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TREELINE DYNAMICS IN SHORT AND LONG TERM PERSPECTIVES – OBSERVATIONAL AND HISTORICAL EVIDENCE FROM THE SOUTHERN SWEDISH SCANDES

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Cover photos: *Front*. Ancient clonal mountain birch, "Old Ingrid", at Mt Getryggen, 905 m a.s.l., 5000 cal. yr BP. *Back*. The spruce clone “Old Rasmus” at Mt Sonfjället, 990 m a.s.l., 9480 cal. yr BP, and the Siberian husky Rasmus.

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ABSTRACT

Treelines in high-mountain regions are constrained by heat deficiency, although the working mechanisms are still not entirely understood. Observational and paleoecological studies on treeline performance may contribute to increased understanding of the treeline phenomenon in general. The present thesis addresses elevational shifts of alpine treelines in the Swedish Scandes. By various analytical tools, the studies embrace widely different temporal scales.

The concept treeline refers to the elevation (m a.s.l.) at a specific site of the upper individual tree of a certain tree species, at least 2 m tall. All the principal tree species in the Scandes are concerned, i.e. mountain birch (*Betula pubescens* ssp. *czerepanovii*), Norway spruce (*Picea abies*) and Scots pine (*Pinus sylvestris*).

Paper I deals with regional treeline dynamics at more than 100 sites over the past 100 years. Concurrent with temperature rise by c. 1.4 °C over the same period, maximum treeline advances of all species amount to about 200 m. Thus, under ideal conditions, treelines respond in close equilibrium with air temperature evolution. However, over most parts of the landscape, treeline upshifts have been much smaller than 200 m, which relates to the combined action of geomorphology, wind, snow distribution and soil depth. After 1975, the birch has lost its role as the most rapidly advancing tree species, being superseded by pine and spruce.

Paper II is a short-term (2005/2007-2010/2011) study of mountain birch treeline performance along a regional maritimity-continentality gradient. Upshift by 3.0 yr^{-1} in the maritime part of the gradient contrasts to retreat by 0.4 m yr^{-1} in the continental part. In the latter area, earlier and more complete melting of late-lying snow patches has seemingly progressed to a state when soil drought sets back the vigour of existing birches and precludes sexual regeneration and upslope advance of the treeline. In the maritime area, extensive and deep snow packs still exist above the treeline and constrain its position, although some release is taking place in the current warm climate.

Paper III explores treeline change by phenotypic transformation of old-established stunted and prostrate spruce individuals (krummholz) growing high above the treeline and is based on analyses of radiocarbon-dated megafossils, preserved in the soil underneath clonal groups of spruce. Living spruce clones, which in some cases may date back to the early Holocene (9500 cal. yr BP), suggests that spruce immigrated from "cryptic" ice age refugia much closer to Scandinavia than conventionally thought. As the krummholz form presupposes open and windy habitats, it is inferred that permanently open spots prevailed in the high-mountain landscape even during periods when treelines in general were much higher than today.

Paper IV reports radiocarbon dates of wood samples, retrieved from newly exposed glacier forefields at three main sites, located high above the modern treelines and embracing the entire Swedish Scandes. It appears that pine colonized early emerging nunataks already during the Late Glacial. Around 9600-9500 cal. yr BP a first massive wave of tree establishment, birch and pine, took place in "empty" glacier cirques. Both species grew 400-600 m above their present day treeline position and accordingly, the summer temperatures may have been 3.5 °C warmer than present (uncorrected for land uplift). During the entire interval 9600 to 4400 cal. yr BP, birch prospered 100-150 m above the uppermost pines. In response to Neoglacial cooling, treelines of both birch and pine descended until their final disappearance from the record 4400 and 5900 cal. yr BP, respectively. Thereafter, these habitats experienced increased snow accumulation and glacier inception.

Keywords: *Betula pubescens* ssp. *czerepanovii*, *Picea abies*, *Pinus sylvestris*, *Larix sibirica*, climate change, climate warming, monitoring, treeline advance, spruce clones, krummholz, megafossils, immigration, Holocene, cryptic refugia, Swedish Scandes, glacier forefields, vegetation history, paleoclimate.

SAMMANFATTNING

Avhandlingen belyser förskjutningar i olika tidsskalor av den alpina trädgränsens läge i de svenska Skanderna. Trädgränsen definieras som den högsta nivån (m ö.h.) för minst 2 m höga individer av en viss art i en definierad del av en fjällsluttning. Avhandlingen består av fyra separata uppsatser, publicerade i olika välrenommerade vetenskapliga tidskrifter.

I Paper I analyseras förändringar av trädgränserna för fjällens vanligaste trädarter, fjällbjörk, gran och tall (*Betula pubescens* ssp. *czerepanovii*, *Picea abies* och *Pinus sylvestris*) mellan 1915 och 2007. Undersökningen omfattar ett 8000 km^2 stort, naturgeografiskt heterogent område, med mer än 100 lokaler. De maximala trädgränsförskjutningarna för samtliga trädarter uppgår till omkring 200 m. Resultaten motsvarar de trädgränsförskjutningar som teoretiskt kan förutsägas utifrån den temperaturhöjning med cirka 1,4 °C som skett under samma tidsperiod, förutsatt ideala förhållanden. För större delen av området råder emellertid andra, icke-ideala förhållanden, varför trädgränsernas uppflyttning i allmänhet blivit avsevärt mindre än 200 m. Den främsta anledningen till detta är lokala topoklimatiska begränsningar, d.v.s. kombinerade effekter av geomorfologi, vind, snöfördelning, jorddjup, etc., som i stora delar av det starkt brutna fjällandskapet mer eller mindre effektivt hindrar träden från att nå sina potentiellt högst belägna växtplatser betingade av temperaturen. Efter 1975 har björken förlorat sin roll som arten med den snabbast expanderande trädgränsen. I stället har tall och gran avancerat med större hastighet. Det innebär att även om klimatets uppvärmning fortsätter, så kommer det subalpina björkbältet att expandera i avsevärt mindre omfattning än vad som ofta förebådats. Möjligtvis kommer det att ersättas av tall.

Paper II behandlar björkens trädgränsdynamik under perioden 2005/2007-2010/2011 längs en regional klimatgradient med avseende på maritimitet/kontientalitet. Trädgränsen har under den aktuella perioden avancerat 3,0 m/år i den maritimt präglade delen av gradienten, vilket kontrasterar signifikant mot en sänkning med 0,4 m/år i området med mer kontinentalt klimat. Skillnaderna diskuteras i termer av klimatförändringens varierande effekter på snötäckets utbredning och varaktighet och dess inverkan på markfuktigheten. En allt tidigare total utsmältning av snölegorna i de kontinentala områdena har av allt att döma resulterat i vattenbrist under sommaren. Torka medför reducerad vitalitet för existerande björkar och förhindrar både sexuell förökning och uppflyttning av trädgränsen. I de maritima delarna kvarligger alltjämt mycket snö under en stor del av sommaren. Trädgränsens position har därför kunnat bibehållas eller flyttas upp. Vissa omständigheter tyder på att trädgränsens stigning i högre grad har varit baserad på fröföryngring efter 1975, jämfört med perioden 1915-1975.

Utgångspunkten för Paper III är erfarenheter från Paper I, som visar att trädgränsens uppflyttning för gran och björk huvudsakligen är resultatet av ökad höjdtillväxt av äldre, i

vissa fall flertusenåriga, mer eller mindre buskformiga individer (krummholz), som vuxit på nivåer långt ovanför trädgränsen. Som ett svar på de senaste hundra årens varmare klimat har dessa antagit trädform, varigenom trädgränsen höjts. För en fördjupad förståelse av den här mekanismen har megafossil, d.v.s. grova vedrester bevarade i marken under gamla grankloner i trädgränsekotonen, ^{14}C-daterats. Resultaten tyder på att granar i exponerad fjällmiljö kan uppnå i det närmaste "evigt" liv genom sin förmåga till vegetativ förökning och möjligheten att växla mellan busk- och trädform i takt med klimatets växlingar. Vissa nu levande kloner existerade av allt att döma redan för 9500 år sedan. Den nu dokumenterat tidiga förekomsten av gran, bekräftar den på senare tid allt tydligare bilden av granen som en tidig invandrare till fjällkedjan. Möjligtvis har granen "övervintrat" den senaste istiden närmare Skandinavien än vad som till helt nyligen varit den gängse uppfattningen.

Paper IV behandlar en för Skandinavien ny metod för historisk trädgränsrekonstruktion. I uppsatsen analyseras ^{14}C-dateringar av totalt 78 större veddelar (megafossil) som nyligen exponerats i anslutning till smältande glaciäris och "perenna" snölegor i tre huvudområden, Helags-Sylarna, Tärna och Abisko, högt ovanför dagens trädgräns. Det framkommer att tall (*Pinus sylvestris*) koloniserade tidigt framsmälta nunatakker redan under senglacial tid. För omkring 9600-9500 år sedan inträffade en första massiv våg av björk- och talletablering i isfria glaciärnischer. Båda arterna växte 400-600 m ovanför sina nuvarande trädgränspositioner, i ett klimat som kan ha varit 3,5 °C varmare än idag.

Under intervallet 9600 till 4400 BP uppträdde björken i ett 100-150 m brett bälte ovanför de översta tallarna. Som ett svar på klimatets successiva avkylning under senare delen av Holocen sänktes både björkens och tallens trädgränser i de aktuella miljöerna, till dess de för 4400 respektive 5900 år sedan helt försvann från lokaler där glaciärer och perenna snöfält började bildas. De analyserade trädresterna, som länge bevarats av glaciäris och perenn snö representerar en period med ett klimat långt varmare än under det senaste århundradet. Med denna analogi från det förflutna kan det därför antas att i en framtid där sommartemperaturerna rent hypotetiskt är 3,5 °C högre än i nutiden, skulle trädgränserna lokalt kunna flyttas upp med ungefär 600 m.

Nyckelord: *Betula pubescens* ssp. *czerepanovii*, *Picea abies*, *Pinus sylvestris*, *Larix sibirica*, glaciärer, vegetationshistoria, paleoklimat, klimatförändring, trädgräns, fjällbjörk, gran, tall, sibirisk lärk, grankloner, megafossil, invandring, Holocen, kryptiska refugier, Skanderna.

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LIST OF PAPERS

This thesis is mainly based on the following four papers, herein referred to by their Roman numerals:

Paper I	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.
Paper II:	Öberg, L. & Kullman, L. 2012. Contrasting short-term performance of mountain birch (*Betula pubescens* ssp. *czerepanovii*) treeline along a latitudinal continentality-maritimity gradient in the southern Swedish Scandes. Fennia 190, 19–40.
Paper III:	Öberg, L. & Kullman, L. 2011a. Ancient subalpine clonal spruces (*Picea abies*) – sources of postglacial vegetation history in the Swedish Scandes. Arctic 64, 183–196.
Paper IV:	Öberg, L. & Kullman, L. 2011b. Recent glacier recession – a new source of postglacial treeline and climate history in the Swedish Scandes. Landscape Online 26, 1–38.

Paper I, II, III and IV are reproduced with the kind permissions of Journal of Ecology, Fennia, Arctic and Landscape Online, respectively.

1. INTRODUCTION

1.1 Treeline position and structure – the modern perspective (Paper I and II)

Treeline position and structure are key elements in mountain and cold-marginal landscape ecology (e.g. Holtmeier 2003; Alftine & Malanson 2004). High-altitude tree growth in general and treeline positions in particular are commonly inferred to be strongly correlated with air and soil temperature and thereby efficient bioindicators of ecological responses to climate change and variability (Tranquillini 1979; Kullman 1998, 2010a; Grace et al. 2002; Holtmeier 2003; Körner 2012). However, some researchers suppose that treeline positions are more or less resilient to climate change (Slatyer & Noble 1992; Masek 2001). The issue of current and future treeline evolution is confounded also by the fact that in many parts of the world treeline structure may bear a clear relationship to prior land use, which may conceal the importance of recent climate variability (cf. Hofgaard 1999; Gehrig-Fasel et al. 2007). In addition, treeline performance may locally be modulated by herbivory and inter/intra specific plant community mechanisms (Cairns et al. 2007; Olofsson et al. 2009; Holtmeier 2012).

It is increasingly recognized that understanding of climate-driven treeline dynamics has to be based on real-scale, multi-site observation series of treeline performance against a background of instrumental meteorological records (cf. Kallio et al. 1986; Woodward 1987; Guisan et al. 2007; Holtmeier 2003). An important rationale for studying treeline dynamism is based on the notion that treeline shifts may have a strong impact on alpine and subalpine biodiversity (Theurillat & Guisan 2001; Dirnböck et al. 2003; Walther et al. 2005; Kullman 2010b).

Paper I reports and analyses results from a multi-site, regional treeline monitoring project, spanning almost a century (1915-2007) and carried out in an area with virtually natural treeline positions. The main intention was to document the pace and extent of elevational treeline response of the principal tree species, i.e. mountain birch (*Betula pubescens* ssp. *czerepanovii*), Norway spruce (*Picea abies*) and Scots pine (*Pinus sylvestris*), relative to instrumentally recorded climate change and topoclimatic landscape variability.

Paper II focuses on mountain birch (*Betula pubescens* ssp. *czerepanovii*) treeline and its performance along a regional climatic maritimity-continentality gradient during the period 2005/2007-2010/2011. The results are discussed in terms of changes in snow cover phenology related to warmer climate.

1.2 Postglacial treeline history (Paper III and IV)

Research presented in this thesis is driven by the premise that improved understanding of past treeline dynamics is essential for modelling future ecological impacts of a potentially warmer (or colder) climate. With respect to treelines, conventional vegetation history methods, such as pollen analysis alone, are inadequate (Hicks 2006; Tinner & Theurillat 2003; Kullman 2008). Equally ambiguous are paleoeclimate reconstructions based on pollen data (Paus 2012). An alternative analytic approach, seeks to reconstruct postglacial treeline shifts by radiocarbon dating of different sources of megafossil tree remains, recovered at sites above the current treeline (Karlén 1976; Kullman 1995, 2012; Eronen et al. 1999; Aas & Faarlund 2000; Kullman & Kjällgren 2006). Megafossils provide an option for unambiguous documentation and direct dating of the presence of a tree species at a specific altitude.

As a complement to recent observational studies (Paper I and II), paleotreeline records afford inputs to general ecological treeline theory by displaying magnitudes and rates of species-specific treeline responses to low-frequency (multicentennial) climate forcing. Moreover, results from megafossil analyses also provide a rare and much needed possibility to calibrate and further develop the methods of pollen and molecular genetical analyses (Kullman 2008), an opportunity recently taken by some paleoecologists (e.g. Segerström & von Stedingk 2003; Giesecke 2005; Hörnberg et al. 2006; Paus 2010, 2012; Carcaillet et al. 2012; Parducci et al. 2012).

The broad temporal spectrum covered by the present thesis offers a possibility to put treeline shifts (implicit climate shifts) over the past century into perspective of the entire Holocene (e.g. Bergman et al. 2005; Kullman & Kjällgren 2006; Kullman 1995, 2012).

Paper III reports a retrospective study of radiocarbon-dated ancient Norway spruce (*Picea abies*) krummholz clones. The main focus is on the long-standing issue of early Holocene immigration and first appearance of spruce in the Swedish Scandes. This is an aspect with implications for possible glacial and late-glacial refuge areas and mechanisms for long-term survival and growth under widely shifting climatic conditions. In fact, many of the resident tree species in the Scandes reproduce at the treeline by the same kind of phenotypic plasticity as displayed by the spruce, i.e. temporal fluctuations in vegetative efforts, which adds generality to this study.

Paper IV deals with subfossil wood remnants recently outwashed from beneath glacier ice and snow bodies, located high above modern treelines. In Scandinavia, this kind of detrital wood is a previously virtually unused source of postglacial vegetation and climate history. The study reports radiocarbon dates of a set of 78 wood samples, retrieved from three main sites, along the Swedish Scandes.

2. STUDY AREAS

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, 2010a).

Paper I and II embrace a large number of sampling sites within an area of ca 8000 km^2, in the southern Swedish Scandes, 61°05′ to 63°25′ N and 12°03′ to 13°11′ E (Fig. 1). Paper III reports and analyses data from the southernmost part of the above-mentioned area. Paper IV accounts for data from three areas, south to north along the Swedish Scandes; Helags/Sylarna, Tärna, and Abisko.

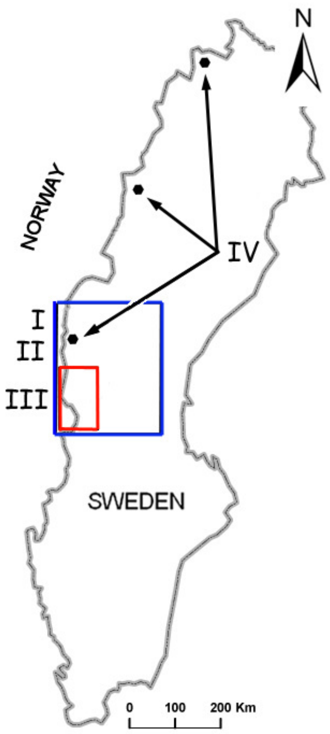

FIG. 1. Location of the studied areas; Paper I and II - *large blue frame*, Paper III - *small red frame*, Paper IV - *arrows*.

In all studied areas, mountain birch (*Betula pubescens* ssp. *czerepanovii*) constitutes the uppermost closed forest and forms the upper treeline, followed in order by the treelines of Norway spruce (*Picea abies*) and Scots pine (*Pinus sylvestris*) about 50 and 100 m below, respectively. Notably Norway spruce is lacking in the Abisko area.

3. METHODOLOGY

Below, the methodological approaches and general premises for the different papers (I-IV) are outlined.

3.1 Treeline and treeline ecotone - definitions

The *treeline* is defined, by convention, as the elevation (m a.s.l.) at a specific location of the uppermost individual of each tree species, with a minimum height of 2 m (cf. Miehe & Miehe 2000; Hofgaard et al. 2009). This is a practical and unambiguous definition, leaving little room for interpretation and allows inter-comparability in space and time. As a rule, this "line" concerns scattered individual trees or small groups which, viewed broadly over an entire mountain slope, often reach virtually the same elevation. Thus, the treeline provides a reasonable expression of the landscape ecological impact of local/regional climate (Kullman 2010a).

The *treeline ecotone* is a broad and indistinct zone, extending from the uppermost outliers of spruce and pine trees, growing in the lower reaches of the subalpine mountain birch belt, up to *tree species line*. In the most continental part of the study area, the birch belt is only fragmentarily developed or even lacking, while it is denser and broader in more snow-rich parts to the north and west (Kullman 2010a).

The *tree species line* is the uppermost occurrence of a certain tree species, irrespective of size.

3.2 Recent treeline shifts (Paper I, II, IV)

The fundament of a regional treeline monitoring network was established around 1915 in the southern Swedish Scandes by Dr Harry Smith (Smith 1920), who documented treeline positions (m a.s.l.) at regularly distributed points in the mountain landscape and with the same definition as specified above. This network is the source of unique baseline information, consisting of almost 400 data collection points and covering c. 8000 km^2.

Around 1975, repeated measurements of treeline positions were accomplished, combined with age structure analyses, for a random selection of 213 of Smith's (1920) original birch sites (Kullman 1979). For pine and spruce, analogous studies, covering the same period of time, have been carried out (Kullman 1981, 1986). Paper I draws on a sub-sample of these historical records. Elevational treeline shifts (or stasis) were quantified separately for the periods 1915–1975, 1975–2007 and for the entire period 1915–2007.

Paper II focuses specifically on elevational change of the birch treeline over the period 2005/2007 – 2010/2011, for simplicity cited as 2007-2011, using a random subsample of spatially very precise treeline records from the years 2005-2007 (Kullman & Öberg 2009) as a benchmark. A total of 44 sites were fairly evenly distributed among two areas representing distinctly different climate characters, with respect to thermic continentality/maritimity.

Paper IV contains a minor case study of recent treeline dynamics in the Abisko-area. Data on treeline elevations in the early 1950s at a small number of sites were compared with analogous measurements carried out in 2009 and 2011.

3.3 Paleotreelines (Paper III, IV)

Paper III focuses on megafossil tree remains, i.e. dead wood and cones, originating around and above the modern treeline. The main emphasis was on radiocarbon-dated megafossil wood remnants preserved in the soil underneath the dense foliage of subalpine and alpine krummholz spruces.

As a general context for discussing and understanding the life histories of the dated spruce clones, megafossils of tree species other than spruce were exhaustively searched, retrieved and radiometrically dated from sites around the sampled spruces. This endeavour comprised peat deposits and shallow ponds distributed from slightly below the modern treeline and up to the highest treeless mountain peaks in the study area.

Paper IV was carried out within three main glacier areas, distributed along a total distance of ~700 km between the southernmost and northernmost part of the Swedish Scandes (Fig. 1).

Recently exposed forefields of alpine glaciers and perennial snow/ice patches were systematically searched for the presence of megafossil wood remnants, useful for radiocarbon dating. In addition, great effort was devoted to scrutinize adjacent alpine tundra, at the same and higher elevations, for megafossils.

3.4 Altitude measurements

Altitudes of monitoring and sampling sites were obtained to the nearest 5 m with a GPS navigator (Garmin 60CS). The GPS unit was calibrated several times during the day against topographical maps".

3.5 Radiocarbon datings

Radiocarbon dating of recovered megafossils was conducted by Beta Analytic Inc., Miami, Florida (USA). Throughout, dates are expressed in the text as calibrated years before present, cal. yr BP ("present" = 1950 AD). Calibration is conducted according to CALIB 5.0.2 (Stuiver et al. 2005) in combination with

INTCAL04. In the text, the intercept values of radiocarbon age are used for simplicity.

4. RESULTS AND DISCUSSION – PAPER I AND PART OF PAPER IV

Treelines of birch, spruce and pine have shifted upslope at 95 % of all studied localities (Fig. 1) during the past 100 years and well in concert with rising trends of summer and winter temperatures. All studied tree species have advanced to broadly the same extent, both with respect to mean and maximum upshifts. This suggests that in one and the same climatic region, treelines of species with different ecologies respond to climate change according to an ultimately common principle. For shorter sub-periods, however, there are inter-specific differences. Over the period of 1915–1975, *Betula* and *Picea* displayed larger and more rapid upshifts than *Pinus*. Eventually, *Pinus* has lined up with *Betula* and *Picea.* Conceivably, this dichotomy is partly a consequence of a delayed response of *Pinus,* owing to its total reliance on seed regeneration, but also relates to a climate that has gradually become more conducive to pine, i.e. drier and with less late-lying summer snow. In contrast to birch and spruce, pine exclusively reproduces with seed. As a consequence, its treeline rise is accomplished by growth of individuals established during the past century. Preconditions for rapid height increment have been very favourable after the 1970s, when pines have developed from seed to tree size.

A minor analogous study of birch performance in the Abisko region (Paper IV) revealed that over the period from the early 1950s to 2010, birch treeline upshift by 105 to 225 m took place. Like the case in the southern Scandes, (Paper I) treeline rise was predominately accomplished by growth form change of old-established krummholz to erect tree forms. This common inter-regional response pattern stresses the pivotal role of climate warming as the main driver and questions the decisive role of strictly local and heterogeneous drivers, e.g. ceasing human impact or reindeer grazing. This is particularly evident as the intensity of prior land use practices appear to have been particularly strong in the Abisko area (Emanuelsson 1987; Hofgaard 1999) and less influential in the southern Scandes (Kjällgren & Kullman 1998; Virtanen et al. 2003; Paper II).

Maximum advance by about 200 m for all species is coincident with 1.4 °C summer and winter warming, which almost perfectly matches the predicted value, based on a lapse rate of 0.6 °C per 100 m altitude and the assumption of a near-perfect treeline-climate equilibrium (Fig. 2, 3). The obtained results conform qualitatively to the outcome of analogous studies in widely different parts of the northern world, although the magnitudes of change differ (Aas 1969; Esper &

Schweingruber 2004; Lloyd 2005; Tape et al. 2006; Danby & Hik 2007; Shiyatov et al. 2007; Devi et al. 2008; Harsch et al. 2009; Hofgaard et al. 2009; Kharuk et al. 2009), supporting the view that this is basically a climate change phenomenon of virtually global significance.

Since several ground-layer species and plant communities have shifted upslope with the same order of magnitude as the treeline (Kullman 2010b, c), it appears that treeline performance can be used as a pointer for widespread shifts in the whole ecosystem.

With respect to the potential and often discussed impact of reindeer grazing and trampling on treeline performance (e.g. Olofsson et al. 2009; Aune et al. 2011), no obvious differences in treeline dynamics were gleaned between areas with heavy and light (or lacking) grazing pressure (cf. Paper I). Moreover, substantial treeline upshift occurred during a period (since the early 20th century) when reindeer numbers in the county of Jämtland increased by about 70 % (Virtanen et al. 2003; SOU 2006).

FIG. 2. *Left*. The position of mountain birch treeline at Mt. Brattriet SW, Härjedalen, in 2006 at 1140 m a.s.l. This steep lee-side slope, prone to large snow accumulation, represents maximum recorded treeline rise for mountain birch by 195 m. Photo: 2006-08-22. *Right*. The pine treeline position in 2007 at Mt. Städjan SW, Dalarna, at 1045 m a.s.l. Typically, pines at the treeline prefer exposed, dry and snow poor sites. Photo: 2007-07-14.

4.1 From Krummholz to tree mode

In most cases, birch and spruce treelines have advanced by *in situ* growth form transformation from old-established krummholz into erect, arborescent modes (Fig. 3). It appears from Paper III that some of these individuals, which mainly reproduce by basal sprouts and layering, have become established long before the 20th century.

FIG. 3. The spruce treeline position in 2007 at Mt. Lillskarven SW, Härjedalen, at 1065 m a.s.l. represents maximum recorded treeline rise by 220 m for spruce. This spruce clone has recently converted from krummholz to upright tree. As typical for the localities displaying the largest spruce treeline upshifts, snow and wind conditions are intermediate. Photo: 2007-08-12.

4.2 Large variation between sites

One important aspect of the present study is the large variation between sites with respect to the magnitude of treeline rise that is, 0–220 m. Based on the results obtained in Paper I, it is suggested that this relates to site-specific topoclimatic constraints. Analogous results are reported from other parts of the Scandes (Aune et al. 2011; Van Bogaert et al. 2011) and also in a global perspective (Harsch et al. 2009; Elliott 2011). Only quite infrequently have treelines reached the potential positions as defined by the regional ambient climate conditions. The largest upshifts, particularly for birch, are accomplished in long, sweeping concave slopes, where diffuse treeline ecotones evolved as a result. These settings may offer optimal insolation, wind shelter, stable soil moisture and physically safe sites for tree growth over a large elevational range (Fig. 4). Commonly, this habitat type previously supported snowfields well into the summer. During the past century, these have tended to melt-out earlier in the growing season, which has created opportunities for tree growth at higher elevations than before. In contrast, treeline stability or only relatively small upshifts have occurred in sites with convex topography, where strong winds, a sparse snow cover and intense reindeer grazing prevents further advance, thereby creating relatively abrupt treelines (Hofgaard et al. 2009).

Spatial heterogeneity of elevational treeline rise in response to the same phase of climate change is a reality which has to be considered when modelling future evolution of the forest-alpine tundra transition. In a hypothetical case of substantial future warming, treelines are unlikely to advance at a broad front over the alpine landscape, in contrast to suggestions made by, e.g. Moen et al. (2004), and a large proportion of the alpine area is likely to remain woodless.

FIG. 4. The locality Lillstensdalsfjället N, where birch treeline rose by 190 m (1915-2007). The former glacier cirque offers optimal insulation, wind shelter, fairly stable soil moisture and physically safe sites for tree growth over a large elevational range. Photo: 2010-09-13.

4.3 Winter temperature rise in favour of conifers

One aspect of relevance for general treeline ecology, which emerges from this study, concerns the role of winter temperature conditions. As evidenced, treelines of conifers have risen substantially more rapidly than the birch treeline during the past 2–3 decades. This course of change coincides with air and soil temperature increases, which were most significant for the winter period. Increased survival rates during this period seem to be the consequence of a substantially reduced incidence of foliage dieback due to winter desiccation (cf. Kullman 2007).

The larger treeline movements (1975–2007) recorded for *Pinus* and *Picea* relative to *Betula* comply with the generalization that rising winter temperatures may favour evergreen coniferous species at the expense of broadleaved deciduous species (cf. MacDonald et al. 2007).

4.4 Reversal of a long-term cooling

Centennial treeline rise by a common maximum for all species of about 200 m represents the effect of a reversal of a long-term cooling trend, forced predominantly by Earth's orbital parameters. As evident from Paper III, this dominant tendency has prevailed since the early Holocene (cf. Kullman & Kjällgren 2006; Paus 2010; Kullman 2012;) and is largely consistent with Greenland ice core proxy paleotemperature data (Oldfield 2005). To the best of our present-day knowledge, the maximum upshifts of the treelines seem to approach positions held during the Medieval Warm Period (AD 900–1300) (Kullman & Kjällgren 2006; Kullman 2012). Anyhow, recent maximum treeline upshifts represent elevational advance from the lowest Holocene level to a position unusual (but not unique) for the past 5000 years or so (Kullman 2004a, 2012; Kullman & Kjällgren 2006).

5. RESULTS AND DISCUSSION - PAPER II

Over the period 2007 to 2011, the birch treeline rose on 48 % of the investigated sites. Retreat and stability were recorded at 11 and 41 % of all sites, respectively. Of those sites with recorded treeline advance, 86 % were in the area with a maritime climate. Moreover, the magnitude of recent treeline change was significantly larger in the climatically maritime than in the continental area.

The study of the clonal age of a treeline birch, typical of those which transformed from krummholz to tree-size during the past century, sustained that it had established much earlier than the modern warming phase (Fig. 5). Decaying wood retrieved from underneath the stools of living and dead stems indicated that this specimen existed already by 4770 cal. yr BP.

Signs of reindeer browsing on twigs and branches were found on about 50 % of the treeline markers in both the maritime and continental area. In most cases, only the tips of annual shoots were browsed and in no case was reindeer impact obviously responsible for cases of treeline retreat during the study period.

Despite virtually similar magnitudes of recent climate warming, short-term positional treeline responses differ significantly between maritime and continental climates. Thus, it appears that treeline dynamics by mountain birch is only indirectly mediated by the course of ambient temperature change and more directly by some variable associated with the maritimity/continentality continuum, most likely snow cover phenology and related soil moisture conditions.

The character of birch decline in the continental area suggests that soil drought and desiccation have recently reached critical levels, as preconditions for sustainable growth and seed regeneration have gradually become decidedly sub-optimal over the past century. Earlier and more complete snow melt and thereby drier soils, is supported by landscape-scale studies, which documents disappearance of snow beds and associated plant communities in the continental area (Kullman 2004b, 2005b).

Predominance of upshifts in the maritime region has a clear spatial relation to sites influenced by a relatively deep and persistent snow cover. This setting, in its most extreme form, does not support establishment and growth of mountain birch (Björk & Molau 2007). In accordance with the current warm phase this constraint is becoming gradually released and new ground with a suitable snow cover and sufficient soil moisture for tree growth by birch is exposed at the margin of receding snow patches (Fig. 6, 7).

It appears that most of the new treeline markers originate from seed establishment over the past 30 years or so. The inference conforms to reports from other parts of the Scandes (Hofgaard et al. 2009; Aune et al. 2011). Treeline advance during the first half of the 20th century was accomplished mainly by transformation of old-growth krummholz birches to arborescent form (Kullman 1979, 2010a).

FIG. 5. *Left*. Ancient mountain birch which grew as a prostrate krummholz-individual, 75 m above the treeline of the early 20th century. *Mid*. Coring at the ground surface level yielded 221 year rings. *Right*. Wood remnants in the soil underneath the stem base were radiocarbondated and indicate that this individual specimen existed here almost 5000 years ago.

6. RESULTS AND INTERPRETATION - PAPER III

The ability of spruce to regenerate clonally by layering close to the treeline is well documented and described in the Scandinavian scientific literature (Kihlman 1890; Kallio et al. 1971; Kullman 1986). The emergent krummholz growth form is interpreted primarily as a response to a harsh, cold and windy winter climate at the taiga-tundra interface or in analogous cold-marginal situations (e.g. Lavoie & Payette 1994; Kullman 1996; Hammer & Walsh 2009).

FIG. 6. Late-lying snow patches and associated meltwater are essential for the existence of subalpine birch forest, but also constrain the elevational position of the treeline. Mt. Storsnasen, 10 July 2011.

FIG. 7. In the maritime area, birch is frequently invading hollows and lee slopes, where previously too much of late-melting snow prevented establishment and growth. Mt. Getryggen, 8 August 2011.

Most of the investigated clones are located in the "advance zone", i.e. between the spruce treeline positions (altitude) held in the early 20th century, and the first decade of the 21st century, i.e. where the treeline shifted upslope by transformation from krummholz to arborescent form (phenotypic plasticity) in response to modern climate warming (Öberg 2008; Kullman & Öberg 2009; Kullman 2010a). 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 was initiated in the late 1930s, as evident in general for the entire study region (Kullman 1986; Paper I).

The clones focused in this study all grow in open landscapes, i.e. patches of exposed and dry-mesic alpine tundra, without fire indications. The vascular plant cover underneath the dense canopy of the clones is generally very poor or virtually lacking, as a consequence of dark and dry conditions. In no case have new spruce genets, i.e. seedlings or saplings, been recorded within the clones of this kind (Kullman & Öberg 2009), neither on the ground nor on the rare coarse woody debris. These observations and other lines of circumstantial evidence support the view that the extant clones are genetically identical with the unearthed ancient wood remains in the soil beneath the canopies.

Typically, large snow drifts pile up over and in lee of the clones. Except for the supra-nival stems, the snow cover provides protection from wind stress and frost desiccation and adds soil moisture, which contributes to their endurance in the harsh alpine environment.

6.1 Radiocarbon ages of megafossil spruce remains

The obtained radiocarbon ages originating from wood pieces and cones, buried underneath the 10 investigated spruce clones focused here, range between 9550 cal. yr BP and the present. Two clones representing well separated localities, attest to the presence of spruce around 9500 cal. yr BP (Fig. 8).

Throughout much of the Holocene and over the entire study region, it appears that spruce has been growing in the area between the present-day (2007) treeline and somewhat below its lower position in the early 20th century. Individual longevity appears to be conditional upon a stunted and persistent horizontal growth form (krummholz), which implies a constantly positive and favourable needle-wood ratio. Such a situation can be durably maintained in a harsh and open environment, where emergence of tall and relatively less productive arborescent stems is prohibited for most of the time by dieback caused by severe winter conditions, which notoriously breaks the apical dominance (Laberge et al. 2000) (Fig. 8).

Since persistence of clonal spruces are conditional on an open landscape, current treeline ecotones with abundant krummholz spruces have probably been virtually as open as today throughout most of the Holocene, even during the thermal optimum in its early part (see below). Obviously, strong winds and associated factors are major forces, which keep some parts of the high mountain landscape open and woodless even during prolonged periods of general warming (cf. Holtmeier & Broll 2010).

FIG. 8. *Left*. Underneath the infra-nival skirt of this spruce, "Old Tjikko", the oldest wood remnants dated 9550 cal. yr BP. Mt. Fulufjället E, 905 m a.s.l. Photo: 2010-10-01. *Right*. The oldest wood remnants belonging to the spruce "Old Rasmus" yielded a date of 9480 cal. yr BP. Mt. Sonfjället W, 990 m a.s.l. Photo: 2004-04-03.

6.2 Holocene arboreal history of birch and pine - the general vegetation context of contemporary spruce performance

The highest parts of the south-central Scandes, including the study region, were obviously deglaciated much earlier than previously proposed. With some regional variation, the highest peaks, i.e. those reaching above 1100-1600 m a.s.l., appear to have been ice-free already by 16 000-17 000 cal. yr BP, while deglaciation of the valleys was substantially delayed (Dahl et al. 1997; Kullman 2000, 2002a; Follestad 2003; Kullman & Kjällgren 2006; Bøe et al. 2007; Goehring et al. 2008; Paus et al. 2006; Paus 2010; Paus et al. 2011).

Within the study area, the view of late-glacial summit deglaciation and attendant local tree growth is sustained by megafossil remains of *Pinus sylvestris,* which were unearthed close to the summit of Mt. Städjan, 1080 m a.s.l., 45 m above the local treeline (Kullman 2004a). The present study attest to the growth of boreal trees around 10 000 cal. yr BP at least 350 m above the treeline position prevailing about a century ago. This indicates a rapid evolution of a climate more favourable to high-elevation tree growth than today, presumably representing a Holocene thermal optimum around 9500 cal. yr BP (cf. Hoek & Bos 2007; Paus 2012). Subsequently, and throughout the Holocene, the upper elevational range of pine declined almost linearly (c. 28 m per millennium) until the late-19th century.

The relatively low frequency of birch megafossils indicates that birch has never played an important role in the treeline ecotone and obviously pine has been the dominating species throughout, in this part of the Scandes. Of course this pattern could be an effect of species-specific decay rates, but since large amounts of both birch and pine megafossils from the same period are found in other areas (Kullman & Kjällgren 2006; Paper IV), this seems to be an unlikely option. Experiences from other parts of the southern Scandes suggest that the mountain birch belt emerged quite late during the Holocene, in response to Neoglacial cooling (Kullman 1995, 2004c, 2012; Barnett et al. 2001). Low abundance of competitive birch, a fairly open landscape and a low fire frequency throughout the Holocene, may have contributed to longevity of clonal individuals.

Aside of the relatively high pine treeline during the early Holocene, macrofossils of thermophilic tree species (*Corylus avellana* and *Quercus robur*) in the current treeline ecotone suggest a climate warmer than present. Likewise, their disappearance from the paleorecord in the mid-Holocene argues for enhanced cooling thereafter.

6.3 Aspects of spruce immigration history

The present study sustains that since the early Holocene, i.e. at least 9500 cal. yr BP, solitary spruces grew at high elevations in a sparse matrix of predominant pine and scattered mountain birches and *Larix sibirica*. The no-analogue character of this arboreal landscape and the climate supporting it is further stressed by occurrences of thermophilic broadleaved deciduous tree species, *Quercus robur* and *Corylus avellana* at high elevations.

Presence of spruce, as evidenced by megafossils, already at the very beginning of the Holocene counters the prevailing idea of a late Holocene immigration and regional spread of spruce into northern and western Scandinavia (e.g. Moe 1970; Huntley & Birks 1983). It now stands out that spruce was one of the first tree species to colonize the virgin postglacial tundras in the southern Swedish Scandes. Virtually all megafossil spruces dating back to the early Holocene cluster far to the west and along the Scandes, locally even west of the main water divide (in Norway). This implies that the traditional view of first Holocene immigration from far-distant ice age refugia in Russia is arguable (cf. Kullman 2000). It may be hypothesized that spruce "hibernated" the last ice age in refugia quite close to Scandinavia (Kullman 2008; Paus et al. 2011). The late-Quaternary history of spruce, and reasonably other taxa in north-western Europe, is an unsettled, complex and scientifically more challenging affair than previously assumed. This issue is in definite need of further "fossil" and molecular genetical evidence (cf. Parducci et al. 2012; Birks et al. 2012).

7. RESULTS AND DISCUSSION - PAPER IV

Climate warming during the past century has imposed recession of glaciers and perennial snow/ice patches along the entire Scandes (Nesje 2009). Perceptible ice loss has continued between 2001 and 2010 (Fig. 9). On the newly exposed forefields, subfossil wood remnants as well as archaeological remains are being outwashed from beneath retreating ice and snow bodies (Kullman 2004c; Nesje et al. 2011).

Paper IV is based on data from three areas from south to north along the Swedish Scandes; Helags/Sylarna, Tärna, and Abisko, where radiocarbon datings of subfossil wood remnants, retrieved from the newly exposed forefields of receding glaciers and perennial snow/ice patches, is used as a source of postglacial treeline and climate history (Fig. 10).

7.1 Subfossil wood remnants

A data set of 78 radiocarbon-dated subfossil tree remants from all three main study areas constitutes the core of this study. Of these, 56 were determined as birch (*Betula pubescens* sensu lato) and 22 as pine (*Pinus sylvestris*).

Many samples were badly decomposed while some were astonishingly well preserved, with intact bark and small twigs and roots (Fig. 23, Paper III). Subfossil wood, released from the ice, decomposes very rapidly and reasonably, the megafossils are now exposed for the first time since the death of the trees. Overall, the sampled megafossils of birch and pine are spread over the time period 13 145 to 4400 cal. yr BP.

Aside of the wood remnants, several strongly compressed "peat cakes", containing a rich flora of macrofossils (e.g. *Betula pubescens, B. nana, Vaccinium uliginosum*, *Empetrum hermaphroditum*) were outwashed on the investigated forefields.

Large expanses of the commonly windswept landscape at adjacent and higher elevations than the megafossil sites were intensively searched for the presence of subfossil tree remains. The result was entirely negative.

7.2 Vegetation history

It is an entirely new and startling discovery that high-alpine sites in the Scandes, 500-600 m above the contemporary treeline and currently occupied by glacier ice and perennial snow, have for long periods of the early- to mid-Holocene harboured stands of trees.

A particularly noteworthy aspect of this study is that from the Late Glacial to the present day, the treeline history appears to be virtually the same along most of the Scandes. This suggests, as deduced also from Paper I and II, a common climatic cause as the main driver of Holocene treeline performance.

The new data from the Abisko-region, in combination with results from an earlier case study (Kullman 1999), provide evidence that pine immigrated to this region much earlier and to substantially higher maximum elevations than commonly inferred by more conventional paleoecological approaches (e.g. Barnekow 1999; Seppä et al. 2004). Besides, the present study suggests that pine was a more frequent constituent of the early Holocene high-mountain landscape than previously assumed (e.g. Barnekow 1999; Bigler et al. 2002; Seppä et al. 2004).

Aside of the sparse late-glacial records, a widespread wave of tree establishment occurred around 9600 cal. yr BP along the entire Swedish Scandes. This pattern is broadly consistent with data presented in Paper III and inferences based on pollen and megafossils retrieved also from other parts of the Scandes (Aas & Faarlund 2000; Barnett et al. 2001; Eide et. al 2006; Bergman et al. 2005; Kullman & Kjällgren 2006; Paus 2010; Paus et al. 2011; Kullman 2012). Early-Holocene tree growth of birch and pine up to 600 m above the current treelines of these species provides a new view on the structure of the early-Holocene high-mountain landscape. The existence of solely birch megafossils 100-150 m above the upper range limit of scattered pine remnants suggests that, strictly locally, birch grew as discrete stands or solitary trees well above a more or less continuous belt of pine or mixed pine/birch throughout the period embraced by the megafossils.

The balance of evidence indicates that the highest early Holocene tree growth was exclusively accomplished by birch and confined to sheltered localities of the kind, which has harboured glacier and snow patches during the late Holocene (Fig. 6). At somewhat lower elevations, however, glacier/snow accumulating sites supported both birch and pine.

7.3 Paleoclimate

The tight and overlapping assemblage of tree megafossils between 9600 and 4400 cal. yr BP suggests that the studied glaciers and snow/ice patches were substantially smaller than today, or did not exist at all during that time span. This is largely in line with glacier histories from other parts of Scandinavia (Snowball & Sandgren 1996; Rosqvist et al. 2004; Bakke et al. 2005; Nesje 2009) and fits with a world-wide pattern of minimum glacier volumes and a warmer-than-present climate during most of the early-to mid-Holocene (e.g. Hormes et al. 2001; Levy et al. 2004; Nicolussi et al. 2005; Buffen et al. 2009; Briner et al. 2010).

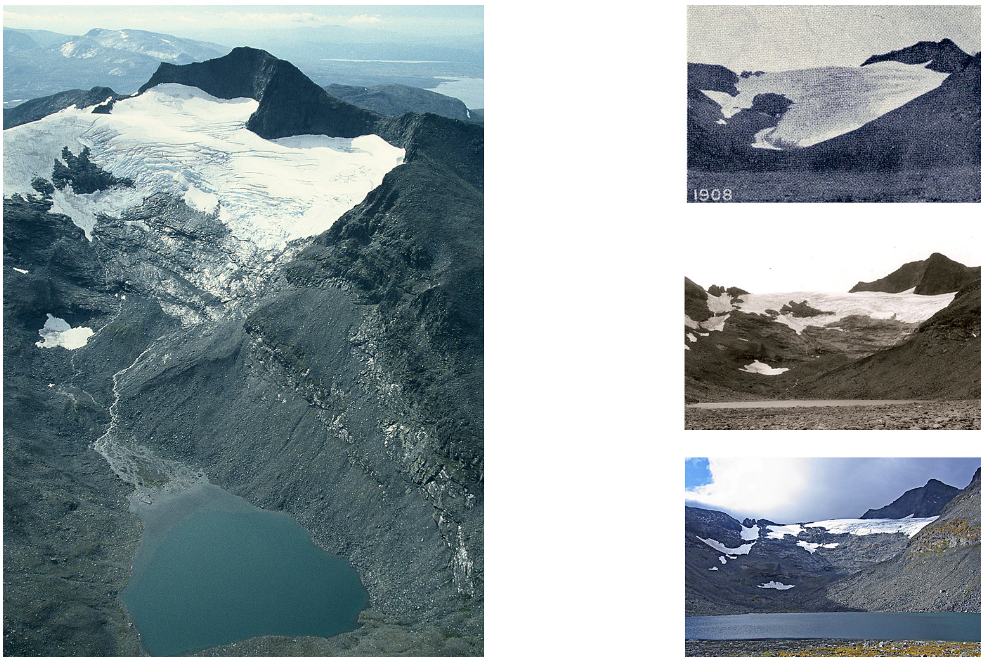

FIG. 9. *Left*. Aerial view of Storsylglaciären. By the early 20th century, the glacier terminated at the small inlet delta by the proglacial lake (Syltjärnen) in the foreground, 1276 m a.s.l. 2005-08-15. *Right top*. Storsylglaciären close to its Neoglacial maximum, in 1908. Photo: Enquist (1910). *Right mid*. By the early 21st century, the glacier had lost approx. 50 % of its prior volume. 2001-08-21. *Right bottom*. Recession has continued during the first decade of the 21st century. 2010-09-10.

FIG. 10. *Left*. Kåppasglaciären. Recently outwashed birch log. 6980 cal. yr BP. *Mid*. Kåppasglaciären. Wood remnant of pine, exposed right at the glacier front. 7680 cal. yr BP. *Right*. Tärnaglaciären. Large piece of a birch stem with bark fragments, exposed in the main drainage stream. 6280 cal. yr BP.

Treelines as much as 600 m higher than present during the early Holocene could tentatively imply summer temperatures 3.5 °C above modern standards (uncorrected for land uplift). By using that estimate as a tentative paleoanalogue for future treeline evolution, it appears that secular warming by 3-3.5 °C, as often anticipated from climate models, may force treelines upslope by 500-600 m in elevation. Hypothetically, this will not occur on a broad front over the present-day alpine landscape. Much like recent climate-driven treeline advance (Paper I), potential future birch treeline upshift will be restricted to sheltered sites where late-laying snow and ice have precluded tree growth for long times in the past.

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9. AUTHOR CONTRIBUTIONS

Lisa Öberg and Leif Kullman conceived, planned and executed the studies in cooperation. Both authors contributed substantially to the analyses and writing of the text of all four papers.

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