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# Ancient Subalpine Clonal Spruces (*Picea abies*): Sources of Postglacial Vegetation History in the Swedish Scandes

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ABSTRACT. This study addresses the long-standing issue of postglacial immigration of *Picea abies* (Norway spruce) into Scandinavia. The main methodological focus is on using megafossil tree remains (wood and cones) of spruce and other species retrieved from the treeline ecotone of the Swedish Scandes as a tool for vegetation reconstruction. The core data come from radiocarbon dating of megafossils preserved in the soil underneath clonal groups of *Picea abies*, formed by rooting of branches that over time give rise to new upright stems. At high elevations, we found living spruce clones, which in some cases may be part of a continuous clonal series dating back to the early Holocene (9500 cal. yr BP). The presence of *Picea* in the Swedish Scandes at this early stage concurs with previous megafossil inferences. This date, which places the arrival of *Picea* very soon after regional deglaciation, is several millennia earlier than the arrival date inferred from pollen data. The persistence of some individual *Picea* clones from the early Holocene thermal optimum to the present implies that permanently open or semi-open spots existed in the high-mountain landscape even during periods when treelines in general were much higher than at present. Initially, *Picea* clones appear to have existed in a regional no-analogue vegetation matrix of widely scattered pine (*Pinus sylvestris*), mountain birch (*Betula pubescens* ssp. *czerepanovii*), Siberian larch (*Larix sibirica*) and thermophilic broadleaved deciduous species. In response to subsequent neoglacial cooling, the alpine character of the landscape has been enhanced through a lowered pine treeline and the disappearance of larch and thermophiles. The endurance of spruces, which escaped fire and other calamities, is due to their inherent phenotypic plasticity. Increasing climatic harshness throughout the Holocene conserved them as crippled krummholz, protected from winter stress by almost complete snow coverage. The appearance of *Picea abies* exclusively in western Scandinavia shortly after the deglaciation could suggest that the species immigrated from "cryptic" ice age refugia much closer to Scandinavia than conventionally thought.

Key words: *Picea abies*, clones, megafossils, immigration, Holocene, cryptic refugia, Swedish Scandes

RÉSUMÉ. La présente étude porte sur la question de longue date relative à l'immigration postglaciaire de *Picea abies* (épinette de Norvège) en Scandinavie. Du point de vue méthodologique, l'accent a été mis sur l'utilisation de restes d'arbres mégafossiles (bois et cônes) provenant d'épinettes et d'autres espèces prélevées de la limite forestière de l'écotone dans les Scandes suédoises en tant qu'outil de réaménagement de la végétation. Les données fondamentales proviennent de la datation au carbone 14 des mégafossiles préservés dans le sol sous des groupements clonaux de *Picea abies*, formés par l'enracinement de branches qui, au fil du temps, donnent naissance à de nouvelles tiges droites. En haute altitude, nous avons trouvé des clones vivants d'épinettes qui, dans certains cas, pourraient faire partie d'une série clonale continue remontant au début de l'Holocène (9500 cal. années BP). La présence de *Picea* dans les Scandes suédoises à ce stade initial vient confirmer les inférences antérieures concernant les mégafossiles. Cette date, qui place l'arrivée de *Picea* peu après la déglaciation régionale, se trouve à être des millénaires avant la date d'arrivée inférée par les données déduites du pollen. La persistance de certains clones *Picea* individuels du début de l'optimum thermique de l'Holocène jusqu'à présent implique qu'il existait des endroits ouverts ou semi-ouverts en permanence dans le paysage des hautes montagnes même pendant les périodes où les limites forestières en général étaient beaucoup plus élevées qu'à présent. Initialement, les clones *Picea* semblent avoir existé au sein d'une matrice de végétation non-analogue régionale de pins largement éparpillés (*Pinus sylvestris*), de bouleaux fontinaux (*Betula pubescens* ssp. *czerepanovii*), de mélèzes de Sibérie (*Larix sibirica*) et d'espèces thermophiliques caduques à feuilles larges. En réaction au refroidissement néoglaciaire subséquent, le caractère alpin du paysage a été amélioré grâce à une limite forestière de pins moins élevée et à la disparition des mélèzes et des thermophiles. L'endurance des épinettes, qui ont échappé aux incendies et à d'autres calamités, est attribuable à leur plasticité phénotypique inhérente. L'intensification de la dureté du climat pendant l'Holocène a donné lieu à leur conservation sous la forme de krummholz rabougri, protégé de la dureté de l'hiver par une couverture de neige quasi-complète. L'apparition exclusive de *Picea abies* dans l'ouest de la Scandinavie peu après la déglaciation pourrait laisser entendre que cette espèce a immigré de refuges « cryptiques » de la période glaciaire beaucoup plus près de la Scandinavie qu'on ne le pensait auparavant.

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Mots clés : *Picea abies*, clones, mégafossiles, immigration, Holocène, refuge cryptique, Scandes suédoises

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## INTRODUCTION

During the past two decades, Late Glacial and early Holocene phylogeography has entered a new and dynamic phase. Analyses of ancient DNA, molecular genetics, and dynamic modeling have revitalized interest in long-standing paleoecological issues (Willis et al., 2000; Hu et al., 2008; Stewart and Cooper, 2008). One challenging question concerns the location of "hibernation" sites for biota during the last glacial phase and also the timing and routes for postglacial re-immigration into deglaciated territories. More specifically, mounting evidence suggests that plants and animals could have thrived in mid- and high-latitude cryptic refugia (Alm, 1993; Kullman, 2000, 2002; Stewart and Lister, 2001) close to the continental ice margins during glacial and late-glacial episodes. These are ideas with potentially far-reaching consequences for population genetics concerning the possibility for species to adapt to future climate change and the consequent evolution of biodiversity (e.g., Barnosky, 2008; Hampe and Petit, 2010). Therefore, more firm evidence is urgently needed.

Despite recent methodological progress, there are no shortcuts to firm knowledge: testing of emerging hypotheses must still rely on "concrete fossil" evidence, rather than only pollen or molecular data (Godwin, 1975; Stewart and Lister, 2001). One option is the use of megafossils: large pieces of wood such as trunks, roots, and cones preserved in peat or lake sediments, which are unlikely to have been moved around in the landscape by wind or other forces (Kullman, 2000; Kullman and Kjällgren, 2006). Although non-quantitative, laborious, and somewhat fortuitous, this method provides data that can show unambiguously that a specific species grew at a specific site at a specific point of time. When conflicting with other paleosources, such as pollen analysis, positive evidence of this kind can hardly be disputed (Stewart and Cooper, 2008). One variant of the megafossil approach, and a new investigation tool, is life-history analysis of long-lived clonally regenerating tree species growing in low-disturbance environments. The feasibility of this tool is demonstrated by several studies (Vasek, 1980; Lavoie and Payette, 1996; Kullman, 2000; May et al., 2009). Here we employ this method to study the early Holocene immigration and first appearance of Norway spruce (*Picea abies*) in the Swedish Scandes and the implications for possible glacial and late-glacial refuge areas.

Together with *Pinus sylvestris* (Scots pine), *Picea abies* is the dominant and economically most important tree species in northern (boreal) Fennoscandia, which makes studies of its Quaternary history particularly relevant. On the basis of pollen analysis, it has long been taken as almost axiomatic that *Picea* was a late Holocene immigrant to northern and central Scandinavia. The predominant paradigm is that the species spread westward over northern Scandinavia from ice-age refugia in central Russia, thousands of kilometers to the east, during the past 3000–4000 years. Spruce is assumed to have reached the Scandes (the study region included) around 2000–2500 years ago (Lundqvist, 1969; Moe, 1970; Tallantire, 1977; Huntley and Birks, 1983; Hafsten, 1992; Lang, 1994; Latałowa and van der Knaap, 2006; Seppä et al., 2009; Tollefsrud et al., 2009). However, another quite different interpretation was advocated long ago by researchers who found stray amounts of *Picea* pollen and even macroremains in early postglacial stratigraphies. Some of these early works are reviewed in more detail by Kullman (2000) and Lindbladh (2004).

During the past decade, the radiocarbon dating of *Picea* megafossils recovered from widespread sites along the mid and northern Swedish Scandes has given an entirely new perspective on this issue (Kullman, 2000, 2002, 2004a). These radiocarbon dates are distributed over virtually the entire Holocene, and about 50% represent wood pieces buried in the soil underneath the canopy of living subalpine and alpine spruce clones of the krummholz type (Kullman, 2000). The term "krummholz" refers to environmentally stunted and crippled individuals with dense infra-nival foliage (cf. Holtmeier, 1981, 1986). Some clones seem to be of high antiquity, as suggested by dead wood embracing the past 8000–9000 years unearthed below their canopies. The oldest living stem belonging to a clone of this kind contained somewhat more than 600 tree rings (Kullman, 2001) (Fig. 1). The propensity for longevity is suggested also by the observation that mortality of extant spruce clones is an extremely rare phenomenon. On these grounds, we have good reason to believe that some subalpine spruce clones are "living relicts" (cf. Laberge et al., 2000; Holtmeier, 2003) with unbroken continuity from the early Holocene immigration or spreading phase. Consequently, we believe that ancient spruce clones could be used to increase our knowledge about the early Holocene performance of *Picea abies* in the Scandes. This approach provides a way to detect the oldest individuals and populations that is more focused and less dependent on chance than the blind, time-consuming search for mega- and macrofossils in stratigraphical contexts such as peat and lake sediments, which are rarely optimal spruce habitats. This thinking is the general background of our study, which was carried out in a subalpine region of the Swedish Scandes, where modern data on Holocene vegetation history are very scarce. Some of the dates have been presented previously in more popular contexts.

The data presented here add to the existing knowledge about early Holocene phylogeographic history in the south-central Scandes. The timing of the first Holocene spruce immigration is a central issue for this entire research field.

FIG. 1. The oldest known living spruce stem, containing somewhat more than 600 tree rings, belongs to this clone at Mt. Storsnasen in the county of Jämtland, Sweden. Photo: 12 July 2007.

An aspect of particular relevance is whether early megafossils represent isolated outposts of only local importance, as maintained by Giesecke (2005), or whether they constitute a more general pattern in the early Holocene landscape. We have reconstructed the vegetation matrix that contained the earliest spruces by radiocarbon dating of megafossil remains of tree species other than spruce, which are preserved in peat and small lakes at high altitudes in the same region. The present study contributes to improved comprehension, in general, of Holocene landscape evolution at the taiga-tundra interface. We also discuss the discrepancy between the results we obtained by applying this type of megafossil analysis to ancient spruce clones and previous results based on traditional analyses of pollen records.

## STUDY AREA

### General Setting: Topography and Geology

The study area (approximately 12 000 km$^2$) is located in the counties of Dalarna and Härjedalen, in the southernmost Swedish Scandes (Fig. 2). With respect to the life history of spruce clones, we focused on investigating six different mountain areas (sites 1 – 6). From north to south, these are (1) Mt. Sonfjället (max. 1278 m a.s.l.), (2) Mt. Barfredhågna (max. 1022 m a.s.l.), (3) Mt. Städjan (max. 1131 m a.s.l.), (4) Mt. Härjehågna (max. 1185 m a.s.l.), (5) Mt. Fulufjället (max. 1039 m a.s.l.), and (6) Mt. Köarskärsfjället (max 875 m a.s.l.). In addition, we retrieved megafossils of Scots pine from two more sites, (7) Mt. Storvätteshågna (max. 1204 m a.s.l.) and (8) Mt. Nipfjället (max. 1192 m a.s.l.). The valley floors range between 750 and 850 m a.s.l.

Characteristically, the mountains investigated are smoothly rounded and reach a maximum of 300 – 400 m above the upper limit of the continuous forest. They all have the character of “islands” in a matrix of broad valleys and uplands covered with boreal coniferous forests and mires. Dominating geological substrates are acidic and nutrient-poor quartzites and Dala sandstone. Extensive frost-shattered boulder fields cover the peak plateaux of most of the highest mountains. At lower elevations, the slopes are clothed with an undifferentiated cover of glacial till. Minor peat accumulations exist near and above the treeline. Small lakes, ponds, and rivulets are scarce as a result of early melting of a relatively thin snow cover (Lundqvist, 1951, 1969).

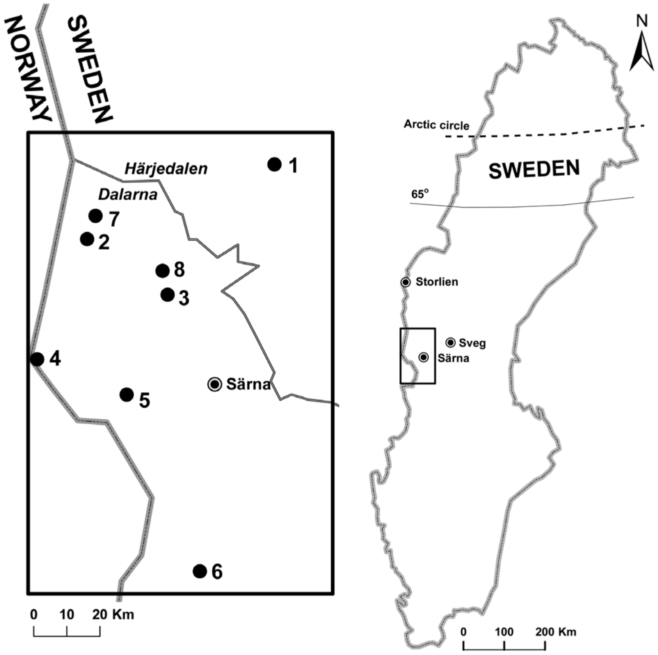

FIG. 2. Location of the study area and the sampling sites at (1) Mt. Sonfjället, (2) Mt. Barfredhågna, (3) Mt. Städjan, (4) Mt. Härjehågna, (5) Mt. Fulufjället, (6) Mt. Köarskärsfjället, (7) Mt. Storvätteshågna, and (8) Mt. Nipfjället.

### Climate

The climate of the study area is moderately continental in character, and the effective humidity is low in comparison with most other parts of the Swedish Scandes. Mean annual temperatures, as recorded by official meteorological stations, range between 2.0 and 0.0˚C, and precipitation varies between 700 and 1000 mm per year (Raab and Vedin, 1995). Data collected at two meteorological stations, Sveg (360 m a.s.l.) and Särna (435 m a.s.l.), represent climatic conditions within the northern and southern part of the study area, respectively. For Sveg, the mean temperatures are -10.5˚C for January, 14.4˚C for July, and 2.1˚ for the year, respectively. Corresponding data for Särna are – 12.1˚, 13.3˚, and 0.8˚C. Annual precipitation is 624 mm for Sveg and 601 mm for Särna. All data were obtained from the Swedish Meteorological and Hydrological Institute (SMHI) and represent the period 1961 – 90.

During the past c. 100 years, regional standard meteorological records display distinct warming for all seasons. Although the Sveg meteorological station is located slightly outside the study area, it is considered to be representative of a larger region of the southern Swedish Scandes that includes the study area (Alexandersson, 2006). Its homogenized long-term data show a positive linear trend of 1.4˚C for the mean annual temperature over the past 131 years (1876 – 2007), with the most consistent warming occurring between 1876 and 1940. The overall climate-warming trend hides a large inter-annual scatter, with a slight reversal of the trend in some decades after the mid-20th century. Precipitation has increased steadily throughout the past century (Alexandersson, 2006), and a tendency for increasing oceanity is perceivable, particularly in the past few decades (Tuomenvirta et al., 2000). A long-term decreasing trend in days with snow cover characterizes the past century (Moberg et al., 2005).

### *Treeline and Treeline Ecotone*

The *treeline* for each tree species at a specific location is defined as the elevation (m a.s.l.) of the uppermost individual attaining a height of 2 m.

The *treeline ecotone* is broad and indistinct, extending from the uppermost outliers of spruce and pine trees in the subalpine mountain birch belt up to the treeless alpine tundra. In this mainly continental part of the southern Swedish Scandes, the birch belt is only fragmentarily developed or even lacking (Samuelsson, 1917; Kullman, 2004a). It is most discrete and extensive in the snow-rich western parts of the area. On Mt. Städjan, Mt. Barfredhågna and Mt. Härjehågna, the uppermost treeline is marked by spruce, while on Mt. Storvätteshågna, pine is the uppermost, followed in order by spruce and birch treeline. On Mt. Köarskärsfjället and Mt. Fulufjället, the spruce treeline reaches almost as high as birch and pine (to 5 – 10 m below them).

As a consequence of climatic continentality, the study area comprises the highest treelines of both Norway spruce (1115 m a.s.l.) and Scots pine (1045 m a.s.l) in the Swedish Scandes, both at Mt. Städjan. Additionally, the second highest treeline of mountain birch (*Betula pubescens* ssp *czerepanovii*) is found at Mt. Sonfjället, 1135 m a.s.l. (Kullman and Öberg, 2009).

During the past 100 years, concomitantly with a linear warming trend of c. 1.3˚C, mountain birch, spruce, and pine shifted their treelines upslope by a maximum of c. 185 m, with mean shifts of 55 – 100 m in the specific area here concerned (Kullman and Öberg, 2009; Kullman, 2010).

The spruce treeline rose mainly by means of this species' high phenotypic plasticity and ability to switch from prostrate krummholz to arborescent growth form in response to climate warming. Pine expanded its treeline by establishing new individuals (genotypic change). In the case of mountain birch, both genotypic and phenotypic treeline changes have occurred, although the latter process seems to have prevailed (Kullman and Öberg, 2009; Kullman, 2010).

The groundcover vegetation within the treeline ecotone is dominated by ericaceous dwarf-shrub heaths (*Vaccinium myrtillus*, *V. uliginosum*, *Betula nana*, *Empetrum hermaphroditum*) with some low herbs, sedges, and grasses, alternating with boulder fields and open mires. As a rule, the heath communities contain a bottom layer with variable proportions of reindeer lichens. The vascular alpine flora is strikingly poor in species (Samuelsson, 1917).

Phytogeographically, the study area belongs to the northern boreal zone (Ahti et al., 1968). A more detailed account of the treeline ecotone and its geoecological and climatic context is provided by Kullman (2005a, 2010).

### *The Coniferous Foothill Forests*

The well-drained, nutrient-poor valley floors at the foothills of the mountains are dominated by lichen-rich pine forest, while spruce often predominates along streams and rivers. With increasing altitude, pine is gradually replaced by spruce, which often forms the uppermost coniferous forest at 600 – 800 m a.s.l. On a smaller scale, spruce is most competitive on humid hillsides and interfluvial uplands with fine-textured, nutrient-rich soils, heavy snow load, and insignificant seasonal ground frost (Engelmark and Hytteborn, 1999).

Observations of charred logs indicate that both the upper coniferous forest and the subalpine region have been influenced by wildfires in the past (Arnborg, 1949, 1951; Sander, 2005). Interviews with local residents indicate that during their lifetime, fires have been few and of minor extension. Stratigraphical studies in the vicinity of Mt. Sonfjället support the theory that wildfires have played only a minor role during the Holocene (Giesecke, 2005).

### *Human Impact*

Humans have used natural resources extensively in the coniferous forests, and to a lesser extent in the treeline ecotone, for haymaking, reindeer husbandry, livestock grazing, lichen harvesting, and selective tree-felling (Ericsson et al., 2000; Ljung, 2004; Ljungdahl, 2007; Öberg, 2009). These practices were most pronounced from the late 19th century until the 1940s, after which they virtually ceased. Despite the more or less heavy use of natural resources, treeline positions within the study area do not seem to have been affected by these land-use activities (Kjällgren and Kullman, 1998). This contention is supported by the accounts of several botanists and geographers working in the study area during the late 19th century and the first half of the 20th (Kellgren, 1891; Smith, 1920).

Grazing and trampling by reindeer (*Rangifer tarandus* L.) are ubiquitous and chronic disturbances to alpine and subalpine vegetation, with a history spanning many millennia of mutual adaptation (Cairns and Moen, 2004; Eriksson et al., 2007; Öberg, 2009). Since 20th century treeline history does not differ between areas with and without semidomestic reindeer, the treeline position per se has probably not been determined by reindeer action (Kullman, 2004a, 2005b; Kullman and Öberg, 2009).

Recent archaeological findings indicate human presence in parts of the study area since about 9000 cal. yr BP (Jönsson, 2009).

## METHODS

Sampling for this study focused exclusively on megafossil tree remains (dead wood and cones). The basic sampling method draws on experiences from similar studies (e.g., Kullman, 2000) in more northerly parts of the Scandes, where we learned by trial and error to distinguish between genuine old-growth spruce clones and more recently established specimens. Criteria for high age were multi-stemmed clones with a muddle of stout, interlacing boles below a dense, infra-nival skirt of branches. Moreover, we found that a minimum depth of 20 – 30 cm for the organic layer of raw humus or peat was essential for long-term preservation of dead wood and cones. Despite their compliance with these criteria, most sampling sites produced no datable megafossils.

In connection with other research projects on treeline dynamics (Öberg, 2002, 2008; Kullman and Öberg, 2009), we had the opportunity to survey large mountain areas for the potentially most rewarding spruce specimens. Intentionally, we tried to get an even spread of sampling sites over a larger region, mainly within the current treeline ecotone where almost all such clones are found. Selectively, we focused on the uppermost clones, supposed to be the oldest (Kullman, 2000).

Subfossil wood was unearthed by digging through the organic layers and down to the upper mineral layer of the soil, usually 10 – 50 cm below the surface. When several wood pieces were retrieved from a single clone, the largest and most decayed specimens were selected for radiocarbon dating. Species confirmation relied on bark fragments attached to the wood, which in most cases left no doubt about the correct identification. A few ambiguous samples were subjected to wood anatomical analysis, conducted by Dr. Thomas Bartholin (National Museum, Copenhagen University), a renowned dendrologist with documented capability to diagnose spruce wood (e.g., Bartholin, 1979). Cones were unambiguously determined to species. Only complete wood pieces (rather than composite samples) were dated. Henceforth, "wood" refers to unspecified woody material, except for roots.

An exhaustive search for megafossils of tree species other than spruce was conducted in peat deposits and shallow ponds from slightly below the modern treeline up to the highest peaks in the study area. Our goal was to obtain a sample that represented forest history and changes in treeline elevation throughout the Holocene.

Radiocarbon dating of recovered megafossils was conducted by Beta Analytic Inc., Miami, Florida. All dates are expressed as calibrated years before the present (cal. yr BP), with "present" = AD 1950. Calibration was conducted using CALIB 5.0.2 software (Stuiver et al., 2005) in combination with INTCAL04. For simplicity, the values given for radiocarbon ages represent the intercept of radiocarbon age with the calibration curve. Where multiple dates are given, we used the midpoint between the oldest and the youngest intercepts. Age determination of individual tree stems was conducted by boring at different stem positions above ground level. The tree rings were counted in the laboratory under a stereomicroscope.

The nomenclature follows Mossberg and Stenberg (2003) for vascular plants and Moberg and Holmåsen (1982) for lichens.

## RESULTS AND INTERPRETATION

### *Holocene Landscape and Climate Context of the Spruce Clones*

We synthesized the broad outline of treeline ecotone evolution during the Holocene from 46 megafossil tree remains (39 pine, 3 birch, 2 larch, 1 hazel, and 1 oak). Table 1 lists the radiocarbon dates and calibrated ages for these remains. Figure 3A shows the dates obtained and the position of each megafossil in relation to the pine treeline prevailing at the end of the Little Ice Age, or around AD 1900 (Kullman and Öberg, 2009).

Early Holocene growth of trees (about 10 000 cal. yr BP) at least 350 m above the treeline position that prevailed about 100 years ago attests to the rapid evolution of a climate more favourable to high-elevation tree growth than at present, presumably representing a Holocene thermal optimum around 9500 cal. yr BP (cf. Hoek and Bos, 2007). Subsequently, and throughout the Holocene, the upper elevational range of pine declined almost linearly (c. 28 m per millennium) until the late 19th century. Possibly a distinct short-term downslope excursion occurred around 8100 – 8200 cal. yr BP (Fig. 3B). This episode may reflect the so-called 8.2 event of near-global climate cooling (e.g., Rohling and Pälite, 2005). Obviously, the long-term process of treeline descent was driven by a progressive general temperature decrease, steadily forced by reduced summer insolation (COHMAP Members, 1988; Shemesh et al., 2001; Marchal et al., 2002) and isostatic land uplift throughout the Holocene. Further indications of climate forcing behind secular treeline evolution are provided by similar megafossil results from adjacent parts of the Swedish and Norwegian Scandes (Kullman and Kjällgren, 2006; Paus, 2010). Pollen records from the same regions are broadly consistent with these megafossil records (Segerström and von Stedingk, 2003; Bergman et al., 2005; Giesecke, 2005).

On the basis of a temperature lapse rate of 0.6˚C per 100 m elevational change (Laaksonen, 1976) and a treeline at least 350 m higher than a century ago, we can tentatively suggest that summer temperatures in the southern Scandes during the early Holocene were about 2.0˚C higher than at present (cf. Nesje et al., 1991). Given a warming trend of slightly more than 1˚C from the late 19th century to the present (Kullman and Öberg, 2009), we may infer that trees growing in the study area at the beginning of the Holocene could prosper in a summer climate 1˚C warmer than during the past few decades. Presumably this is an underestimate, since the potential position of the early Holocene pine treeline could obviously

TABLE 1. Radiocarbon dates of megafossil pine and some other tree species from different sites within the study area.

| Species | Site no. | Lab. no. | $^{14}$C yr BP | 2σ cal. yr BP | Intercept cal. yr BP | Material | Altitude (m a.s.l.) | Source |
|---|---|---|---|---|---|---|---|---|
| Pine | 1 | Beta-246095 | 5680 ± 50 | 6570–6390 | 6450 | Wood | 1015 | This study |
| Pine | 7 | Beta-158304 | 4310 ± 70 | 5040–4710 | 4875 | Wood | 1010 | Kullman, 2004a |
| Pine | 7 | Beta-158306 | 6770 ± 60 | 7700–7560 | 7630 | Wood | 1080 | Kullman, 2004a |
| Pine | 7 | Beta-158307 | 1590 ± 50 | 1570–1360 | 1465 | Wood | 920 | Kullman, 2004a |
| Pine | 7 | Beta-158308 | 5930 ± 80 | 6940–6560 | 6750 | Wood | 990 | Kullman, 2004a |
| Pine | 7 | Beta-158314 | 8380 ± 50 | 9500–9280 | 9390 | Wood | 1070 | Kullman, 2004a |
| Pine | 7 | Beta-169411 | 8050 ± 70 | 9120–8660 | 8890 | Wood | 1035 | Kullman, 2004a |
| Pine | 7 | Beta-169412 | 6040 ± 60 | 7010–6730 | 6870 | Wood | 1035 | Kullman, 2004a |
| Pine | 7 | Beta-172305 | 9070 ± 70 | 10380–10150 | 10265 | Wood | 1180 | Kullman, 2004a |
| Pine | 7 | Beta-172316 | 8040 ± 60 | 9050–8710 | 8880 | Wood | 940 | Kullman, 2004a |
| Pine | 7 | Beta-172317 | 8500 ± 60 | 9550–9440 | 9445 | Wood | 1180 | Kullman, 2004a |
| Pine | 7 | Beta-178795 | 9230 ± 50 | 10540–10240 | 10390 | Wood | 1180 | Kullman, 2004a |
| Pine | 7 | Beta-178798 | 5840 ± 50 | 6750–6510 | 6630 | Wood | 1010 | Kullman, 2004a |
| Pine | 7 | Beta-179446 | 4440 ± 70 | 5310–4850 | 5080 | Wood | 940 | Kullman, 2004a |
| Pine | 7 | Beta-179447 | 4360 ± 50 | 5050–4840 | 4945 | Wood | 950 | Kullman, 2004a |
| Pine | 7 | Beta-180218 | 3440 ± 70 | 3870–3490 | 3680 | Wood | 945 | Kullman, 2004a |
| Pine | 2 | ST-396 | 7330 ± 130 | 8290–7995 | 8145 | Wood | 940 | Lundqvist, 1959 |
| Pine | 2 | ST-397 | 6840 ± 140 | 7800–7580 | 7690 | Wood | 900 | Lundqvist, 1959 |
| Pine | 2 | ST-398 | 6520 ± 170 | 7560–7330 | 7745 | Wood | 915 | Lundqvist, 1959 |
| Pine | 2 | ST-5747 | 910 ± 90 | 975–765 | 870 | Wood | 910 | Kullman, 1980 |
| Pine | 2 | ST-5750 | 835 ± 90 | 935–710 | 825 | Wood | 910 | Kullman, 1980 |
| Pine | 8 | Beta-57644 | 1190 ± 90 | 1170–1070 | 1120 | Wood | 990 | Kullman, 2000 |
| Pine | 8 | Beta-169410 | 8050 ± 70 | 9120–8660 | 8890 | Wood | 1160 | Kullman, 2004a |
| Pine | 8 | Beta-173414 | 7720 ± 80 | 8630–8380 | 8505 | Wood | 1150 | Kullman, 2004a |
| Pine | 8 | ST-12023 | 1155 ± 110 | 1230–950 | 1090 | Wood | 975 | Kullman, 2000 |
| Pine | 3 | Beta-158302 | 4680 ± 50 | 5580–5310 | 5445 | Wood | 1045 | Kullman, 2004a |
| Pine | 3 | Beta-158303 | 4160 ± 80 | 4660–4440 | 4550 | Wood | 1015 | Kullman, 2004a |
| Pine | 3 | Beta-158305 | 10500 ± 60 | 12870–11980 | 12425 | Wood | 1100 | Kullman, 2004a |
| Pine | 3 | Beta-178793 | 6140 ± 100 | 7260–6750 | 7005 | Wood | 1085 | Kullman, 2004a |
| Pine | 3 | Beta-178794 | 8190 ± 60 | 9300–9010 | 9155 | Wood | 1035 | Kullman, 2004a |
| Pine | 3 | Beta-178797 | 7890 ± 60 | 8990–8550 | 8770 | Wood | 1055 | Kullman, 2004a |
| Pine | 5 | Beta-195539 | 6610 ± 60 | 7590–7420 | 7480 | Trunk | 890 | This study |
| Pine | 5 | Beta-195540 | 8230 ± 60 | 9420–9020 | 9240 | Trunk | 920 | This study |
| Pine | 5 | Beta-195541 | 7800 ± 70 | 8760–8420 | 8580 | Trunk | 920 | This study |
| Pine | 5 | Beta-195542 | 8380 ± 60 | 9510–9270 | 9440 | Trunk | 920 | This study |
| Pine | 5 | Beta-195543 | 8570 ± 60 | 9600–9490 | 9540 | Branch | 935 | This study |
| Pine | 5 | Beta-195544 | 8340 ± 60 | 9490–9220 | 9410 | Trunk | 905 | This study |
| Pine | 5 | Beta-195545 | 8050 ± 70 | 9120–8660 | 9000 | Trunk | 905 | This study |
| Pine | 5 | Beta-195550 | 8690 ± 80 | 9920–9520 | 9600 | Trunk | 1030 | This study |
| Birch | 7 | Beta-178448 | 4440 ± 70 | 5310–4850 | 5080 | Wood | 920 | Kullman, 2004a |
| Birch | 7 | Beta-178799 | 8360 ± 60 | 9500–9250 | 9375 | Wood | 915 | Kullman, 2004a |
| Birch | 5 | Beta-195546 | 320 ± 60 | 510–280 | 370 | Trunk | 935 | This study |
| Larch | 2 | Beta-178796 | 8160 ± 70 | 9290–9000 | 9145 | Twig + 1 cone | 915 | Kullman, 2004a |
| Larch | 5 | Beta-195537 | 7390 ± 60 | 8350–8040 | 8180 | Cones | 890 | This study |
| Hazel | 7 | Beta-158309 | 8670 ± 40 | 9720–9540 | 9630 | Acorn | 910 | Kullman, 2004a |
| Oak | 7 | Beta-158310 | 8560 ± 40 | 9560–9500 | 9530 | Nutshell | 910 | Kullman, 2004a |

not be attained given the relatively low maximum peak altitudes in the study area (cf. Kullman, 2004a).

Only a few megafossils of tree birch have been recovered at the elevations surveyed (Table 1), and the small number of datings obtained does not allow any detailed comparison with pine. It is clear, however, that tree birch grew at fairly high elevations in the early Holocene, virtually as early as the first Holocene pine dates. We suggest tentatively that birch has never played any important role in the treeline ecotone, and consequently, pine has been the dominating species in that ecotone throughout the Holocene. Experiences from other parts of the southern Scandes indicate that a discrete mountain birch belt evolved quite late in the Holocene in response to neoglacial cooling (Kullman, 1995, 2004b; Barnett et al., 2001).

It is particularly interesting that megafossil remains (cones and twigs) of *Larix sibirica* (larch) have been recovered at two sites in the treeline ecotone (Fig. 4). These remains range in age between 9100 and 8200 cal. yr BP (Table 1). Until quite recently, *Larix* was not assumed to have grown in any part of Scandinavia during the Holocene. Analogous discoveries of macroremains of this species have also been made at scattered localities farther north in the Scandes (Kullman, 1998a). In addition, pollen records from the alpine region of northern Sweden and central Norway indicate the presence of *Larix* in the early Holocene (Bergman et al., 2004; Paus, 2010). According to present-day climatic correlates (Putenikkin and Martinsson, 1995), the occurrence of *Larix* is indicative of low winter and high summer insolation, implying a dry continental and strongly seasonal climate during the early Holocene (cf. MacDonald et al., 2008). A climate drier than at present is further suggested by the fact that both larch and pine megafossils have been recovered from small ponds in the treeline ecotone (Fig. 4).

In addition to the relatively high pine treeline during the early Holocene, macrofossils of thermophilic tree

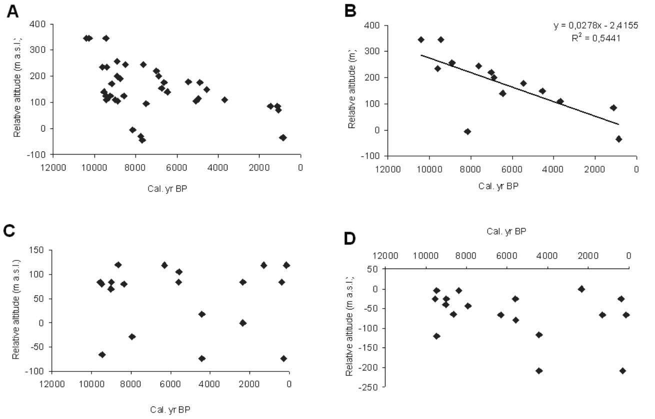

FIG. 3. A) Radiocarbon dates of pines from all six spruce sample sites relative to the elevation of the pine treeline at the early 20th century (zero line), not adjusted for land-uplift. For the basic data, see Table 1; B) Linear regression of the uppermost megafossil pine date in sequential 500-year periods plotted on a calendar-year scale. Further details as in Figure 3A; C) Radiocarbon dates of megafossil *Picea abies* from sites 1 to 6 in relation to the spruce treeline position in 1915; and D) The same dates as in Figure 3C, but in relation to the spruce treeline position in 2007.

FIG. 4. Megafossils retrieved from a small pool (Site 5b). From left to right, a large spruce cone (9030 cal. yr BP), two smaller larch cones, and a larch twig (8160 cal. yr BP, composite date). Photo: 12 July 2007.

species (hazel, *Corylus avellana*, and oak, *Quercus robur*) in the current treeline ecotone (Table 1) speak for a climate warmer than present. Likewise, their disappearance from the paleorecord in the mid-Holocene argues for enhanced cooling thereafter. The presence of species belonging to this group of truly warmth-demanding trees during the early Holocene is consistent with pollen data from the high mountains of the study area (Lundqvist, 1951; Giesecke, 2005). This aspect of the early Holocene tree landscape is further sustained by macrofossil and pollen data gathered in other high-mountain regions of the south-central Scandes (Kullman, 1998b; Bergman et al., 2005).

### *Clonal Spruces: Growth and Site Characteristics*

The ability of *Picea abies* to regenerate clonally by layering close to the treeline is well documented and described in the Scandinavian literature (Kihlman, 1890; Kallio et al., 1971; Kullman, 1986). The same strategy prevails for *Picea* species in other parts of the world, for example, in the European Alps (Holtmeier, 2003), Russia (MacDonald et al., 2008; Kharuk et al., 2009) and in North America (Payette et al., 1985; Gamache and Payette, 2004). At the Arctic treeline in North America, living *Picea* clones in fire-free landscapes have been found to be at least 3000 years old (Payette and Morneau, 1993). Even greater ages are postulated for extant tree islands in the forest tundra of northern Russia (Lavrinenko and Lavrinenko, 1999). Obviously, this growth form is primarily a response to a harsh, cold, and windy winter climate at the taiga-tundra interface or in analogous cold-marginal situations (e.g., Lavoie and Payette, 1994; Kullman, 1996; Hammer and Walsh, 2009).

Typically, the state of wood preservation was poor in our samples; most of the cellulose content was decayed and only the structural lignin components were preserved. The basic preconditions for long-term preservation of wood fragments were provided by a cold and dry continental climate. In addition, deep layers of continuously accumulating needle litter, transforming into raw humus or peat, further promoted conservation. Dead trunks and branches often remained in situ before falling to the ground. In the upright position, the wood dries and hardens to a state quite resistant to further weathering and biological decay before it is incorporated into the soil beneath the canopy of the clone.

The general appearance of the clonal spruces is shown in the photographs of Figures 5 and 6. The majority are multi-stemmed (5–20 stems, > 1 m high), with a maximum height of 4–8 m. As a rule, each clone is characterized by an infra-nival "skirt" of dense foliage (cf. Lavoie and Payette, 1994) that covers an area of 15–30 $m^2$. Quite often, this near-ground and snow-protected part of the clone appears to be the most vital part and is estimated to contain the largest photosynthetically active biomass.

Most of the clones we investigated are located at altitudes between the position of the spruce treeline in the early 20th century and its present position (Fig. 3C, D). This is the "advance zone," where the treeline shifted upslope by transformation from krummholz to arborescent form (phenotypic plasticity) in response to recent climate warming (Öberg, 2008; Kullman and Öberg, 2009; Kullman, 2010). Within this zone, no extant stem was higher than 2 m in the early 20th century. Emergence of upright stems distinctly protruding from the infra-nival krummholz morphs began here in the late 1930s, as is evident in general for the entire study region (Kullman, 1986). This course of life-history evolution is expressed by some of the clones that were specifically analyzed in this respect (Figs. 5 and 6).

The clones we focused on in this study all grow in open landscapes, on patches of exposed and dry-fresh alpine tundra without fire indications. Closer inspection reveals that they occupy minor depressions in the local topography and quite often are found in association with running water.

FIG. 5. A) "Old Tjikko" (Site 5a). The oldest wood remnants, dated 9550 cal. yr BP, were found beneath the infra-nival skirt of this spruce. Its upright stem has evolved with climate warming since the late 1930s. Photo: 1 October 2009. B) "Fossil" wood, representing four different time slices of the Holocene, was recovered in the soil under this spruce. From left to right, samples dated at 5600, 385, 9550, and 9000 cal. yr BP. Photo: 12 July 2007.

Surrounding plant cover is commonly dwarf-shrub heath with different admixtures of reindeer lichens.

Clonal spruces appear to be distributed without obvious relation to the aspect or inclination of a site and are generally located on landscape segments prone to intermediate snow conditions. Typically, large snowdrifts pile up over and in lee of the clones, protecting them (except their supra-nival stems) from wind stress and frost desiccation. The moisture snow adds to the soil also helps the clones to endure the harsh alpine environment (Fig. 6).

### *Radiocarbon Ages of Megafossil Spruce Remains*

A total of 19 dates, originating from 10 spruce clones, were the particular focus of this study (Table 2). In some cases, more than one wood sample was retrieved and dated for a specific spruce clone. In addition, we dated two spruce cones recovered from peat deposits, which had no spatial association with any living spruce.

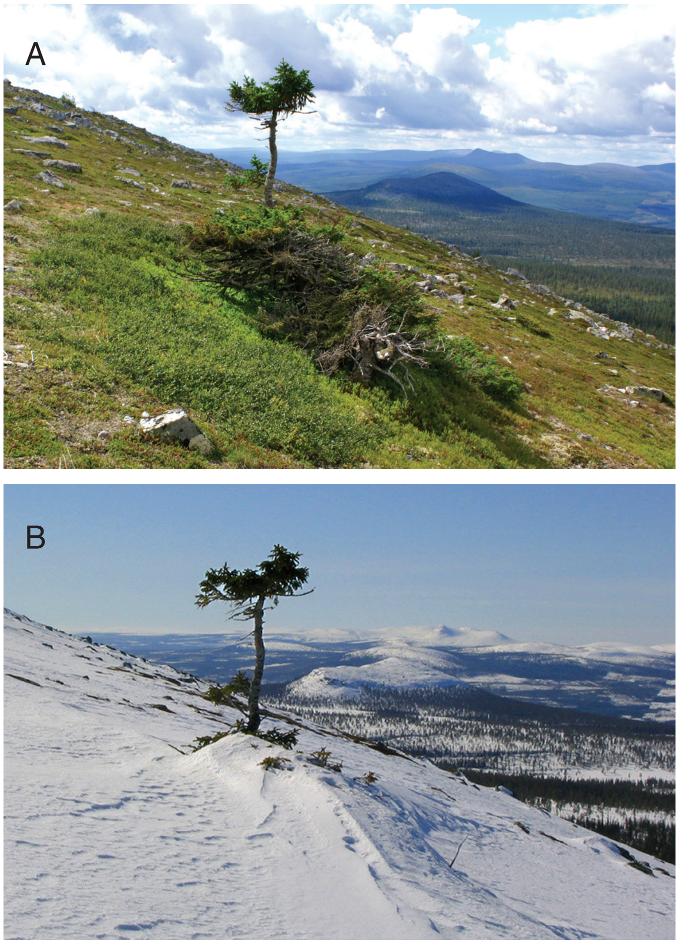

FIG. 6. A) The "Old Rasmus" spruce (Site 1b) demonstrates the modal evolution of the species in the treeline ecotone during the past century. Its oldest remnants yielded a date of 9480 cal. yr BP, and its stoutest living stem contained about 400 year rings at the root neck. The upright stem started to protrude from the infra-nival cushion in the 1930s, in close accord with the first warming peak of the 20th century. Photo: 12 July 2006. B) Large snow drifts result in a particularly lush ground cover of *Vaccinium myrtillus* (seen in photo A), as well as providing protection and moisture to the prostrate clones. Photo: 3 April 2004.

The ages we obtained range from 9550 cal. yr BP to the present. Two clones and one cone, representing well-separated localities, attest to the presence of spruce around 9500 cal. yr BP. As indicated above, treelines were generally much higher in that period than at present as a consequence of a warmer climate. Presumably, spruce benefited from these conditions to establish itself at strictly localized sites with ample soil moisture and snow protection.

It appears that throughout the Holocene and over the entire study region, spruce has been growing in the area between its present-day (2007) treeline and a point somewhat below the lower position of that treeline in the early 20th century (Fig. 3C, D). None of the dated spruce remains displayed any physical connection with living parts of the clones. This could, a priori, suggest that they do not represent the same genet as the living spruce. However, different lines of circumstantial evidence support the view that the extant clone is genetically identical with the ancient wood remains. A first indication in that direction is that wood

TABLE 2. Radiocarbon dates of megafossil spruce from six different sites within the study area. Site numbers with the same letter refer to the same clone.

| Site no. | Lab. no. | $^{14}$C yr BP | 2σ cal. yr BP | Intercept cal. yr BP | Material | Latitude | Longitude | Altitude (m a.s.l.) | Source |
|---|---|---|---|---|---|---|---|---|---|
| 1a | Beta-246094 | 2300 ± 40 | 2360 – 2180 | 2340 | wood | 62° 16.980′ | 13° 30.475′ | 945 | This study |
| 1b | Beta-246091 | 8450 ± 60 | 9540 – 9320 | 9480 | wood | 62° 16.665′ | 13° 28.162′ | 990 | This study |
| 1b | Beta-246092 | 7530 ± 40 | 8400 – 8310 | 8370 | wood | 62° 16.665′ | 13° 28.162′ | 990 | This study |
| 1c | Beta-246093 | 2300 ± 50 | 2360 – 2160 | 2340 | wood | 62° 16.660′ | 13° 28.171′ | 995 | This study |
| 2 | Beta-108767 | 8490 ± 70 | 9530 – 9380 | 9465 | cone | 62° 03.226′ | 12° 24.325′ | 860 | Kullman, 2000 |
| 3a | Beta-179449 | 3970 ± 50 | 4540 – 4280 | 4420 | wood | 61° 54.835′ | 12° 53.026′ | 998 | Kullman, 2004a |
| 3b | Beta-238423 | 3940 ± 80 | 4580 – 4150 | 4420 | cone | 61° 54.502′ | 12° 52.814′ | 907 | This study |
| 3b | Beta-238424 | 260 ± 60 | 480 – 0 | 300 | wood | 61° 54.502′ | 12° 52.814′ | 907 | This study |
| 4a | Beta-238419 | 7890 ± 70 | 8990 – 8540 | 8640 | wood | 61° 43.355′ | 12° 09.438′ | 985 | This study |
| 4b | Beta-238418 | 5550 ± 60 | 6440 – 6280 | 6310 | wood | 61° 43.312′ | 12° 09.343′ | 984 | This study |
| 4b | Beta-238421 | 1400 ± 70 | 1410 – 1180 | 1300 | wood | 61° 43.312′ | 12° 09.343′ | 984 | This study |
| 4b | Beta-238422 | 160 ± 60 | 310 – 0 | 135 | wood | 61° 43.312′ | 12° 09.343′ | 984 | This study |
| 4c | Beta-238420 | 4800 ± 60 | 5640 – 5330 | 5580 | wood | 61° 43.256′ | 12° 09.540′ | 971 | This study |
| 5a | Beta-195547 | 4870 ± 60 | 5720 – 5480 | 5600 | cone | 61° 38.356′ | 12° 40.589′ | 905 | This study |
| 5a | Beta-195548 | 350 ± 60 | 520 – 290 | 385 | trunk | 61° 38.356′ | 12° 40.589′ | 905 | This study |
| 5a | Beta-195549 | 8630 ± 60 | 9720 – 9520 | 9550 | trunk | 61° 38.356′ | 12° 40.589′ | 905 | This study |
| 5a | Beta-195551 | 8050 ± 70 | 9120 – 8660 | 9000 | trunk | 61° 38.356′ | 12° 40.589′ | 905 | This study |
| 5b | Beta-195538 | 8140 ± 60 | 9270 – 9000 | 9030 | cone | 61° 38.218′ | 12° 40.933′ | 890 | This study |
| 6 | Beta-264389 | 7100 ± 70 | 8020 – 7790 | 7940 | wood | 61° 10.255′ | 13° 07.994′ | 826 | This study |

samples of widely different ages were found right underneath the same clone. The clones, with their dense basal canopies, produce a deep layer of desiccated needle litter superimposed on a 20 – 50 cm thick layer of raw humus or peat, which does not allow root penetration of spruce seedlings (cf. Laberge et al., 2000; Holtmeier, 2003; Malanson et al., 2009). In no case have new spruce genets (seedlings or saplings) been recorded within these or other clones (Kullman and Öberg, 2009), a clear indication that seed regeneration is virtually impossible underneath these clones. The possibility that spruce seeds have intermittently germinated in the debris formed by different clones, living and dying at the same specific spot, is not supported by any recent observations. In fact, the remains of one dead clone (indeed a rare phenomenon) have been observed for more than 30 years, without indication of germination of spruce or other plant species (L. Kullman, pers. observ.). Taken together, these circumstances make it less likely that the old clones in the treeline ecotone are the outcome of multiple seed regeneration episodes at the same spot (cf. Holtmeier, 1974).

It appears that individual longevity of spruce is conditional upon a stunted and mainly horizontal growth form (krummholz), which implies a relatively large leaf-to-wood ratio. Such a situation can be maintained more easily in a harsh and open environment, where severe winter conditions prevent the emergence of tall and relatively less productive arborescent stems (Laberge et al., 2000). By implication, current treeline ecotones with abundant krummholz spruces have probably been virtually as open as today throughout the Holocene, even during the early part of the thermal optimum when lower-than-present $CO_2$ concentrations and the associated less-efficient use of water by plants (cf. Cowling and Sykes, 1999), in combination with strong windiness (Paus, 2010), may have helped to maintain the open landscape. Without this openness, it is unlikely that so many clones would have survived to the present day. Obviously, strong wind and associated factors are major forces that keep some parts of the high-mountain landscape open and woodless even during prolonged periods of warming (cf. Holtmeier and Broll, 2010). This interpretation is quite in line with the results from megafossil research in adjacent regions (Kullman and Kjällgren, 2006), as well as with the recent regional study of treeline performance over the past century (Kullman and Öberg, 2009). The latter study showed that in strongly wind-exposed topography, some old krummholz spruces within and above the treeline remained in that stage, and thus treelines were unable to take full advantage of climate warming to advance uphill and reach the potential thermal limit. This fact also implies that even in the hypothetical case of a warmer future, large expanses of the alpine world would remain unforested.

### *Aspects of Immigration History*

From around 9500 cal. yr BP to the present, scattered spruces have grown at high elevations in a sparse matrix of predominant pine and scattered mountain birches and larches. The no-analogue character of this arboreal landscape and the climate behind it is further stressed by occurrences of thermophilic broadleaved deciduous tree species, *Quercus robur* and *Corylus avellana,* at high elevations. Low abundances of spruce and some other tree species are not peculiar oddities, since similar occurrences, supported by macroremains, are recorded farther north in the Scandes (Kullman, 1998b, 2000). Rather, they represent the regional climatic situation and associated plant invasion patterns.

The presence of spruce already at the very beginning of the Holocene, as evidenced by megafossils, counters the prevailing idea of a late Holocene immigration and regional spread of *Picea abies* into northern and western Scandinavia (e.g., Moe, 1970; Huntley and Birks, 1983; Tollefsrud et al., 2008, 2009). Indisputably, *Picea abies* was among the first tree species to colonize the virgin postglacial tundra in the southern Scandes.

It stands out quite clearly from this and earlier studies (Kullman, 2000) that the majority of genuinely early (> 7000 cal. yr BP) spruce megafossils line up from north to south along the Swedish Scandes. The same broad pattern can also be deduced from existing pollen records (Lundqvist, 1969; Segerström and von Stedingk, 2003; Giesecke and Bennett, 2004; Hörnberg et al., 2006) if a less conservative interpretational paradigm is used: that is, if we accept that a pollen threshold of ca. 1% could in some cases represent actual local occurrence (cf. Segerström and von Stedingk, 2003; Terhürne-Berson, 2005; Zazula et al., 2006). Given these premises, pollen records from southern Norway could support early Holocene occurrence of spruce even to the west of the main watershed of the Scandes (Velle et al., 2005; Eide et al., 2006; Bjune et al., 2009). In this context, it should be considered also that Tollefsrud et al. (2008) found a strongly deviating genetic structure of spruce populations in central Scandinavia (the study area included). This structure could suggest a different and earlier immigration history for this area than for the rest of Scandinavia. Taken together, these circumstances are compatible, although not conclusively, with an immigration route from the west in this part of Scandinavia.

The ca. 1800 km distance to the putative refuge areas in central Russia and the difficulty of spreading, against prevailing westerly winds, over the Baltic Sea or temporary land bridges (as speculated by Tollefsrud et al., 2008), speak against the orthodox notion of an eastern origin for Scandinavian spruce. Nevertheless, there is macrofossil evidence for late-glacial presence of spruce just to the southeast of Sweden, in Latvia and Lithuania (e.g., Heikkilä et al., 2009). These occurrences could a priori have served as sources for the first spruce immigration into Sweden. However, neither megafossil nor pollen records are available to suggest the presence of spruce in eastern and southeastern Sweden (above the highest coast line) as early or earlier than is now recorded for the Scandes and adjacent regions in the west. In favour of first arrival from the west to the Swedish Scandes is the rapidity with which spruce, according to the megafossil record, appears in the early Holocene, for example, on late-glacial nunataks in the Scandes (Kullman, 2000; Paus et al., 2011). Reasonably, these circumstances could argue for late-glacial "bridgeheads" quite close to the Scandes, near the continental ice sheet. Megafossils indicate that birch trees existed early during the late-glacial period (Younger Dryas included) on the Arctic coast of northern Norway (Kullman, 2008). Predominant westerly winds (cf. Koç et al., 1993) may have contributed to rapid spread from such putative source areas.

In fact, there is mounting evidence in general that postglacial tree migration from full glacial areas has originated from relatively nearby minor cryptic refugia, rather than being mediated by expansion from far distant refugia (Payette et al., 2002; Schauffler and Jacobson, 2002; Brubaker et al., 2005; Anderson et al., 2006, 2009; Opgenoorh et al., 2009; Hampe and Petit, 2010).

In a uniformitarian perspective, spruce in krummholz form is equally or even more hardy than mountain birch (Kullman, 2010). Consequently, there is actually no rational reason to discard, on the basis of climatic tolerance, the theory that spruce and other boreal trees grew throughout the Wechselian in ice-age refugia close to the ice sheet, although their presence is still in need of macro- or megafossil verification. The results of this study have highlighted the capacity of spruce for a virtually eternal life, provided that it is kept in prostrate krummholz form by a harsh climate. Certainly, the latter presumption was fulfilled throughout the glacial phase in proglacial habitats. In a complex topography, with local ample snow accumulation providing foliage protection during the coldest parts of the winters, long-term glacial survival is not untenable (cf. Petit et al., 2008; Anderson et al., 2009).

Despite the firm foundation of fossil data, some interpretations launched above are hypothetical and in definite need of further "fossil" and molecular genetical evidence. Nonetheless, it is evident that the late-Quaternary history of *Picea abies*, and reasonably of other taxa in northwestern Europe, is an unsettled, complex, and scientifically more challenging affair than has generally been assumed.

## CONCLUSIONS

Living clonal spruces, growing in open cold-marginal landscapes, have attained ages of 9500 years and possibly more. They represent a highly conservative structural element of the landscape and the legacy of a warmer-than-present early Holocene climate. Ancient spruce clones constitute high-resolution tools that enable detection of small and scattered early Holocene populations beyond the reach of other approaches such as pollen analysis.

Radiocarbon-dated spruce clones attest to a pattern of widespread spruce occurrences at high elevations along the Swedish Scandes in the early Holocene. This circumstance demonstrates that the first arrival of spruce in Sweden occurred several millennia earlier that has traditionally been believed.

Together with predominant pine, mountain birch, Siberian larch, and broadleaved deciduous species, spruce constituted a regular component of the early Holocene high-mountain vegetation, although with low abundance.

Longevity of spruce clones presupposes open and wind-exposed habitats. Consequently, their local environments have probably been as open as they are today even during the warmest parts of the Holocene. Presumably, they may remain open even in the hypothetical case of future climate warming.

Rapid postglacial immigration and spread of spruce along the entire Swedish Scandes could indicate that multiple "cryptic" glacial refugia existed much closer to Scandinavia than was previously thought.

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