

Contrasting short-term performance of mountain birch (*Betula pubescens* ssp. *czerepanovii*) treeline along a latitudinal continentality-maritimity gradient in the southern Swedish Scandes

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Positional treeline shift is a fundamental aspect and indicator of high-mountain vegetation response to climate change. This study analyses treeline performance during the period 2005/2007–2010/2011 in the Swedish Scandes. Focus is on mountain birch (*Betula pubescens* ssp. *czerepanovii*) along a regional climatic maritimity-continentality gradient. Treeline upshift by 3.0 yr⁻¹ in the maritime part differed significantly from retreat by 0.4 m yr⁻¹ in the continental part of the transect. This discrepancy is discussed in terms of differential warming-induced snow cover phenology patterns and their influence on soil moisture conditions. In the continental area, earlier and more complete melting of prior relatively rare late-lying snow patches, even high above the treeline, has progressed to a state when melt water irrigation ceases. As a consequence, soil drought sets back the vigor 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. Thereby, the birch treeline expands upslope as the alpine snow patches shrink, but continue to provide sufficient melt water throughout the summer. Treeline rise appears to have been based primarily on seed regeneration over the past few decades. This is a novelty, since prior (1915–2007) treeline advance was accomplished mainly by *in situ* shifts in growth form of relict krummholz birches, in some cases millennial-old, prevailing above the treeline. By the snow phenology mechanism, birch can benefit from climate warming in the maritime region, which contrasts with the situation in the continental region. This discrepancy should be accounted for in projective models. In a hypothetical case of sustained warming, the subalpine birch forest belt may expand less extensively than often assumed, although advance may continue for some time in snow rich maritime areas.

Keywords: Swedish Scandes, treeline, revisitation study, climate warming, regeneration, *Betula pubescens* ssp. *czerepanovii*

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Introduction

Performance of cold-marginal treelines (in a broad sense) is commonly seen as a key element in the context of climate-driven transformation of the high-mountain landscape (Payette et al. 2001; Holtmeier 2003; Kullman 2010a, 2012; Harsch &

Bader 2011; Malanson et al. 2011; Öberg & Kullman 2011a). It is generally accepted that treelines are ultimately constrained and structured by heat deficiency, although the finer ecological and eco-physiological mechanisms are still not fully understood (Grace et al. 2002; Hoch & Körner 2003; Holtmeier 2003; Lloyd 2005; Körner 2012). Some

theoretical doubt and discussion have been raised as to the responsiveness of treelines to climate change (e.g. Noble 1993; Kupfer & Cairns 1996; Körner 1999). Nevertheless, a wealth of empirical data world-wide have evidenced increased high-mountain tree establishment and upward treeline shifts in concert with post-Little Ice Age climate warming, let be with intra-regional variations of different magnitudes and rates (Kullman 1979; Juntunen et al. 2002; Esper & Schweingruber 2004; Lloyd 2005; Caccianiga & Payette 2006; Kapralov et al. 2006; Tape et al. 2006; Danby & Hik 2007; Shiyatov et al. 2007; Batllori & Gutiérrez 2008; Devi et al. 2008; Harsch et al. 2009; Kharuk et al. 2009; Kullman & Öberg 2009; Elliott & Kipfmüller 2011; Leonelli et al. 2011; Öberg & Kullman 2011a; Kirilyanov et al. 2012; Singh et al. 2012). Paleoecological data further support the contention of substantial treeline displacements in covariance with climate change throughout the Holocene (Tinner & Kaltenrieder 2005; Kullman & Kjällgren 2006; MacDonald et al. 2008; Paus 2010; Öberg & Kullman 2011a, 2011b). To some extent, contrasting results and opinions with respect to treeline mobility may relate to different treeline definitions and to the fact that some studies are based on just a few sites and therefore possibly biased with respect to the omnipresent topoclimatic continuum (cf. Kullman & Öberg 2009).

At the local scale, the basic control of treeline performance (elevation, structure and species composition) is more complex and spatially variable than just a plain function of ambient temperature. For example, the treeline position is locally modulated by strong winds, snow cover duration, effective soil moisture, geomorphology, soil depth, human impacts, herbivory, pathogens and historical legacy, all interacting in non-linear feedback systems (Walsh et al. 1994; Holtmeier & Broll 2005; Lloyd 2005; Gehrig-Fasel et al. 2007; Kullman & Öberg 2009; Aune et al. 2011; Leonelli et al. 2011). In particular, the role of wind seems to be much underrated (Seppälä 2004; Gamache & Payette 2005; Holtmeier & Broll 2010; Kullman 2010a). Strong wind exposure and associated snow cover redistribution may frequently constrain the treeline at a lower elevation than would be the case in less exposed mountain environments (Kullman & Öberg 2009; Elliott & Kipfmüller 2010).

The current concern with the alleged anthropogenic forcing of the world's climate and associated

ecological impacts has commonly focused on treeline change as a sensitive indicator (early warning) of pending broadscale transformation of alpine and arctic ecosystems and landscapes (Neilson 1993; Holtmeier 2003; Graumlich et al. 2005; Nagy 2006; Payette 2007; Kullman 2010a, 2010b; Malanson et al. 2011).

For the case of predictive and dynamic modelling of the forest-alpine tundra interface and sub-alpine/alpine vegetation (cf. Kullman 2012), empirical data ("experiments by nature") on treeline performance along macroclimatic and topoclimatic gradients are mandatory (e.g. Fagre et al. 2003; Körner 2005; Holtmeier & Broll 2007; Batllori & Gutiérrez 2008). This contention was particularly stressed by a recent regional and observational multi-site study, focusing on positional treeline change by different tree species over the past century, 1915–2007, in the southern Swedish Scandes (Kullman & Öberg 2009; Kullman 2010a). Treeline rise was recorded on 95% of all revisited localities, although with site-specific extent and a strong relationship to local topography and associated wind, snow cover and soil moisture conditions. The maximum magnitude was about 200 m in elevation, much the same for all three investigated species, viz. *Betula pubescens* ssp. *czerepanovii* (mountain birch), *Picea abies* (Norway spruce) and *Pinus sylvestris* (Scots pine), although with differential rates over shorter sub-periods. This figure is more or less what should be predicted from a lapse rate of 0.6 °C per 100 m altitude (Laaksonen 1976) and for a treeline system in equilibrium with recorded summer temperature warming (1.4 °C) during the observation period. Relative to the interval 1915–1975 and in contrast to *Picea* and *Pinus*, treeline rise of *Betula* slowed down during the sub-period 1975–2007 (Kullman & Öberg 2009).

Retarded treeline rise of birch after the mid-1970s was particularly discernible in the most continental (southernmost) part of the investigated region, where it also manifested as declining vigor of many treeline markers, i.e. individual treeline trees. As trees have reached increasingly higher elevations, they have faced wind stress to such a degree that further upshift is largely impaired. In addition, soil drought, as a consequence of earlier seasonal snow melt, was suggested as a proximate cause for flattened treeline advance (Kullman & Öberg 2009). This is within a region where a relatively thin snow cover and scarcity of late-lying snow patches have "always" provided marginal

conditions for the comfort of mountain birch, which displays a close spatial association with the most snow rich parts of the terrain (Samuelsson 1917; Kullman 2010a, 2012). Mountain birch has its ecological optimum in cool, maritime climates and depends more on soil humidity than *Picea* and *Pinus* (Hämet-Ahti & Ahti 1969; Wielgolaski 1975; Kullman 1981, 1986). During the warm and dry early Holocene, the treeline ecotone in the whole study area was mainly composed of the relatively drought-resistant *Pinus sylvestris* (Kullman 1995; Öberg & Kullman 2011b).

The relatively high rate of treeline rise, as recorded predominantly in maritime areas of the southern Scandes (Kullman & Öberg 2009), may be understandable in terms of a snow cover that over quite large areas of mountain slopes supplies sufficient melt water for sustained vitality of existing and upcoming treeline birches. In many parts of this landscape, a surplus of late-melting snow still appears to control the treeline, which responds with uphill advance as the constraint im-

posed by late-lying snow eventually weakens when the summer climate warms and earlier snow melt takes place (Fig. 1).

Divergent treeline patterns and responses between continental and maritime climates are possibly coupled to soil moisture conditions, the amount of snow and the timing of its seasonal melting (cf. Grace 1997; Gansert 2004; Payette 2007; Aune et al. 2011). This is an aspect of general relevance for the generation of realistic landscape-scale models for an anticipated warmer future. In fact, snow cover phenology is suggested to be more essential for high-mountain plant life than direct effects of ambient air temperature (cf. Holtmeier & Broll 2005; Körner 2005; Schmidt et al. 2006; Kullman 2007a, 2007b; Wipf et al. 2009). Increasing soil drought and moisture stress in response to warming-induced earlier snow melt in the summer is frequently discussed in connection with treeline performance in different parts of the world (e.g. Barber et al. 2000; Lloyd & Fastie 2002; Daniels & Veblen 2004; Millar et al. 2004;



Fig. 1. 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.

Gamache & Payette 2005; Wilmking et al. 2005; Holtmeier & Broll 2007; Shrestha et al. 2007; Batllori & Gutiérrez 2008; Green & Pickering 2009).

Betula pubescens ssp. *czerepanovii* possesses eminent capabilities both for seed-based and vegetative reproduction. The latter option relies on fast-growing basal sprouts, which provides a steady turn-over of stems as the old ones eventually die from senescence or physical damage (Kallio & Mäkinen 1978; Kullman 1981). It has been hypothesized that by this mechanism individual *Betula* specimens may, under certain circumstances, survive almost eternally, fluctuating between krummholz and arborescent modes as climate favourability shifts (Kallio & Mäkinen 1978; Jonsson 2004; Kullman 2010a). Treeline rise by mountain birch in the Swedish Scandes during the first half of the 20th century was accomplished predominantly by a swift phenotypic height-growth response of a pool of ancient krummholz specimens existing above the former treeline, hypothetically as relicts from a period with warmer climate, prior to the neoglacial cooling phase, initiated more than 3500 years ago (Kullman 2003; Öberg & Kullman 2011a). In very recent time, however, increasing seed viability and resultant reproduction has been discerned for *Betula* in moderately moist leeward slopes, where the depth and duration of the snow cover have diminished in favour of birch growth and establishment (Kullman 2007b; Kullman & Öberg 2009). Presumably, a common shift to sexual regeneration at the treeline is imminent in maritime climates (cf. Holtmeier & Broll 2007). The present study focuses on both these principal modes of birch treeline regeneration and their relative roles in connection with recent climate warming along a regional continentality-maritimity gradient.

Based on the background outlined above, we hypothesize (1) that summer warming and associated snow phenology have recently forced contrasting responses of the *Betula* treeline between regions with continental and maritime climatic conditions, respectively and (2) that recent treeline regeneration is predominantly seed-based in the former and vegetative in the latter region. We tested these assumptions by a revisitation study using accurate positional baseline data, retrieved over a relatively short observation period. Thereby, the possible operation (or not) of distinct climatic events of importance for population dynamics may be observed (cf. Holtmeier & Broll 2005; Danby & Hik 2007). In addition, any confounding

processes, e.g. herbivory, human impact or other non-climatic disturbances, can be better understood by a short-time approach than revisitation studies with longer intervals.

Study area

The study comprises treeline sites distributed along a regional transect, extending 250 km northward from the southernmost mountains with an alpine treeline in the Swedish Scandes, 61° 05' to 63° 25'N (Fig. 2). The mountains reach 900–1800 m a.s.l. (highest in the north) and the valley floors are at 600–800 m a.s.l. The regional climate displays a clear spatial discontinuity between weakly maritime in the north to a more continental character in the south. Accordingly, the transect can be divided into two distinct, sharply separated parts, with respect to climatic maritimity-continuity, calculated as the sum of the mean temperature difference between July and June and between day and night during June (Raab & Vedin 1995). The southern, continental part (C) is characterized by a value of 30–40 and the northern, maritime part (M) by 25–30. Other indices provide a similar view of a radical change of climate character at virtually the same point along the transect (e.g. Tuhkanen 1980). Southwards, annual precipitation decreases by about 300 mm and the proportion of snow decreases by 10%. In the south, the number of days with snow cover and the maximum snow depth is relatively low. Moreover, the seasonal snow melt is earlier and windiness becomes less pronounced towards the south (Raab & Vedin 1995).

The difference in macroclimatic character exerts a discernible influence on the treeline position, which is more than 300 m higher in the very south compared to the northern extremity (Kjällgren & Kullman 1998). In addition, the floristic composition of the subalpine birch forests just below the treeline clearly reflects contrasts in climate character between north and south (Hämet-Ahti 1963).

The focal point of the study, i.e. the birch treeline, is by convention narrowly defined as the maximum elevation (m a.s.l.), at a given site, of trees with a minimum height of 2 m (cf. Miehe & Miehe 2000; Batllori & Gutiérrez 2008). This strict definition is practical for the purpose of intercomparisons over time and space. The chosen critical stem height implies that treeline markers are not

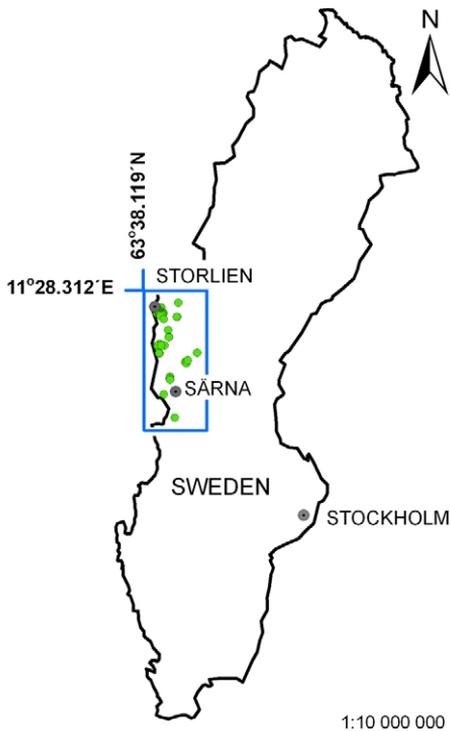


Fig. 2. Location map showing the extent of the study transect and the individual treeline sites.

entirely covered by snow and thereby the treeline is coupled to the climate of the free atmosphere during the entire year. Since the treeline is usually formed by isolated trees in a matrix of alpine tundra, the impact of intraspecific competition and shelter is minimized and therefore the relation to climate and climate change is optimized (cf. Körner 2007; Kullman 2010a).

It may be argued that the treeline, based on the uppermost individual birch within each transect, is sensitive to disturbance without relevance for the treeline ecotone as a whole. In the present case, however, this caveat is largely reduced by the use of a large number of sampling localities. Moreover, since the study is short-term and involves relocation and repeat photography of individuals, any such putative events are under control. Thus, we are quite confident that treeline change under these premises provide a reliable view of the dynamic situation prevailing in the treeline ecotone in general.

Any kind of “forest limit” is impractical for the current purposes, as the transition zone (ecotone) between closed forest and alpine tundra is spatially variable and unique in structure for each individual mountain slope, which also impacts the responsiveness to climate change and variability (Kullman 2010a, 2012; Harsch & Bader 2011). Obviously, the closed forest has self-stabilizing properties, which further invalidates its use for ecological monitoring (cf. Körner 1999; Dullinger et al. 2004; Kullman 2010a).

The uppermost treeline in the study area is formed by *Betula pubescens* ssp. *czerepanovii*, which usually forms a subalpine belt above the coniferous (boreal) forest, where *Picea abies* and *Pinus sylvestris* alternate as dominants. As a rule, the treeline of *Betula* extends about 50 and 100 m above the treelines of *Picea* and *Pinus*, respectively (Kjällgren & Kullman 2002).

With increasing continentality at the geographical scale, the width of the subalpine birch belt as well as the vertical distance between the birch treeline and the treelines of conifers decline. In the south, the birch treeline attains its highest levels in the Swedish part of the Scandes, 1140 m a.s.l., while values around 800 m a.s.l. prevail in the north.

The subalpine birch forest has been utilized for extensive grazing by semi-domestic reindeer (ongoing) and livestock (until the 1940s). However, the treeline, as defined below, is virtually pristine in character (Kilander 1965; Kullman 1979; Kjällgren & Kullman 1998). One reason may be that treeline markers of mountain birch are often situated high above the closed forest, in steep and boulder-rich terrain, not easily accessible to man and grazing animals (cf. Sundqvist et al. 2008). Moreover, mountain birch has a strong regeneration capacity, also at the sapling stage, which reduces its sensitivity to physical disturbance, e.g. herbivory (Kallio & Mäkinen 1978; Kullman 2010a). Further support for treeline naturalness is given by the fact that regional treeline dynamics during the past century are much the same for *Betula*, *Picea* and *Pinus*, despite their widely different regeneration strategies and varied utilization by herbivores and humans (Kullman & Öberg 2009). With respect to human impact, Swedish treelines differ from those in most other parts of Europe (cf. Gehrig-Fasel et al. 2007; Rössler et al. 2008; Potthoff 2009), as recent treeline dynamics is merely a consequence of natural forces (cf. Nagy 2006).

More detailed data concerning the differentiation of climate, geology, plant cover and human impact along the concerned transect are given by Kullman & Öberg (2009). The Holocene vegetation history, with particular respect to treeline and forest vegetation is quite well-known (Seegerström & von Stedingk 2003; Bergman et al. 2005; Kullman & Kjällgren 2006; Öberg & Kullman 2011a, 2011b).

Materials and methods

The present study draws on a multi-site regional sample of treeline positions gathered in ~500 m wide belt transects by the early-20th century (Smith 1920) and with resurveys carried out in the mid-1970s (Kullman 1979) and 2005–2007 (Kullman & Öberg 2009). Here we focus specifically on elevational change of the *Betula* treeline over the period 2005/2007–2010/2011, for simplicity henceforth 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. All sites were visited with four years in between. A total of 44 sites were fairly evenly distributed among two areas (C and M), representing different climate types, with respect to thermic continentality/maritimity (see above).

By the survey in 2005–2007, the treeline positions were accurately defined by the use of a GPS navigator (Garmin 60 CS) repeatedly calibrated against topographical maps. Consistently, the deviations were less than 5 m. Reported data are rounded off to the nearest 5 m. In addition, the treeline markers were photographed, which further helped to relocate the exact positions for the individual birch trees, which constituted the treeline 2005–2007. Centred on the treeline markers as starting points, a ~500 m wide belt transect, trending upslope, was systematically scrutinized for the accurate positions of any new birch individuals fulfilling the treeline criteria of an upright stem, at least 2 m tall. In those cases, where stasis or upslope displacement could not be documented, the belt transect was extended downslope until the first individual birch complying with the treeline definition was found.

The regeneration mode behind recorded treeline rise was assessed from the presence or not of birch specimens (irrespective of size) by the mid-1970s (Kullman 1979) at the same elevation as the new treeline, 2010/2011. Absence was tak-

en as evidence of treeline rise accomplished by seed-based establishment of new individuals during the past 30 years or so.

Repeat photography was carried out from identical vantage points in order to document growth and vitality changes of treeline markers (if any) and to provide further detail to the analysis of treeline performance over the study period. Some treeline sites were visited at several occasions during the four-year period, also during winter and spring, in order to assess snow cover conditions, weather injuries and other disturbances, e.g. herbivory.

The option of height growth increment of ancient krummholz birches growing above the treeline, as a potential mechanism of treeline shift (Kullman 1979, 2010a), is tested by radiocarbon-dating of wood remnants preserved in the soil beneath the canopy of a living and representative tree-sized birch, which grew as krummholz prior to the early 20th century and attained tree-sized after the early 20th century (Kullman 1979, 1993). The concerned birch (Mt. Getryggen, 905 m a.s.l., area M) is 3.7 m high (2010), with three living stems of similar stature and one dead stem, 1.9 m high. Maximum winter snow depth under the canopy is 0.8 and 0.3 m at the wind and lee side, respectively. By the early 20th century, this individual birch grew 75 m above the contemporary treeline (Kullman 1979). Radiocarbon-dating of unearthened subfossil *Betula* wood, physically connected to below-ground parts of the living birch, was conducted by Beta Analytic Inc., Miami (USA). The radiocarbon ages are expressed as calibrated years before present (cal. yr BP), which refer to the intercept of the radiocarbon age with the calibration curve (for further details, see Öberg & Kullman 2011b).

Browsing by semi-domestic reindeer (*Rangifer tarandus* L) and other herbivores is sometimes thought to influence the potential for birch treelines to respond positively to climate warming (e.g. Olofsson et al. 2009; Aune et al. 2011). This motivated us to assess each treeline marker for signs of herbivory.

The nomenclature of vascular plant taxa is according to Mossberg & Stenberg (2003).

Climate evolution over the past century

Climate evolution over the past century is represented by the official weather stations Storlien/

Visjövalen (595 m a.s.l.) and Särna (435 m a.s.l.), in area M and C, respectively. These stations have long and fairly homogeneous records and display similar trends in covariance with the entire region (cf. Alexandersson 2006; SMHI 2012). Throughout, summer and winter refer to the mean temperatures of June–August and December–February, respectively. For the period 1915–2011, summer temperatures rose by 1.1–1.4 °C and winter temperatures by 0.9–1.4 °C. For both periods, the highest figures were recorded at Storlien/Visjövalen. During the four-year period in particular focus here, summer temperatures were 1.0 and 0.8 °C warmer than the average for 1915–2011, for Storlien/Visjövalen and Särna, respectively. Corresponding figures for the winter are –0.1 and –1.3 °C, respectively. Precipitation in the region has increased by 5–10% over the same period of time, and most significantly by 10–20% during the summers over the past two decades. Concurrently, winter precipitation remained fairly stable (Alexandersson 2006; SMHI 2012). The days with snow cover have decreased (Moberg et al. 2005).

Growing season soil temperatures are suggested as a general constraint of treeline position (e.g. Körner & Paulsen 2004). In order to account for this aspect, we analyzed root-zone temperature records annually (1985–2001) at a treeline site, under the canopy of a birch copse in the northern part of the study area (Mt. Storsnasen, 850 m a.s.l.), where the maximum snow depth is ~0.7 m. A view of this site in summer and winter is given in Figure 3. Temperatures were recorded by resist-

ance termistors (TO-03R), manufactured by T. Johnsson Inc. Umeå, Sweden. The sensors were installed at a depth of 30 cm in the upper mineral soil, right below the organic raw humus layer. At this depth, short-term temperature variations are significantly damped (cf. Körner 2007), as evidenced by daily measurements over some weeks during all seasons. Readings have been carried out 2–3 times per month, which should provide an integrated view of seasonal trends in soil temperature, comparable between different years (cf. Harris 2001). Based on these measurements, we present an annual index of the summer temperature favourability. This refers to the highest reading for the July–August period, which always contained the highest annual record. Soil temperature measurements 1985–2011 are displayed in Figure 4. A strong rising linear trend (+3.4 °C) of growing season soil temperature is evident for the period 1985–2011.

Proxy support for a changing mountain climate in the study area, with direct relevance for birch performance, is provided by continuous glacier and snow patch recession (cf. Kullman 2004b, 2007a, 2007b; Öberg & Kullman 2011a). In addition, a photographic landscape-scale time series (2008–2011) of annual birch leaf unfolding and landscape-scale snow melt in the northern part of the transect is compared with a photo of the same view captured by Dr. Harry Smith on June 11 in 1914. At this date, the birches were totally devoid of leaves and snow covered most parts of the surveyed landscape (Fig. 5). During the four years



Fig. 3. Summer and winter views of the site for soil temperature records. Mt. Storsnasen, 29 July 2010 and 3 March 2011.

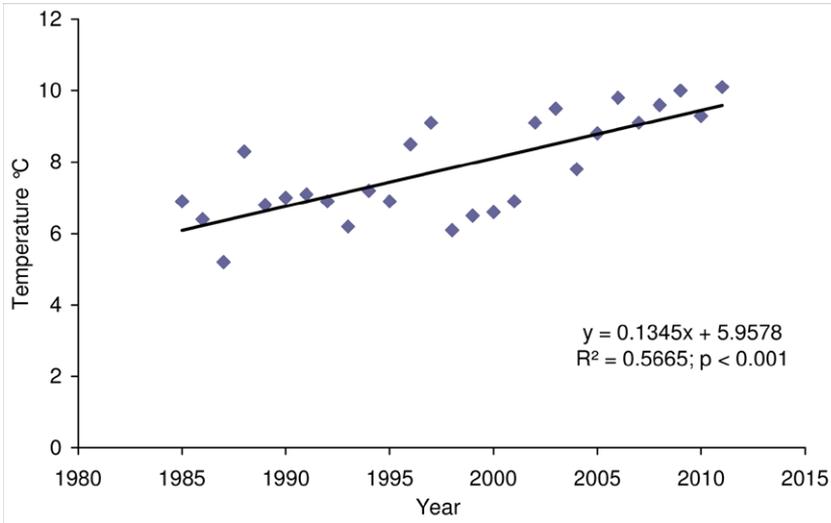


Fig. 4. Maximum summer (July-August) root-zone temperatures obtained annually at the treeline (Fig. 3).

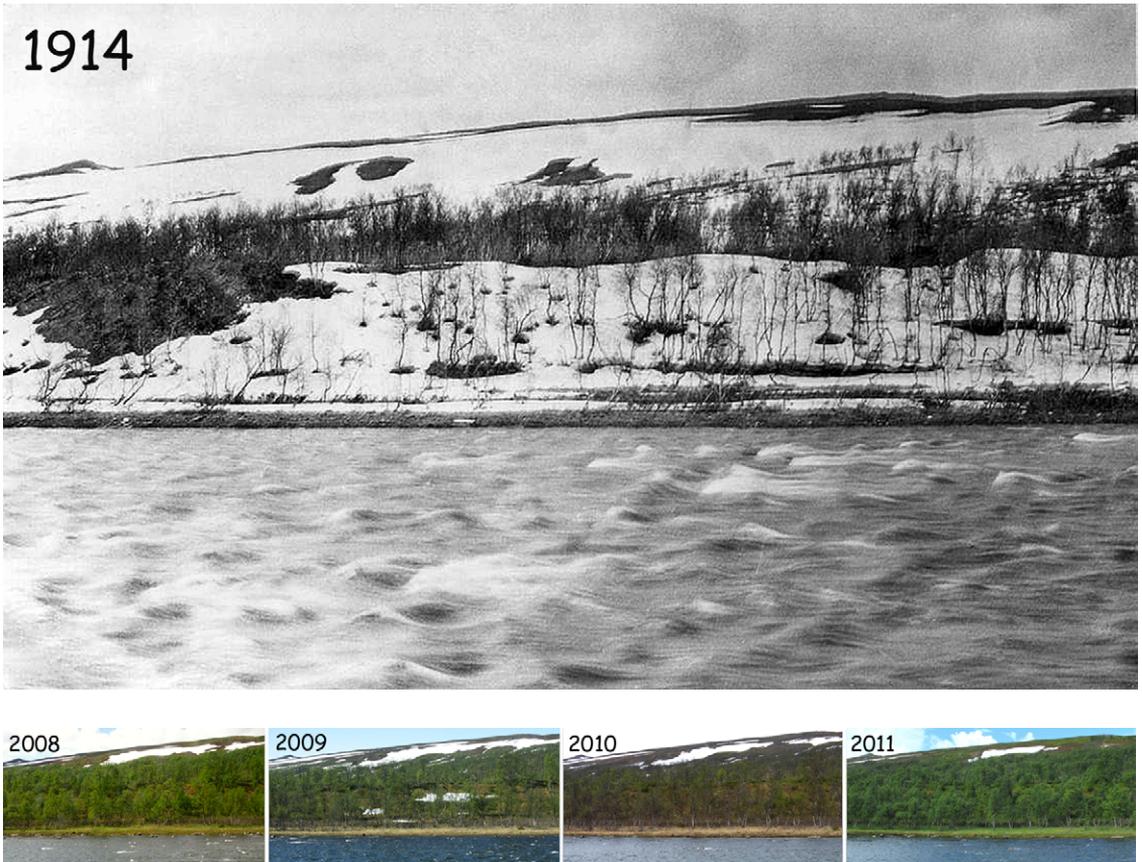


Fig. 5. Phenological view of the east-facing slope of Mt. Lillulvåfjället. The initial image (top) was captured by H. Smith, 11 June 1914. The following sequence (from left to right) represents the situation at virtually the same date of the years 2008, 2009, 2010 and 2011.

here concerned, snow melt has been well underway and birch leafing entirely completed at the same date (± 2 days). Overall the subalpine/alpine landscape in the Scandes has become drier since the 1930s or so (Smith 1957; Komárková & Wielgolaski 1999; Kullman 2007a, 2007b, 2010b).

Results

Treeline change 2007 to 2011 was assessed at 44 sites – 24 in area M and 20 in area C. Of the total sample, 21 sites (48%) displayed treeline rise by 5 m or more (max. 45 m), 18 sites were indifferent (41%), while 5 sites (11%) showed retreat by 5 m or more (max 35 m). A total of 18 out of 21 sites (86%) with treeline advance was confined to area M. The investigated sites represent all aspects, although with a preponderance for south and north. Detailed statistics concerning the magnitude of treeline change within area M and C, respectively, is given in Table 1. Figure 6 accounts for the extent of treeline change in relation to latitudinal position within the geographical transect. Clustering of sites with upslope treeline displacement in the north (area M) is evident, while stability and retraction prevail in the south (area C). It is visually striking that the sharp transition between the maritime and the continental parts of the transect (see above) almost exactly coincides with these fundamentally different treeline performances.

The magnitude of treeline change is significantly larger in area M than in area C (t-test, $p=0.0007$). Area C displays a negative average shift. Of those sites representing treeline descent, 4 out of 5 were in area C. The annual rates for the whole transect and the two sub-areas (M and C) are 1.4, 3.0 and -0.4 m/year, respectively (Table 2).

The etiology behind treeline retraction was a complex and time transgressive affair, involving gradual foliage loss, dieback of stems and their final breakage (Fig. 7). The main pattern was a reduction in maximum stem height to below 2 m. When the dominant stem had died, short sprouts always existed at the trunk base. In no case was treeline retreat associated with death of individual treeline markers. In some cases, observations in late summer evidenced dead and drying leaves, indicative of severe drought during the summer. Since stem and twig dieback occurred above as well as below the maximum snow depth position, it appears unlikely that frost desiccation could be responsible for this process. At the localities with recorded treeline stasis, the treeline markers did not increase perceptibly in height and they frequently displayed reduced vitality of the same kind as described above (Fig. 8).

All sites (area M and C) with treeline stability, retraction, or discernible loss of vigor are in particularly wind-exposed landscape sections, virtually without late-lying snow patches located above the treeline (Fig. 9). The only case of lowered

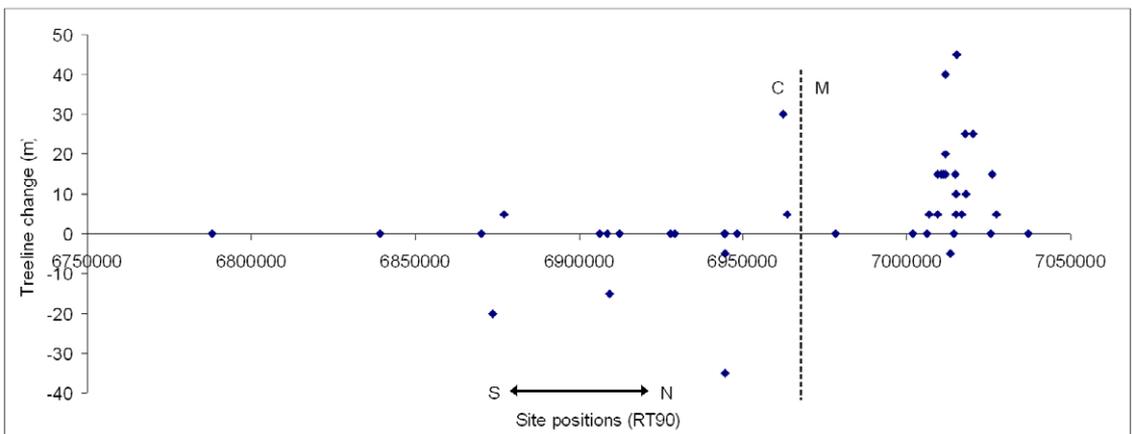


Fig. 6. Treeline change at all individual sites, plotted against the latitudinal position along the entire maritimty-continental transect, according to the geographical positional system RT90. The hatched line separates the maritime (M) and the continental areas (C).

Table 1. Treeline positions (m a.s.l.) 2007, 2011 and change (m) over the period 2007-2011. Geographical coordinates are given as degrees lat. long. Localities above and below the horizontal line belong to area M and C, respectively.

Locality	Coordinates		2007	2011	Δ 2007-2011	Size (m)	Aspect
	N	E					
Åreskutan	6324888	1304651	1010	1010	0	2.1	S
Gräslidfjället	6311718	1210158	960	975	15	2.1	N
Rekdalshöjden	6317546	1202836	830	845	15	2.2	N
Rekdalshöjden	6317387	1202467	845	845	0	2.4	SW
Högåsen	6318746	1221447	725	730	5	2.3	S
Lillhammaren	6313523	1213724	845	870	25	2.0	N
Lillhammaren	6313657	1213927	815	825	10	2.1	NE
Storsnasen	6314869	1220393	905	930	25	2.1	NE
Storsnasen	6312208	1222679	925	930	5	2.0	E
Storsnasen	6313078	1221553	970	975	5	2.0	SE
Hårdeggen	6312291	1227936	930	940	10	2.0	N
Hårdeggen	6311922	1227562	920	920	0	2.0	S
N Tväråklumpen	6312293	1221885	930	975	45	2.0	SE
Getryggen	6311196	1221825	940	935	-5	2.2	E
Getryggen	6310405	1220651	890	905	15	2.1	SE
Getryggen	6310356	1219731	935	975	40	2.1	S
Getryggen	6310240	1218395	930	950	20	2.0	SW
Middagsvalen	6308634	1302892	840	845	5	2.4	N
Middagsvalen	6308313	1302704	835	835	0	2.6	S
Mettjeburretjakke	6310222	1224516	970	985	15	2.2	SW
Mettjeburretjakke	6309774	1224444	1010	1025	15	2.3	W
Storulvåfjället	6309142	1219864	920	925	5	2.5	N
Storulvåfjället	6309059	1219864	905	920	15	2.0	S
Gåsen	6305172	1229550	940	940	0	2.3	W
Predikstolen	6252778	1242090	995	995	0	2.2	S
Falkvålen	6244889	1244770	945	950	5	2.9	N
Falkvålen	6244255	1244480	940	970	30	2.0	S
Storskarven	6236194	1222364	995	995	0	2.0	E
Lillskarven	6234489	1234489	1080	1080	0	2.3	E
Hamrafjället	6233915	1216563	1085	1085	0	2.5	SSW
Hamrafjället	6234039	1217606	1060	1055	-5	2.0	SSE
Hamrafjället	6234180	1218687	1025	990	-35	2.5	SE
Varggransfjället	6227736	1357732	940	940	0	2.4	N
Brattnet	6225348	1223175	1135	1135	0	2.4	S
Brattnet	6225300	1222298	1140	1140	0	2.0	S
Sonfjället	6216590	1328154	1015	1000	-15	2.4	W
Sonfjället	6216227	1328190	980	980	0	5.0	SSW
Sonfjället	6214956	1332040	1135	1135	0	2.1	S
Sonfjället	6218341	1333862	1040	1040	0	2.1	N
Molnet	6158597	1251963	1095	1100	5	2.0	S
Städjan	6156665	1251374	985	965	-20	2.1	E
Städjan	6154939	1252584	965	965	0	2.1	S
Fulufjället	6137925	1238508	945	945	0	3.4	S
Köarskärsfjället	6110890	1307922	875	875	0	2.2	S

Table 2. Absolute change and annual rate of change, separately for area M, C and the entire transect.

	Area M	Area C	All
Change m (mean \pm S.D.)	11.9 \pm 12.5	-1.8 \pm 12.1	5.7 \pm 14.0
Change m yr ⁻¹ (mean \pm S.D.)	3.0 \pm 3.1	-0.4 \pm 3.0	1.4 \pm 3.5



Fig. 7. Treeline retraction over the four-year study period, exemplified at two sites. *Left*. Almost complete dieback of the main stem, although with live basal sprouts. Mt. Stådjan, 6 June 2011. *Right*. Slight reduction in height of the tallest stem implies that this old-growth birch does not fulfill the 2 m treeline definition. Mt. Sonfjället (Gråsidan), 1 August 2011.

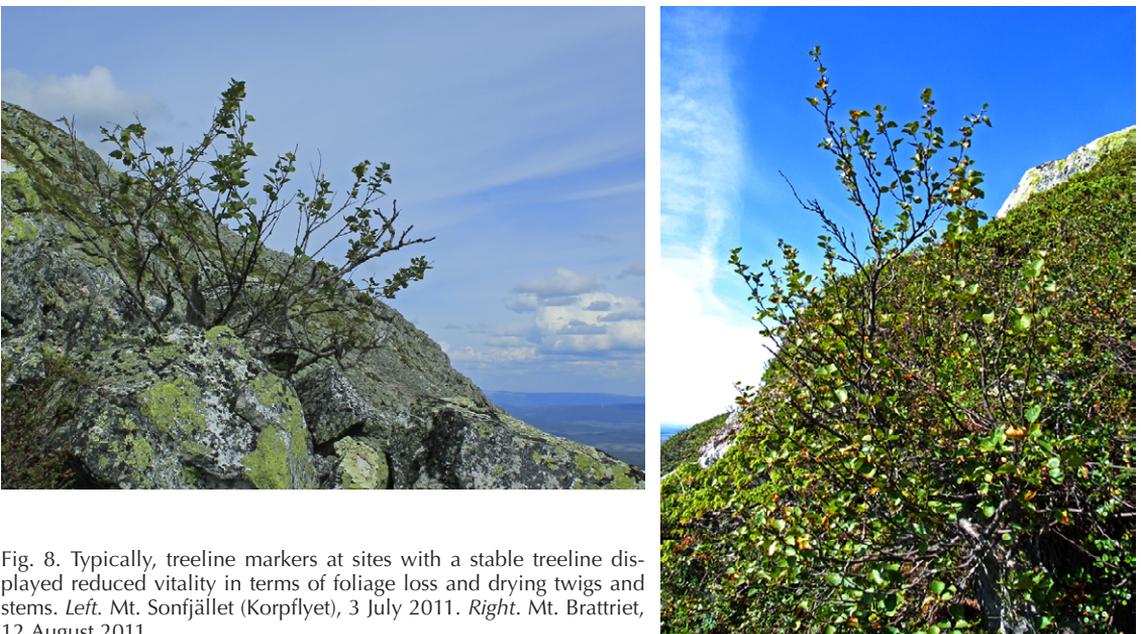


Fig. 8. Typically, treeline markers at sites with a stable treeline displayed reduced vitality in terms of foliage loss and drying twigs and stems. *Left*. Mt. Sonfjället (Korpflyet), 3 July 2011. *Right*. Mt. Brattriet, 12 August 2011.



Fig. 9. Characteristic site with stable treeline, which is positioned right at the rim of closed birch forest. The terrain higher upslope is strongly windswept and virtually no late-lying snow patches accumulate here. Mt. Hårdeggen, 8 August 2009.

treeline in area M was due to geomorphic instability in the form of a minor landslide. In no case could reindeer browsing, which is quite strong along the entire transect, account for treeline lowering or substantial physiognomic recession.

Predominant treeline rise and infilling during the present study period are largely confined to habitats where establishment and growth were previously constrained by too much late melting snow. This discrepancy in snow cover characteristics and phenology between area M and C, particularly during late spring and early summer, has been documented by surveys at each locality (Kullman 1979, updated). The typical character of this course of change is highlighted from Mt. Getryggen (area M), one of the most intensively studied mountains in this respect (Fig. 10, 11).

Notably, the majority of birches representing recent treeline rise are quite low and slender speci-

mens, 2–2.2 m high and with basal trunk diameters of 3–8 cm (see Fig. 11E). Treeline rise has been accomplished by saplings which were recorded as near-tree sized by 2005–2007, when they grew slightly above the contemporary treeline. Annual height growth during the study period was in the range 15–25 cm, which resulted in height increment by 0.5–1 m during the four year period, thereby passing the critical limit of 2 m. Widely scattered saplings, 0.5–1.5 m high, occur within a zone 0–25 m above the new and most recent treeline.

The study of the clonal age of a treeline birch, which transformed from krummholz to tree-size during the past century, clearly sustains its ancient age and establishment much earlier than the modern warming phase (Fig. 12). Coring of the stem at the root collar revealed that this specimen existed, presumably as krummholz, in the late-18th cen-



Fig. 10. 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.

tury. Two pieces of decaying wood were excavated and radiocarbon-dated underneath the stools of living and dead stems. One sample yielded a modern age within the range AD 1490–1950 (Beta-230891) and another dated 4770 cal. year BP (Beta-264397).

Most of the new treeline markers, which appeared during the study period, seemed to originate from seed that had germinated in recent time, apparently during the past 2–3 decades. In some cases, however, they were recorded as low-growing (< 2 m tall) shrubs by surveys of the same transects carried out in the mid-1970s (Kullman 1979). Multiple stems and stools of decaying stems bases further indicate a pre-recent origin. Thus, with respect to the mode of reproduction and mechanism of treeline rise, the present phase of birch treeline advance (mainly in area M) relies both on seed reproduction and accelerated height

growth of old-growth krummholz specimens, i.e. a kind of phenotypic plasticity (Kullman 1979, 2010a; Öberg & Kullman 2009). Overall, the importance of the latter mechanism seems to have diminished substantially relative to the situation prevailing at the time of the survey carried out in the mid-1970s (Kullman 1979).

Signs of reindeer browsing on twigs and branches were found on 58 and 51% of the treeline markers in area M and C, respectively. In most cases, only the tips of annual shoots were browsed and in no case was reindeer impact obviously responsible for treeline retreat during the study period.

Characteristically, treeline markers in area M grow in spots with predominant *Vaccinium myrtillus* and some species typical of moderate snow beds, e.g. *Alchemilla alpina* and *Viola biflora*. In area C, treeline birches are confined to more monospecific and xerophilic *Vaccinium myrtillus*-heaths.

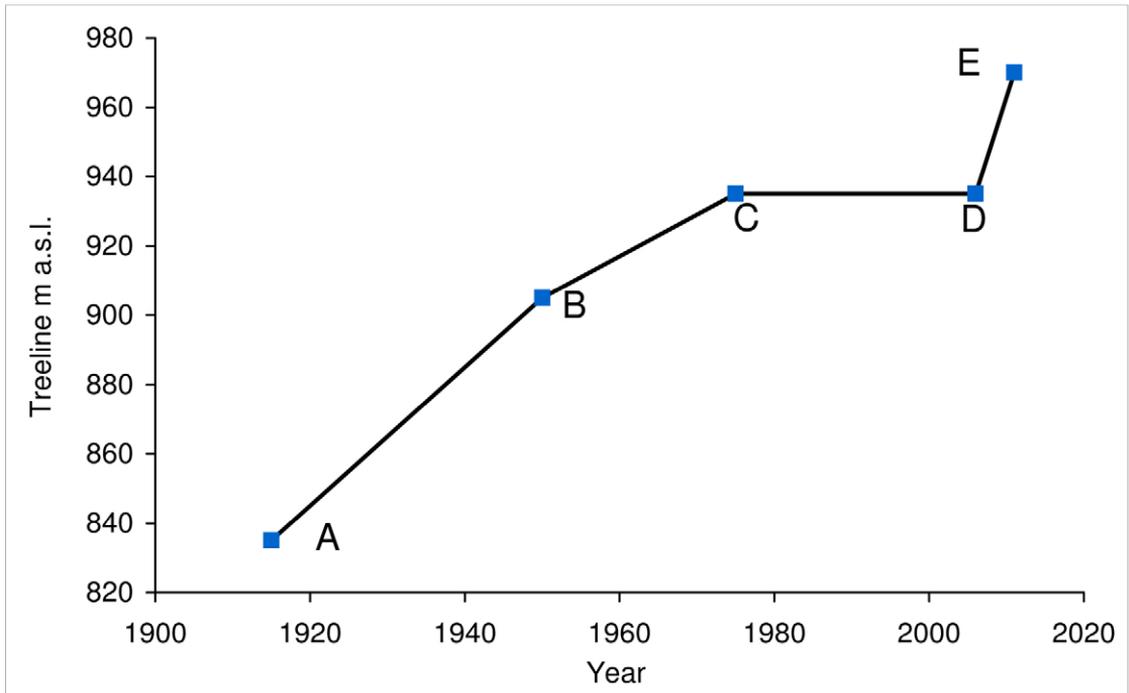


Fig. 11. *Upper*. The temporal course of treeline change along a local elevational transect on the south-facing slope of Mt. Getryggen, according to observations at different points of time. A. 830 m a.s.l. (Smith 1920), B. 905 m a.s.l. (Kilander 1955), C. 930 m a.s.l. (Kullman 1979), D. 930 (Kullman & Öberg 2009), E. This study. *Lower*. Present-day character of the trees marking past and present treeline positions (A-E). 30 April 2011.

Discussion

As outlined below, we consider both of the initially launched hypotheses to be validated by the obtained results. Current treeline performance displays a temporally tight and ultimate relationship with the character of the prevailing thermal climate and appears to be independent of herbivory,

e.g. reindeer grazing. This result contrasts with generalizing hypotheses that reindeer grazing may have a substantial inhibitory effect on warming-induced treeline upshifts (Cairns & Moen 2004; Olofsson et al. 2009; Van Bogaert et al. 2011). A similar conclusion has also been reached for treeline areas in northernmost Sweden (Hedenås et al. 2011). However, this circumstance does not



Fig. 12. *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 radiocarbon-dated and indicate that this individual specimen existed here almost 5000 years ago.

rule out the possibility that in a reindeer-free system the abundance of birches would be higher than is currently the case. On the other hand, observations in ungrazed mountain areas do not support this option (Kullman 2004a, 2005).

Despite virtually similar magnitudes of recent climate warming, short-term positional treeline responses differ significantly north and south of a distinct breakpoint, separating a maritime climate in the north (area M) from more continental conditions in the south (area C). Treeline rise is relatively most prevalent and extensive in the former area, while stability and retreat characterize the latter. This discrepancy indicates 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 maritimty/continentality continuum, most likely snow cover phenology and related soil moisture conditions. This assumption is based on tendencies gleaned in more extensive studies over longer periods of time (Kullman 1979; Kullman & Öberg 2009).

In the south (area C), the treeline is generally positioned relatively close to the mountain peaks, which potentially may hamper its ability to reach the potential limit (see discussion by Odland 2010). However, this circumstance can hardly account for the differential performance along the studied geographical transect. This contention is based on the fact that both treeline position and vitality declined in the south, which needs a tem-

poral change of growth preconditions. Moreover, it is well documented that most of the mountains in the continental area have supported tree and forest growth virtually up to the highest peaks during periods with more favourable climates during earlier parts of the Holocene (Öberg & Kullman 2011b; Kullman 2012)

When contemplating the role of effective soil moisture in alpine/subalpine regions it is important to make a distinction between moisture provided by liquid precipitation and by the gradual melting of late-lying snow patches. To a large extent, the seasonal water balance of high-mountain ecosystems is a function of snow cover characteristics, in particular its spring/summer phenology (e.g. Peterson 1998; Beniston 2003; Hall & Fagre 2003). The fundamental role of melt water in alpine/subalpine plant ecology is widely recognized (e.g. Smith 1957; Holway & Ward 1963; Philipp 1978; Kullman 1986; Keller & Körner 2003; Smith et al. 2003; Shrestha et al. 2007; Millar et al. 2012). Drying-out of the topsoil and associated nutrient shortage represents a recurrent hazard during the summer over those parts of the Scandes where there is no continuous supply of melt-water (Østbye 1975; Wielgolaski & Kärenlampi 1975). Sustained snow melting throughout the summer is vital for establishment and growth of mountain birch (Kullman 1986; Atkinson 1992; Sveinbjörnsson et al. 1992). Thus, projections of future evolution of treeline vegetation based solely on wet precipitation models

therefore risk to be misleading (e.g. Young et al. 2011).

The character of birch decline in the continental area suggests that soil drought and desiccation have recently reached critical levels, when pre-conditions for sustainable growth and seed regeneration have gradually over the past century become decidedly sub-optimal. An expression of this situation is provided by an age structure study of mountain birch at a typical site in the treeline ecotone (area C), which displays a pronounced “geriatric” age frequency pattern, with a preponderance of low-vitality ancient trees, representing peak regeneration in the mid 19th century. This sharply contrasts with insignificant sexual regeneration over the warmer and drier 20th century and particularly during recent decades (Kullman 2012). The coupling between the present state of treeline performance, earlier and more complete snow melt and thereby drier soils, is supported by landscape-scale studies, which document disappearance of snow beds and associated plant communities in the continental area (Kullman 2004a, 2005), despite increased summer precipitation. Obviously, under these circumstances, the drought-intolerant mountain birch (Vaartaja 1955) and its treeline are no longer able to benefit from recent climate warming. Due to gradually enhanced moisture stress, trees and treelines in this area are not responding to rising temperatures with upslope advances as they did during earlier warming phases of the 20th century (Kullman & Öberg 2009). This kind of shift in response pattern, implying that moisture stress rather than heat deficiency is limiting for treeline rise, is reported also from continental Alaska and Sierra Nevada (e.g. Taubes 1995; Lloyd 1997; Driscoll et al. 2005; Millar et al. 2012). In contrast to retarded birch treeline advance, more drought-resistant evergreen conifers, pine in particular, are currently more expansive. At some localities in the continental area, pine is even “leap frogging” over the sparse and disintegrating birch belt (Kullman 2004a, 2010a, 2010b, 2012). This currently emerging situation has a paleoecological analogy. During the early Holocene, when temperatures were about 3 °C higher than present, no birch belt existed and pine formed the transition between forest and alpine tundra (Nesje et al. 1991; Kullman 1995; Barnett et al. 2001; Kullman & Kjällgren 2006; Öberg & Kullman 2011b).

The relatively more frequent treeline rise in the maritime region is consistent with air and soil tem-

perature evolution, birch phenology series and glacier/snow pack performance. Upshifts, in contrast to stability and retraction, have a clear spatial relation to sites influenced by a relatively deep and persistent snow cover, as assessed by field surveys at each locality during spring and early summer (Kullman 1979, updated). This is a setting that in its most extreme form does not support establishment and growth of mountain birch (Björk & Molau 2007). In accord 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. 1).

It appears that most new treeline markers have originated from seed establishment of new individuals over the past 30 years or so. In contrast, during earlier parts of the 20th century, treeline upshifts were mainly accomplished by transformation of krummholz birches to more erect and arborescent forms as climate warming initiated a surge of fast-growing stems (Kullman 1979, 2010a). These originated from a pool of relictual shrub birches, some of which have prevailed above the treeline for several past millennia (Fig. 12), characterized by neoglacial cooling (Kullman 2003, 2010a). Gradually during the past century, this pool seems to have become “depleted” as most individuals have turned into tree form and a shift from predominant vegetative to sexual reproduction has taken place quite recently in snow rich and maritime areas. This contention is supported also by a virtually new phenomenon, implying that, within snow rich areas, birch saplings (20–30 years old) are quite commonly established up to 300–700 m above the treeline (Kullman 2004b, 2007a, 2007b; Sundqvist et al. 2008; Öberg & Kullman 2011a). This indicates that treeline vegetation is currently in a strongly progressive phase in these environments. An analogous reproductional shift may account for extensive upslope advances of many vascular plant species in the alpine zone of the maritime area, i.e. a kind of “thermophilization/xerophilization” of the alpine plant cover in general (Kullman 2007a, 2007b, 2010b).

The annual rate of treeline advance for the entire area (M + C), i.e. 1.4 m year⁻¹, is double the figure assessed for the period 1915–2007, which contained both warm and cool phases (Kullman & Öberg 2009), indicating that treeline change is currently performing in distributional equilibrium with the prevailing climate. Similar rates during

the past 20 years are reported for the Ural Mountains (Russia) (Kharuk et al. 2009). In this context, it should be stressed that the short-term temperature equilibrium, empirically demonstrated in this study, invalidates generalizations that, at the scale of years to decades, the birch treeline is out of equilibrium with climate (e.g. Staland et al. 2010). Given sufficient soil moisture, there is a tight coupling between climate warming and treeline responses, as described and discussed from widely different regions (Weissberg & Baker 1995; Luckman & Kavanagh 2000; Daniels & Veblen 2004; Elliott 2011; Singh et al. 2012).

Since the air temperature rise during the study period has been quite modest, in contrast to more consistent soil temperature increase, there is reason to stress the contribution of high soil temperatures for the present phase of birch treeline rise in particular and for treeline life in general (cf. Karlsson & Nordell 1996; Körner & Paulsen 2004; Gehrig-Fasel et al. 2008; MacDonald et al. 2008).

A main conclusion from the present study is that one and the same climatic fluctuation does not everywhere lead to the same pattern and magnitude of birch treeline change (cf. Kullman & Öberg 2009; Virtanen et al. 2010; Elliott & Kipfmüller 2011). In the present context, snow cover phenology appears to have a pivotal role for differential treeline dynamics. This circumstance has essential implications for projections of treeline performance in an allegedly warmer future. It now appears that such modelling needs to account for divergent responses along the ubiquitous continentality-maritimity gradients in the Scandes. Existing models (e.g. Moen et al. 2004; Young et al. 2011) do not make this distinction, which results in quite unrealistic outputs, projecting a threat to the persistence of an extensive treeless alpine zone in Scandinavia. In a hypothetical case of continued warming, mountain birch is likely to advance substantially only in the most maritime and snow rich districts of the Scandes, where sufficient soil moisture would still be available (cf. Öberg & Kullman 2011a). In this context, it is important to stress also that recent treeline rise is manifested by small and sparsely distributed trees. We can see no indication whatsoever for a pending landscape-scale transformation from alpine tundra to closed birch forest, as young seedlings and sapling are only sparsely spread above the treeline. However, infilling of snow glades in the upper birch forest belt by seeded birches occurs commonly in the maritime area (Kullman 2007b; Kullman & Öberg

2009), which implies some densification of the treeline ecotone. In a long-term perspective, putative warming and soil drought may reach critically high levels also in the maritime region, which would cause disintegration and extirpation of the birch belt and its replacement with the more drought-resistant *Pinus sylvestris* (Kullman & Kjällgren 2006; Kullman 2010a). An analogous projection, based on recent vegetational trajectories, has been made for *Betula pubescens* ssp. *czerepanowii* in the Ural Mountains of Russia (Kapralov et al. 2006).

Conclusions

- During the period 2007/2008–2010/2011, treeline advance and stability/retreat prevailed in areas with maritime and continental climate, respectively.
- Current treeline performance occurred in a context of historically high summer and winter air temperatures and raised root zone temperatures.
- Treeline rise was proximately conditioned by release from snow cover constraint on birch establishment and growth.
- Treeline stability and retreat related to soil drought as a consequence of more or less complete melt-out of most snow patches already during the early summer.
- Prior treeline rise (1915–2007), predominantly accomplished by increased height growth of relict krummholz birches, has recently given way to seed-based establishment of new trees above the former treeline (2005–2007).
- The discrepant response pattern between treelines in maritime versus continental climates, despite a similar course of climate change, should be accounted for in projective vegetation models for high mountain regions.
- In case of continued warming, the subalpine birch forest is unlikely to expand on a broad front over the alpine tundra since the continental type of snow phenology conditions and associated birch responses will eventually come to prevail over much of the Scandinavian mountain world.

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