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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 photo: Old clonal spruces at Mt. Sonfjället, 990-995 m a.s.l.: The spruce "Old Rasmus", 9480 cal. yr BP (*right*) and "Old Raisa", 2340 cal. yr BP (*left*).

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

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ABSTRACT

Against the background of past, recent and future climate change, the present thesis addresses elevational shifts of alpine treelines in the Swedish Scandes. By definition, *treeline* refers to the elevation (m a.s.l.) at a specific site of the upper trees of a specific tree species, at least 2 m tall.

Based on historical records, the first part of the thesis reports and analyzes the magnitude of treeline displacements for the main trees species (*Betula pubescens* ssp. *czerepanovii*, *Picea abies* and *Pinus sylvestris*) since the early 20th century. The study covered a large and heterogeneous region and more than 100 sites. Concurrent with temperature rise by c. 1.4 °C over the past century, maximum treeline advances of all species amount to about 200 m. That is virtually what should be predicted from the recorded temperature change over the same period of time. Thus, it appears that under ideal conditions, treelines respond in close equilibrium with air temperature evolution. However, over most parts of the landscape, conditions are not that ideal and treeline upshifts have therefore been much smaller. The main reason for that discrepancy was found to be topoclimatic constraints, i.e. the combined action of geomorphology, wind, snow distribution, soil depth, etc., which over large parts of the alpine landscape preclude treelines to reach their potential thermal limit.

Recorded treeline advance by maximum 200 m or so over the past century emerges as a truly anomalous event in late Holocene vegetation history.

The second part of the thesis is focused more on long-term changes of treelines and one specific and prevalent mechanism of treeline change. The first part of the thesis revealed that for *Picea* and *Betula*, treeline shift was accomplished largely by phenotypic transformation of old-established stunted and prostrate individuals (krummholz) growing high above the treeline. In obvious response to climate warming over the past century, such individuals have transformed into erect tree form, whereby the treeline (as defined here) has risen. As a means for deeper understanding of this mode of positional treeline change, extant clonal spruces, growing around the treeline, were radiocarbon dated from megafossil remains preserved in the soil underneath their canopies. It turned out that Picea *abies* in particular may attain almost eternal life due to its capability for vegetative reproduction and phenotypic plasticity. Some living clones were in fact inferred to have existed already 9500 years ago, and have thus persisted at the same spot throughout almost the entire Holocene. This contrasts with other tree species, which have left no living relics from the early Holocene, when they actually grew equally high as the spruce. Thereafter they retracted by more than 300 m in

elevation supporting that also on that temporal scale, treelines are highly responsive to climate change.

The early appearance of *Picea* in the Scandes, suggests that *Picea* "hibernated" the last glacial phase much closer to Scandinavia than earlier thought. It has also immigrated to northern Sweden much earlier than the old-established wisdom.

The experiences gained in this thesis should constitute essential components of any model striving to the project landscape ecological consequences of possible future climate shifts.

SAMMANDRAG

Mot bakgrund av historiska, nutida och framtida klimatförändringar, belyser avhandlingen förskjutningar av den alpina trädgränsens läge i de svenska Skanderna. Trädgränsen definieras som den högsta nivå (m ö.h.) vid vilken minst 2 m höga individer en viss art förekommer i en bestämd fjällsluttning.

Den första delen, som baseras på historiska data, beskriver och analyserar förändringar av trädgränserna för våra vanligaste trädarter (*Betula pubescens* ssp. *czerepanovii*, *Picea abies* and *Pinus sylvestris*) sedan 1900-talets början. Studien omfattar ett stort, heterogent område med mer än 100 lokaler. De maximala trädgränsförändringarna för samtliga trädarter uppgår till omkring 200 m och stämmer därmed väl överens med det värde som teoretiskt kan förutsägas utifrån den temperaturhöjning med cirka 1,4 °C som skett under samma tidsperiod. Det förefaller alltså som om trädgränserna i det närmaste skulle kunna vara i jämvikt med klimatet, förutsatt ideala förhållanden. För större delen av området råder emellertid andra, icke-ideala förhållanden, varför trädgränsernas förändring där i allmänhet blivit avsevärt mindre. Den främsta anledningen till detta kan hänföras till topoklimatiska begränsningar, d.v.s. en kombinerad effekt av geomorfologi, vind, snöfördelning, jorddjup, etc., som i stora delar av fjällandskapet hindrar träden från att nå sina potentiellt högst belägna växtplatser med avseende på temperaturen.

Den konstaterade maximala uppflyttningen av samtliga studerade arters trädgränser på omkring 200 m framstår som en mycket ovanlig typ av händelse i vegetationshistorien under senare delen av Holocen.

I avhandlingens andra del ligger fokus på trädgränsens dynamik över en längre tidsperiod och på en speciell, vanligt förekommande mekanism för förändring av trädgränsens läge. Den första studien avslöjar att trädgränsens uppflyttning för *Picea* och *Betula* till stora delar ägt rum genom fenotypiska anpassningar av äldre, mer eller mindre buskformiga individer (krummholz), som vuxit på nivåer långt ovanför trädgränsen. Som ett svar på de senaste hundra årens varmare klimat har nu dessa tidigare lågvuxna individer transformerats till trädform, varigenom trädgränsen stigit. För en fördjupad förståelse av den här mekanismen har megafossil, som extraherats ur marken under gamla grankloner i trädgränsekotonen, kol 14-daterats. Resultaten tyder på att *Picea abies* kan uppnå i det närmaste "evigt" liv genom sin förmåga till vegetativ förökning och fenotypisk flexibilitet. Vissa nu levande kloner existerade redan för 9500 år sedan och har alltså funnits på samma plats under så gott som hela Holocen. I detta avseende skiljer sig *Picea abies* markant från andra trädarter, vilka inte lämnat kvar levande

relikter från tidig Holocen, när dessa arter faktiskt växte på samma höga nivåer som *Picea*. Därefter har samtliga arters trädgränser sänkts med drygt 300 m fram till början av 1900-talet, vilket tydligt visar trädgränsernas känslighet och respons för klimatförändringar även i ett längre tidsperspektiv.

Den tidiga förekomsten av *Picea* kan innebära att granen har "övervintrat" den senaste istiden närmare Skandinavien än man tidigare trott, och att den invandrat till norra Sverige långt tidigare än den länge rådande uppfattningen.

Resultaten från avhandlingens båda delar kan tjäna som viktiga komponenter i modeller som syftar till att projicera landskapsekologiska konsekvenser av framtida klimatändringar.

Nyckelord: *Betula pubescens* ssp. *czerepanovii*, *Picea abies*, *Pinus sylvestris*, klimatförändring, övervakning, trädgräns, kloner, megafossil, invandring, Holocen, kryptiska refugier, svenska fjällkedjan, Skanderna

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LIST OF PAPERS

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

Paper I   Kullman, L. & Öberg, 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. In press. Ancient subalpine clonal spruces (*Picea abies*) – sources of postglacial vegetation history in the Swedish Scandes.

Paper I is reproduced with the kind permission of Journal of Ecology.

1. INTRODUCTION

1.1 Treeline position and structure – the modern perspective

Treeline position and structure are key elements in mountain and cold-marginal landscape ecology, interacting with wind patterns, distribution and duration of snow cover, albedo, shading, soil frost, litter accumulation, nutrient circulation, biodiversity, carbon cycle, etc. (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 potentially integrating bioindicators of ecological responses to climate change and variability (Tranquillini 1979; Grace 1989; Kullman 1998a, 2010a; Theurillat & Guisan 2001; Grace et al. 2002; Juntunen et al. 2002; Gunnarson & Linderholm 2002; Holtmeier 2003; Körner & Paulsen 2004; Millar et al. 2004; Payette 2007). However, some researchers suppose that treeline positions are more or less resilient to climate change (Slatyer & Noble 1992; Masek 2001; Körner 2003; Rössler et al. 2008). The issue of current and future treeline evolution is confounded also by the fact that in many parts of the world treeline performance and structure bear a clear relationship to prior land use, which may conceal the relative importance of recent climate variability (cf. Hofgaard 1999; Gehrig-Fasel et al. 2007; Bryn 2008). In addition, treeline performance is affected and locally modulated by herbivory and inter/intra specific plant community mechanisms (Holtmeier 2003; Cairns et al. 2007; Olofsson et al. 2009).

With the general background and potential complexities outlined above it is increasingly recognized that understanding of climate-driven treeline functions and mechanisms have to be based on real-scale, high-resolution observation series of treeline performance against a background of instrumental meteorological records (cf. Kallio et al. 1986; Woodward 1987; Ewald 2001; Guisan et al. 2007; Holtmeier 2003). Such endeavours, carried out at sites with minimal human impact in the past, are imperative to the generation of realistic ecosystem models for possible future climate change scenarios (Oldfield 2005; Wieser & Tausz 2007). Except for the evolution of pure and basic science, a solid ground for modelling treeline dynamism is of paramount interest from 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; Bryn 2006; Kullman 2010b).

1.2 Postglacial treeline history

Contemporary landscapes and ecosystems can hardly be comprehended without knowing and considering their long-term historical backgrounds (cf. Reichholf

2008). Research presented in this thesis is driven by the premise that improved understanding of past treeline dynamics is essential for forecasting future ecological impacts of a potentially warmer climate. With respect to treelines, conventional vegetation history methods, such as pollen analysis alone, are inadequate. The main problem is that it is virtually impossible to know whether trace amounts of pollen represent local occurrence near the sampling site or pollen spread from far distant sources (Lang 1994; Hicks 2006; Tinner & Theurillat 2003; Kullman 2008). An alternative analytic approach, originally intended for paleoclimate research, seeks to reconstruct postglacial treeline shifts by radiocarbon dating of megafossil tree remains, recovered at sites above the current treeline (Karlén 1976; Aas & Faarlund 2000; Kullman 1994, 1995; Eronen et al. 1999; Payette et al. 2002). Megafossils provide an option for unambiguous documentation and direct dating of the presence of a species at a specific altitude.

As a complement to recent observational programmes, 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 method of pollen analysis (Kullman 2008), an opportunity already taken by some paleoecologists (e.g. Segerström & von Stedingk 2003; Hörnberg et al. 2006; Paus 2010).

It is important to make the distinction that megafossil analysis can tell little about the history of closed forest communities. In that respect, pollen analysis is a sharper tool, although this aspect of vegetation history is outside the scope of the present thesis.

From the perspective of global change ecology, the careful study of historical treeline records offers a possibility to put treeline shifts (implicit climate shifts) over the past century, with instrumental climate data, into perspective of the entire Holocene (e.g. Kullman & Kjällgren 2006). This approach provides indications of the possible anomalous nature of 20th century climate warming, as a currently much debated consequence of increasing atmospheric loads of anthropogenically introduced "greenhouse gases" (IPCC 2007).

A variant of the megafossil approach is life-history analyses of long-lived clonally regenerating tree species, growing as stunted krummholz in low-disturbance, subalpine-alpine environments. The feasibility of this tool is demonstrated by several studies (Vasek 1980; Kullman 2000; Lavoie & Payette 1996; May et al. 2009).

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 is to document the pace and

extent of elevational treeline response of the principal tree species relative to instrumentally recorded climate change and topoclimatic landscape variability.

Paper II reports a retrospective study based on radiocarbon-dated ancient Norway spruce (*Picea abies*) krummholz clones. The main focus is on the long-standing and somewhat controversial 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 (e.g. Jonsson 2004), which is a further incentive for this study.

2. STUDY AREA

The study area is located in the southern Scandes (Caledonides) in Sweden, the counties of Jämtland and Dalarna (Fig. 1). In an area of ca 8000 km², ranging from 63°25′ to 61°05′ N and 12°03′ to 13°11′ E, the present treeline positions of the dominating species mountain birch (*Betula pubescens ssp. czerepanovii*), Scots pine (*Pinus sylvestris*) and Norway spruce (*Picea abies*) were recorded at more than 100 systematically distributed sites (Paper I). In the southernmost part of the same area, elevational treeline change and forest history of the main tree species were analysed for the entire Holocene, in a subarea of ca 1200 km². A sub-set of localities were particularly focused on with respect to the life-history analyses of ancient spruce clones (Paper II).

3. METHODOLOGY

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).

3.1 Treeline and treeline ecotone - definition

The *treeline* is defined 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. This is a practical and unambiguous definition, leaving little room for interpretation and allows inter-comparability in space and time.

The *treeline ecotone* is a broad and indistinct zone, extending from the uppermost outliers of spruce and pine trees in the subalpine mountain birch belt up to *tree species line,* boardering the treeless alpine tundra. In the most continental part of the study area, the birch belt is only fragmentarily developed or even lacking, while it is most discrete and reaches its largest extension 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.

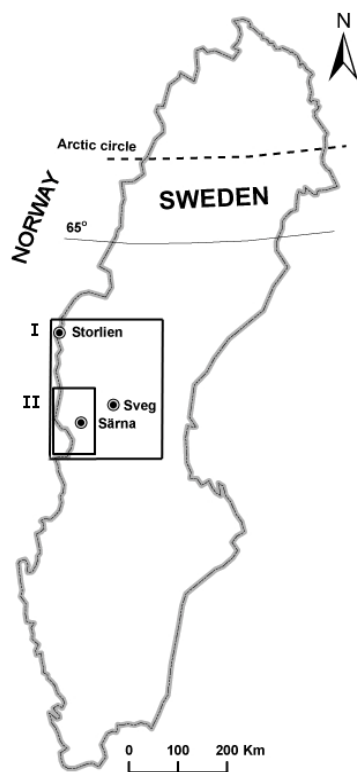FIG. 1. Location of the areas studied in Papers I (*large frame*) and II (*small frame*) respectively, and the meteorological stations Sveg and Särna.

3.2 Monitoring (Paper I)

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 km².

Around 1975, repeated measurements of treeline positions were carried out by Leif Kullman for 213 of Smith's 391 original birch sites (Kullman 1979). For spruce and pine and a few birch sites, no records existed before 1975. In these cases, treeline positions by 1915 were estimated by age determination of trees growing downslope of the current treeline. This made it possible to find out the highest level for trees with more than 60 tree rings 2 m above the ground level, i.e. likely to have been tree-sized by 1915 (Kullman 1981, 1986). During the re-surveys in the mid-1970s, the uppermost tree within each transect (henceforth termed 'treeline marker'), was tallied and photographed for future recognition, thereby increasing the precision of subsequent surveys.

The most recent update of the data set was carried out between 2005 and 2007 (Öberg 2008; Kullman & Öberg 2009). A sub-sample comprising about 50% of the sites investigated by the mid-1970s were randomly selected and re-surveyed. Treeline markers representing the past and present treelines were accurately positioned using modern GPS technique and tallied with respect to size and vitality and their surrounding landscapes were re-photographed.

By the methodological approach outlined above, elevational treeline shifts (or stasis) of *Betula pubescens ssp. czerepanovii* , *Picea abies* and *Pinus sylvestris* are quantified separately for the periods 1915–1975, 1975–2007 and for the entire period 1915–2007. These data constitute the base of the present study, which has the character of an assemblage of individual case histories, each one reporting observations of reality, integrating climate change with unique site characteristics and histories.

3.3 Sampling strategy (Paper II)

The study in Paper II focuses on megafossil tree remains, i.e. dead wood and cones. The basic sampling methodology draws on experiences from similar studies in more northerly parts of the Scandes (e.g. Kullman & Kjällgren 2006; Kullman 2000). The main emphasis was on megafossil wood remnants preserved in the soil underneath the dense foliage of krummholz spruces growing around the current treeline.

In connection with other research projects on treeline dynamics (Öberg, 2002, 2008; Kullman & Öberg, 2009), we had the opportunity to survey extensive mountain areas for potentially and particularly ancient spruce specimens. Intentionally, an

even spread of sampling sites over a larger region were aimed for, mainly within the current treeline ecotone, where such clones almost exclusively exist. Selectively, the uppermost clones were focused on, as they were supposed to be the oldest (Kullman 2000). This assumption was based on exhaustive megafossil studies of the pine treeline history (Kullman 2002; Kullman & Kjällgren 2006). These have evidenced that the first postglacial trees colonized high elevations of early emerging nunataks.

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 around the spruce sampling sites. 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. The ambition was to obtain a sample representing the main outlines of elevational treeline change and forest history throughout the Holocene.

Radiocarbon dating of recovered megafossils was conducted by Beta Analytic Inc., Miami, Florida. Throughout, dates are expressed as calibrated years before present (BP), with "present" = 1950 AD. Calibration is conducted according to CALIB 5.0.2 (Stuiver et al. 2005). Where multiple dates are given, we used the midpoint between the oldest and the youngest intercepts. When mentioned in the text, the intercept values are used for simplicity. Age determination of individual tree stems was conducted by boring at different stem positions above the ground-level. The tree rings were counted in the laboratory, under a stereomicroscope.

4. RESULTS, DISCUSSION AND CONCLUSIONS - PAPER I

Treelines of the principal boreal tree species in the southern Scandes have shifted upslope at 95 % of all studied localities during the past 100 years and well in concert with rising trends of summer and winter temperatures. The magnitudes have been highly variable and site-specific. This regional and multi-site study indicates that the treeline is more sensitive to small and short-term changes in climate than previously known. Maximum advance by about 200 m for all species is concomitant 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. 2a). The obtained results conform to the outcome of analogous studies in widely different parts of the world (Aas 1969; Meshinev et al. 2000; Shiyatov 2003; Esper & Schweingruber 2004; Lloyd 2005; Mazepa 2005; Tape et al. 2006; Danby & Hik 2007; Payette 2007; Shiyatov et al. 2007; Vittoz et al. 2008; Devi et al. 2008; Harsch et al. 2009; Hofgaard et al. 2009; Kharuk et al. 2009; Van Bogaert et al. 2010), supporting

the view that this is basically a climate change phenomenon of virtually global significance.

Spatial heterogeneity of elevational treeline responses to the same climate phase has to be considered when modelling future evolution of the forest-alpine tundra transition. Even in a hypothetical case of substantial climate warming, treelines are unlikely to advance at a broad front and a large proportion of the alpine area will remain woodless.

A causal relationship between climate variability and treeline performance is supported also by the fact that treeline rise was halted or locally even slightly reversed in response to relatively cold periods during the 1960–1980s. In conjunction with that phase, low winter temperatures (air and soil) and a sparse snow cover caused severe landscape-scale defoliation and even mortality of both older trees and young saplings growing at the treeline (Kullman 1997). Analogous responsiveness has been observed in the same area in summer 2010, likely as a consequence of a period of extremely low temperatures in combination with a thin snow cover during the previous winter, which resulted in deep ground frost (unpublished data).

In parallel to regional-scale upshifts of treelines, also large uphill migrations of several resident ground-layer species, many with woodland (boreal) affinities have taken place in the same region during the past 50–60 years (Kullman 2010b,c). Many of them have shifted upslope with roughly equally the same magnitudes as the treelines.

Additionally, the present studies show that there has been a remarkable advance of the tree species lines, by 400-700 m over the past 50 years (cf. Kullman 2007a, 2010a). This phenomenon may indicate a potential for further treeline rise in a near future, given that the past trend of warming is not discontinued. With the data retrieved by the present study, a unique baseline for further scientific monitoring is available.

The evidence presented in Paper I strengthens the view of an ongoing and profound all-level (trees to ground-layer) transformation of the subalpine-alpine tundra system, most likely attributable to climate forcing (cf. Sundqvist et al. 2008) (Fig. 2a-c). This implies that treeline performance can be used as a superior pointer for widespread shifts in the whole ecosystem.
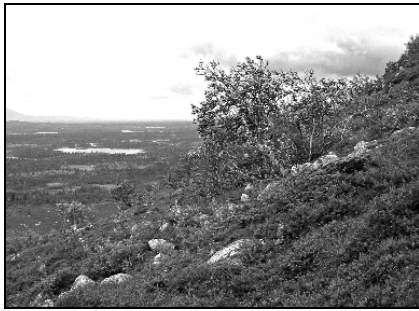
FIG. 2a. The position of mountain birch treeline in 1915, captured in 2006 (*left*), and 2006 (*right*) at Mt. Brattriet SW, Härjedalen, 945 and 1040 m a.s.l. respectively. This steep lee-side slope, prone to large snow accumulation, represents the largest treeline rise for mountain birch by 195 m. Photos: 2006-08-22.

FIG. 2b. The spruce treeline position in 1915, captured in 2007 (*left*), and 2007 (*right*) at Mt. Slagufjället S, Härjedalen, 895 and 940 m a.s.l. respectively. Photos: 2007-07-11.

FIG. 2c. The pine treeline position in 1915 (*left*), captured in 2006, and 2006 (*right*) at Mt. Jakobshöjden SW, Dalarna, 900 and 995 m a.s.l. respectively. Typically, pine at the treeline prefers exposed, dry and snow poor sites. Photos: 2006-07-02.

4.1 Treeline advance

During the entire observation period (1915–2007) all 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 genotypic spread, but also relates to a climate that has gradually become more conducive to pine, i.e. drier and with less late-lying snow. In contrast to birch and spruce, pine exclusively reproduces with seed. As a consequence, its treeline rise is accomplished by individuals established during the past century. Preconditions for rapid height increment have been very favourable after the 1970s, during which period pines have developed from seed to tree size (Fig. 2c, *right*).

4.2 Krummholz

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). Some of these individuals, which mainly reproduce by basal sprouts and layering, have become established long before the 20th century (Kullman 1993, 2000, 2005b; Öberg 2008; Paper II).

Old krummholz-spruces that have been reproductively 'silent' for centuries or more, have started to produce cones (Fig 4) and at least in some cases, reproduce sexually (Fig. 5) over the past 10 years or so. In the case of pine, the new treeline markers have produced some offspring in their vicinity during the past decade.

Sparsely scattered young saplings of all concerned tree species have recently migrated to maximum positions 500–700 m higher than the local treelines, i.e. *the tree species line* has advanced much more than the treeline (Kullman 2001, 2007a,b). The majority of these saplings have become established since the late-1980s in concert with substantially increased seed viability of treeline trees (Kullman 2007a,b,c).

FIG. 3. *Left*. This spruce clone at Mt. Lillskarven SW, 1065 m a.s.l., raised the treeline by 220 m (1915-2007) by increased height growth and vitality as a response to the 20th century climate change. As typical for the localities displaying the largest spruce treeline upshifts, snow and wind conditions are intermediate. Photo: 2007-08-12. *Right*. Spruce treeline marker at Mt. Middagsvalen N, 835 m a.s.l., where the treeline raised by 30 m (1915-2007) due to new recruitment in the 1930s. Only rarely has this type of treeline rise occurred for spruce and birch. Photo: 2009-08-09.

FIG. 4. Old krummholz spruce clone "Old Pompe" at Mt. Getryggen E, 770 m a.s.l. (*left*), that recently converted to upright tree, carrying cones (*right*). Radiocarbon dated macrofossil wood yielded an age of 5700 cal. yr BP (Beta-263552). Photo: 2010-08-31.

FIG. 5. Krummholz spruce, dating ca 1300 cal. yr BP, at Mt. N. Tväråklumpen SE, 1090 m a.s.l. (*left*), with cones (*middle*) and offspring (*right*). Photo: 2009-08-01 (*left* and *right*), 2004 (*middle*).

4.3 Large variation between sites

One of the most important aspects of the present study is the large variation between sites with respect to the magnitude of treeline rise, that is, 0–220 m. Obviously, this relates to site-specific topoclimatic constraints. Only quite infrequently have treelines reached the potential positions as prescribed by regional ambient temperature conditions. The largest upshifts, particularly for birch, are accomplished in long, sweeping concave slopes. These settings may offer optimal insolation, wind shelter, stable soil moisture and physically safe sites for tree growth over a large elevational range (Fig. 6). Commonly, this habitat type previously supported snowfields well into the summer. During the past century, they have tended to melt earlier in the growing season, which creates new opportunities for tree growth at higher elevations than before.

FIG. 6. The locality Lillstensdalsfjället N, where birch treeline rose by 190 m (1915-2007) to 1070 m a.s.l. The former glacier cirque offers optimal insolation, wind shelter, fairly stable soil moisture and physically safe sites for tree growth over a large elevational range. Photo: 2010-09-13.

At virtually all studied sites, old-growth spruce and birch (krummholz) existed upslope of the current treeline. This excludes that possibility that cases with small or minor treeline shifts were due to stochastic absence of individual apt to evolve to tree size by phenotypic adjustment.

4.4 Winter temperature rise in favour for 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 (Kullman 2007c).

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).

4.5 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, forced predominantly by Earth's orbital patterns. This dominant tendency has prevailed since the early Holocene (Kullman & Kjällgren 2006) 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 have reached slightly above the positions held during the Medieval Warm Period (AD 900–1300) and several preceding millennia (Kullman 2003, 2004a,b; Kullman & Kjällgren 2006). Thus, recent treeline upshifts represent elevational advance from the lowest Holocene level to a position most likely not reached in the past 7000 years (Kullman 2004a,b; Kullman & Kjällgren 2006), i.e. a truly anomalous event in Holocene vegetation history.

5. RESULTS AND INTERPRETATION - PAPER II

5.1 The 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 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).

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) (Fig. 7).

FIG. 7. Ancient multi-stemmed spruce clone, inferred to have existed already by 7940 cal. yr BP, at Mt. Köarskärsfjället S. This clone rapidly attained tree-size during the 1930s (*left*). During some relatively cold decades, 1960-1980s, this and many other spruces in the treeline ecotone suffered severe needle loss in response to winter desiccation, from which they have started to recover in recent decades (*right*). Photo: 1943 July (Gösta Lundqvist, *left*), 2010-06-15 (*right*).

FIG. 8. *Left.* Old-growth multi-stemmed spruce clones with transformed from krummholz to upright tree form in response to 20th century warming. *Right.* A muddle of inter-lacing boles exist underneath the dense infra-nival skirt of branches. Mt Härjehågna E, 985 m a.s.l. Photo: 12 July 2007.

The clones focused in this study all grow in open landscapes, i.e. patches of exposed and dry - fresh 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 (Fig. 8). In no case have new spruce genets, i.e. seedlings or saplings, been recorded within the clones (Kullman & Öberg 2009).

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.

5.2 Radiocarbon ages of megafossil spruce remains

The obtained radiocarbon ages originating from wood pieces buried underneath the 10 spruce clones focused here, range between 9550 cal. yr BP and the present. Two clones and one cone, representing well separated localities, attest to the presence of spruce around 9500 cal. yr BP (Fig. 9).

Throughout the whole 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. None of the dated spruce remains displayed any physical connection with living parts of the clones. This could, *a priori*, suggest that they are not representing 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. In some cases, wood of widely different ages were sampled right underneath one and the same clone, indicating long-term continuity at a very narrow site. Moreover, and most important, seed regeneration is found to be virtually impossible underneath their dense basal canopies (cf. Laberge et al. 2000; Holtmeier 2003). This makes it less likely that these clones in the treeline ecotone are the outcome of multiple seed regeneration episodes at the same spot (cf. Holtmeier 1974).

Digging in raw humus soils and peat deposits at numerous sites outside the spruce clones has in no case revealed any wood remnants of spruce.

It appears that individual longevity is conditional upon a stunted and mainly horizontal growth form (krummholz), which implies a constantly positive and favourable needle - wood ratio. Preferably, such a situation can be efficiently 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

severe winter conditions, which notoriously break the apical dominance (Laberge et al. 2000) (Fig. 10).

FIG. 9. *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: 2010-08-13.

FIG. 10. Spruce clone "Old Molly" at Mt. Åreskutan S, 980 m a.s.l. Datings of macrofossil, retrieved from the ground right below its infra-nival skirt of dense foliage, revealed 6400 cal. yr BP (Beta-282008). Heavy loads of high-density snow and ice are the main reasons for stem breakages in this steep slope. Photo: 2007-08-23.

By implication, 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 wind 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). This inference is quite in line with the results from megafossil research in adjacent regions (Kullman & Kjällgren 2006). Moreover, Paper I show that in strongly wind-exposed topography treelines were unable to take full advantage of climate warming and advance uphill to reach the potential thermal limit.

5.3 Holocene vegetation history - inferred from megafossil and life-history analyses of long-lived spruce clones

The highest parts of the south-central Scandes, including the study region, were obviously deglaciated much earlier than previously proposed (e.g. Lundqvist 1998; Påsse 2001; Svendsen et al. 2004). With some regional variation, the highest peaks, i.e. those reaching above 1100-1300 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, 2002; Follestad 2003; Kullman & Kjällgren 2006; Bøe et al. 2007; Goehring et al. 2008; Paus et al. 2006; Paus 2010).

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. One pine log recovered there, dated c.12 500 cal. yr BP (Kullman 2004b). 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 and 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). Subsequently, and throughout the Holocene, the upper elevational range of pine declined almost linearly (c. 28 m per millennium) until the late-19th century.

According to the low frequency of birch megafossils relative to pine, birch has never played any important role in the treeline ecotone and obviously pine has been the dominating species throughout. This concurs with experiences from other parts of the southern Scandes and indicates that a discrete mountain birch belt evolved quite late during the Holocene, in response to Neoglacial cooling (Kullman 1995, 2004a; Barnett et al. 2001). Relatively rare findings of birch megafossils are unlikely due to easier decay of subfossil wood of this species.

Studies in other subalpine/alpine regions have shown that birch may be preserved in great quantities since the early Holocene (e.g. Kullman 1995). Low abundance of birch implies that the spruce has not been particularly much affected by competitive exclusion, a circumstance which 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.

5.4 Spruce immigration history

During the early Holocene, i.e. prior to 9500 cal. yr BP, scattered 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. Apparently, spruce was not a rare and peculiar oddity in the mountain landscape, since similar occurrences are recorded at several localities further north in the Scandes (Kullman 1998b, 2000). Rather, they represent low-abundance floral elements, predictable from the prevailing regional climatic situation and associated plant invasion patterns.

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 *Picea abies* into northern and western Scandinavia (e.g. Moe 1970; Huntley & Birks 1983; Tollefsrud et al. 2008, 2009). It now stands out that *Picea abies* 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 late Holocene immigration from far-distant ice age refugia in Russia is arguable (cf. Kullman 2000). Alternatively, it may be hypothesized that spruce "hibernated" the last ice age in refugia quite close to Scandinavia. It stands out quite clearly that the late-Quaternary history of *Picea abies*, and reasonably other taxa in north-western Europe, is an unsettled, complex and scientifically more challenging affair than generally assumed. This issue is in definite need of further "fossil" and molecular genetical evidence.

6. FUTURE RESEARCH

As a logical continuation of the research presented in this thesis, I see some scientifically rewarding avenues for continued research, which are tentatively outlined below.

6.1 Mountain birch forest – a threatened nature type in a warmer climate?

As concluded in Paper I, spatial elevational treeline responses to climate change are markedly heterogeneous and site-dependent, and even in a hypothetical case of substantial future climate warming, treelines are unlikely to advance at a broad front and likely a large proportion of the alpine area will remain treeless.

A relevant objective for future research would be to test the possibility that future climate warming will bring about a complete ecosystem shift, implying that the subalpine birch forest belt in the Scandes becomes largely replaced by stands of foremost pine and some spruce and possibly local "pockets" of mountain birch

This tentative hypothesis draw on the results from the long-term (centennial) regional monitoring (Paper I), which has evidenced that the pace of birch treeline ascent was retarded during the past few warming decades, relative to pine and spruce. It has also turned out that over extensive areas, mountain birch is showing signs of reduced vitality, in great contrast to pine and spruce.

The societal importance of a landscape transformation, as outlined above, may have far-reaching consequences for various sectors of the society, e.g. reindeer husbandry, conservation (biodiversity) and tourist industry. Thus, reliable and real-scale data for the purpose of projective landscape modelling are urgently needed as a basis for proactive response and adaptation measures.

Such a project would imply intensive field investigations, which address the basic questions by different and complementary methods at a site found to be particularly suited for the present purpose, preferably Mt. Getryggen.

The main analytical approach could be age structure analyses of birch populations along local-scale ecological transects running between snow patch depressions and exposed ridges. In addition, regeneration dynamics, growth rates and vitality status are assessed in permanent plots at the same sites, established in 1980. Another vital part of the project is the establishment of tree ring chronologies from mature birches growing in the permanent plots, mainly as a measure to elucidate any drought stress affecting the birches differently along the studied gradients.

Any tendencies to conifer invasion into the birch forest are temporally and quantitatively investigated by systematic mapping and aging of all individual pines and spruces growing on this study slope, which embraces the detailed studies outlined above. These studies should be complemented with phenological observations and soil temperature recordings.

6.2 Recent glacier retreat – a new source of high-mountain paleovegetation reconstruction and clues for the future alpine landscape

Predominant climate warming during the past 100 years has fundamentally altered the preconditions for physical and biological systems in alpine and subalpine regions. Climate models predict continued warming by about 3°C until the end of the 21st century. For the purpose of proper landscape management in such a hypothetic situation, there is an urgent need to project the consequences for future evolution of the alpine/subalpine landscape. Responses of the alpine treeline and the forest-alpine tundra ecotone are crucial in this respect since an encroaching tree cover has a steering effect on the plant cover structure and biodiversity patterns.

An important project would be to elucidate the possibility of future tree growth at high altitudes by use of a paleoanalogue approach. This implies an attempt to find out whether birch (or other species) grew as high as predicted for the future by mainstream climate models, during the early Holocene when temperatures were c. 3° warmer than today. For that purpose, a new source of information can be used. This is based on different kinds of "fossil" plant material, i.e. pieces of subfossil tree trunks and peat with plant macroremains, exposed on the forefields of receding glaciers, as evidenced by Kullman & Öberg (2010).

This material represents a unique possibility and reliable way to obtain spatial-precise reconstructions of major facets of high-alpine vegetation in a distant and warmer past. Aside of its purely scientific value, this project has a strong pedagogic side as it provides a concrete view of climate impact on both the living and physical landscape.

7. ACKNOWLEDGEMENTS

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