976. Lacustrine sediments and tree-limit variations as indicators of Holocene climatic fluctuations in Lappland, northern Sweden. *Geografiska Annaler* 55A, 29-63.
- Karlén, W. & Kuylénstirena, J. 1996. On solar forcing of Holocene climate: Evidence from Scandinavia. *The Holocene* 6(3), 359-365.
- Koch, J., Clague, J.J. & Osborn, G. 2014. Alpine glaciers and permanent ice and snow patches in western Canada approach their smallest sizes since the mid-Holocene consistent with global trends. *The Holocene* 24(2), 1639-1648.
- Kullman, L. 1995. Holocene tree-limit and climate history from the Scandes Mountains, Sweden. *Ecology* 76, 2490-2502.
- Kullman, L. 1998. Palaeoecological, biogeographical and palaeoclimatological implications of early Holocene immigration of *Larix sibirica* Ledeb. into the Scandes Mountains, Sweden. *Global Ecology and Biogeography Letters* 7, 181-188.
- Kullman, L. 2002. Boreal tree taxa in the central Scandes during the Late-Glacial: implications for Late-Quaternary forest history. *Journal of Biogeography* 29, 1117-1124.
- Kullman, L. 2004. Early Holocene appearance of mountain birch (*Betula pubescens* ssp. *tortuosa*) at high elevations in the Swedish Scandes: megafossil evidence exposed by recent snow and ice recession. *Arctic, Antarctic, and Alpine Research* 30, 172-180.
- Kullman, L. 2006. Late-glacial trees from arctic coast to alpine tundra. *Journal of Biogeography* 33, 376.
- Kullman, L. 2010. A richer, greener and smaller alpine world: review and projection of warming-induced plant cover change in the Swedish Scandes. *Ambio* 39, 159-169.
- Kullman, L. 2013. Ecological tree line history and palaeoclimate – review of megafossil evidence from the Swedish Scandes. *Boreas* 42, 55-567.
- Kullman. 2017a. Melting glaciers in the Swedish Scandes provide new insights into palaeotree line performance. *International Journal of Current Multidisciplinary Performance* 3(3), 607-618.

- Kullman, L. 2017b. Further details on Holocene treeline, glacier/ice patch and climate history in Swedish Lapland. *International Journal of Research in Geography* 3(4), 61-69.
- Kullman, L. 2018. *Larix* an overlooked taxon in boreal vegetation. A review with perspective on incongruencies between megafossil and pollen records. *Geo-Öko* 39, 90-110.
- Kullman, L. 2019. Early signs of a fundamental subalpine ecosystem shift in the Swedish Scandes – the case of the pine (*Pinussylvestris* L.) treeline ecotone. *Geo-Öko* 40, 122-175.
- Kullman, L. & Kjällgren L. 2000. A coherent postglacial tree-limit chronology (*Pinussylvestris* L.) for the Swedish Scandes: aspects of paleoclimate and "recent warming", based on megafossil evidence. *Arctic, Antarctic and Alpine Research* 32, 419-428.
- Kullman, L. & Kjällgren L. 2006. Holocene pine tree-line evolution in the Swedish Scandes: Recent tree-line rise and climate change in a long-term perspective. *Boreas* 35(1), 159-168.
- Kullman, L. & Öberg, L. 2009. Post- Little Ice Age tree line rise and climate warming in the Swedish Scandes: a landscape ecological perspective. *Journal of Ecology* 97, 415-429.
- Kullman, L. & Öberg, L. 2013. Melting glaciers and ice patches in Swedish Lapland provide new insights into the Holocene arboreal history. *Geo-Öko* 33, 121-146.
- Kullman, L. & Öberg, L. 2015. 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. *Arctic* 68(2), 141-152,
- Kullman, L. & Öberg, L. 2019. Smältandeglaciärer – fornatiders klimat, trädochskogar. Förlag BoD, Stockholm.
- Laaksonen, K. 1976. The dependence of mean air temperature upon latitude and altitude in Fennoscandia. *Annales Academiae Scientiarum Fennicae* A3 199, 1-19.
- Lundqvist, J. 1969. Beskrivning till jordartskarta över Jämtlandslän. Sveriges Geologiska Undersökning Ser. Ca 4, 1418,
- Lundqvist, J. 1986. Late Weichselian glaciation and deglaciation in Scandinavia, *Quaternary Science Reviews* 5, 269-292.
- Lundqvist, J. 1994. Inlandsisens avsmältning. In: *Berg och Jord. Sveriges Nationalatlas*. Bra Böcker, Höganäs, pp, 124-131.
- Luoto, T.P., Kaukolehto, M., Weckström, J., Korhola, A. & Väliranta, M. 2014. New evidence of warm early Holocene summers in subarctic Finland based on an enhanced regional chironomid-based temperature calibration model. *Quaternary Research* 81 (1), 50-62.
- Moe, D. 1970. The post-glacial immigration of *Picea abies* into Fennoscandia. *Botaniska Notiser* 123, 61-66.
- Mörner, N.A., Solheim, J.-E., Humlum, O. & Pedersen, S.I. 2020. Changes in Barents Sea ice edge positions in the last 440 years: A review of possible driving forces. *International Journal of Astronomy and Astrophysics* 10, 97-164.
- Nesje, A., Pilø, L.H., Finstad, E. and 7 others. 2011. The climatic significance of artefacts related to prehistoric reindeer hunting exposed by melting ice patches in southern Norway. *The Holocene* 22(4), 485-496.
- Nicolussi, K. & Patzelt, G. 2000. Discovery of early Holocene wood and peat on the forefield of the Pasterze Glacier, Eastern Alps, Austria. *The Holocene* 10, 191-199.
- Öberg, L. & Kullman, L. 2011. Recent glacier recession-a new source of postglacial treeline and climate history in the Swedish Scandes. *Landscape Online* 26, 1-38.

- Parducci, L., Jørgensen, T., Tollefsrud, M.M and 22 others. Glacial survival of boreal trees in northern Scandinavia. *Science* 355, 1083-1086.
- Pässe, T. & Andersson, L. 2005. Shore-level displacement in Fennoscandia calculated from empirical data. *Geologiska Föreningen i Stockholms Förhandlingar* 127, 253-268.
- Paus, A. 2010. Vegetation and environment of the Rødalen alpine area, Central Norway, with emphasis on the early Holocene. *Vegetation History and Archaeobotany* 19, 29-51
- Paus, A. 2013. Human impact, soil erosion, and vegetation response lags to climate changes: challenges for the mid-Scandinavian pollen-based transfer-function temperature reconstructions. *Vegetation History and Archaeobotany* 22, 269-284.
- Paus, A., Velle, G. & Berge, J. 2011. The Lateglacial and early Holocene vegetation and environment in the Dovre mountains, central Norway, as signalled in two Lateglacial nunatak lakes. *Quaternary Science Reviews* 29, 1780-1793.
- Paus, A. & Haugland, V. 2017. Early- to mid-Holocene forest-line and climate dynamics in southern Scandes Mountains inferred from contrasting megafossil and pollen data. *The Holocene* 27, 361-383.
- Schenk, F., Väiliranta, M. & Muschitiello, F. and 7 others 2018. Warm summers during the Younger Dryas cold reversal. *Nature Communications* 9, 1634.
- Schlüchter, C. & Jörin, U. 2004. Holz und Torffunde als Klimaindikatoren. *Alpen ohne Gletscher. Die Alpen* 2004(6), 34-47.
- Segerström, U. & von Stedingk, H. 2003. Early-Holocene spruce, *Picea abies* (L.) Karst., in West central Sweden as revealed by pollen analysis. *The Holocene* 13, 897-906.
- Seppä, H., Alenius, T., Bradshaw, R., Giesecke, T., Heikkilä M. & Muukkonen, P. 2009. Invasion of Norway spruce (*Picea abies*) and the rise of the boreal ecosystem in Fennoscandia. *Journal of Ecology* 97, 629-640.
- Smith, H. 1920. *Vegetation och dess utvecklingshistoria i det centrala svenska högfjällområdet*. Almqvist & Wiksells, Uppsala.
- Väiliranta, M., Kaakinen, A., Kuhry, P., Kulti, S., Salonen, J.S & Seppä, H. 2011. Scattered late-glacial and early Holocene tree populations as dispersal nuclei for forest development in north-eastern European Russia. *Journal of Biogeography* 38, 922-932.
- Väiliranta, M., Salonen, J.S., Heikkilä, and 10 others 2015. Plant macrofossil evidence for an early onset of the Holocene summer thermal maximum in northernmost Europe. *Nature Communications* 6. DOI: 10.1038/ncomms7809.
- Zahle, R., Huang, Y.-T., Bigler, C., Wood, J.R., Dalén, L., Wang, X.-R., Segerström, U. & Klaminder, J. 2018. Growth of plants on the Late Weichselian ice-sheet during Greenland interstadial-1? *Quaternary Science Reviews* 185, 222-239.