



A one hundred-year study of the upper limit of tree growth (*Terminus aboreus*) in the Swedish Scandes illustrated and updated change in an historical perspective

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Positional treeline change since the early 20th century and up to 2017 was assessed along three elevational transects on Mt. Gettryggen in the southern Swedish Scandes. Baseline data, representing the year 1915, were compared with later intermittent records up to 2017. Concerned species were *Betula pubescens* ssp. *czerepanowii*, *Picea abies*, *Pinus sylvestris* and *Alnus incana*. These species responded with different degrees of continuous upshift and substantial inter-site variability. *Betula* displayed the largest advance, by 215 m. This maximum magnitude of change compares with data from widely different parts of the Swedish Scandes. This common performance indicates that regionally recorded summer warming by 1.5 °C is the ultimate cause. In a long-term historical perspective, most congenial conditions for birch and pine growth at high elevations prevailed around 10500 – 9400 cal. yr BP, when the local treelines reached 1355 and 1250 m a.s.l., respectively. The former elevation coincides with the upper limit of *Vaccinium myrtillus* and the low-alpine belt. With the exception for *Pinus*, recent treeline upshifts were accomplished predominantly by phenotypic responses of millennial-old krummholz specimens. Only occasionally, has treeline advance by *Betula* and *Picea* originated from seed regeneration during the past century. These circumstances may set the limit for further advance where and when the pool of high-altitude old-established krummholz specimens becomes depleted as existing krummholz individuals have already transformed to tree mode.

INTRODUCTION

Impacts and consequences of climate change and variability on the living landscape and its various compartments have become a common scientific and landscape management concern in recent days. Climate models disseminate a prospective view of ubiquitous and calamitous climate warming over the rest of the present century (IPCC 2013). Subalpine and alpine ecosystems, prevailing at their edge of climatic tolerance, are supposed to display first and straightforward responses to altered climatic conditions. Accordingly, alpine treelines and treeline ecotones, primarily considered to depend on altitudinally decreasing summer air and soil temperatures, emerge as primary monitoring targets and “early warning lines” in this context (Tranquillini 1979; Grace et al. 2002; Körner & Paulsen 2004; Kullman 2007, 2015a, b; Holtmeier 2003; Müller et al. 2016). They have by tradition been held to display clearly interpretable indications of changed growth conditions and pending landscape transformations in response to altered climatic conditions (Kullman 1998a, 2012, 2015b, 2017a; Fagre et al. 2003; Holtmeier 2003; Lloyd 2005; Nagy 2006; Harsch & Bader 2011). However, a close association with climate change has been disputed by

certain authors (e.g. Olofsson et al. 2009; Van Bogaert et al. 2011), an option questioned by Kullman (2015b). Thus, further inquiry into this issue seems motivated.

Treeline studies in different parts of the world display large inter-site variations with respect to degree of upslope treeline shifts during the past 100 years of climate warming (Aas 1969; Kullman 1979, 2017a, 2018; Hiller et al. 2001; Kapralov et al. 2006; Danby & Hik 2007; Kullman & Öberg 2009; Harsch et al. 2011; Mamet & Kershaw 2012; Gaire et al. 2014). In many cases, this circumstance relates to topoclimatic and ecological constraints in combination with ground cover and herbivory (Kullman 1979, 2007b; Shiyatov 2003; Dalen & Hofgaard 2005; Selsing 2010; Elliott 2011; Leonelli et al. 2011, 2016; Holtmeier & Broll 2011; Nagy et al. 2013; Aakala et al. 2014; Schickhoff et al. 2015). A general problem within treeline science is that many recent studies suffer from unprecise treeline definitions (cf. Hustich 1979; Kullman 2010; Schickhoff et al. 2015), which impairs adequate inter-site and temporal comparisons. Moreover, recent treeline shifts may locally result from abandoned land use, contemporaneous with climate change, which further complicates cause attribution of past and modelling of future performance.

It may be a truism that the past has an influence on the present and future landscape structure. Therefore, recent treeline dynamics can be properly understood only with a longer retrospective and observational

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view on the concerned ecosystem and its dynamics. In the Scandes, modern treeline change has to be evaluated in perspective of a virtually consistent retraction towards lower elevations throughout most of the Holocene, with an elevational nadir right before the onset of the modern episode of climate warming in the early 20th century (Kullman 2013, 2015b,c).

Effects of climate warming over the past century, subsequent to the dire, dark and cool centuries of the Little Ice Age (Lamb 2005; Grove 1988), offer a unique opportunity to improve our understanding of the relationship between landscape-scale high-elevation tree growth and thermal conditions. Despite predictions of pending climate warming and extensive forest encroachment on the alpine tundra (Kellomäki et al. 1997; Moen et al. 2004; ACIA 2005; Kaplan & New 2006), there is little factual evidence of ongoing change in that direction, at the general landscape scale (Kullman 2016b). This discrepancy between models and the real world performance may be a consequence of lacking understanding of climate-treeline relationships, giving rise to over-simplified models, not subjected to proper validation tests. These aspects constitute the background and rationale of the present study, which mainly focuses on factual elevational dynamics of precisely defined treelines during the past 100 years of the dominating tree species in the southern Swedish Scandes. Concerned species are mountain birch (*Betula pubescens* ssp. *czerepanovii*), Norway spruce (*Picea abies*) Scots pine (*Pinus sylvestris*) and Grey alder (*Alnus incana*). A particular focus is on change during the past 10–15 years, as a measure of endurance of treeline shifts. Moreover, different modes of treeline shifts are highlighted. The results are viewed in perspective of local and regional Holocene treeline history.

STUDY AREA

Location, climate, physiogeography and land use

The present study focuses on treeline performance on Mt. Getryggen in the southern Swedish Scandes, 63° 11' N; 12° 19' E (Fig. 1). The mountain peak is at 1382 m a.s.l., while surrounding valley bottoms linger about 700–750 m a.s.l. The bedrock consists of amphibolite and gneisses and is covered with glacial till, fluvi-glacial deposits and peat. Predominant soils in the treeline ecotone are shallow Spodosols. The study site is ideal for monitoring treeline movements. An even topography and adequate soils provide possibilities for upslope tree advancement over the mountain slopes. Particularly important is the fact that this mountain has been in the focus of different generations of treeline researchers since the early 20th century. Thus, modern treeline dynamics may be evaluated against a proper baseline record, a truly unique circumstance.

With respect to the climate character, the concerned mountain is within a transition zone between sub-oceanic and sub-continental influences (Raab & Vedin 1995). The nearest official meteorological station (Storlien/Visjövalen, 642 m a.s.l., 20 km to the northwest) accounts for climate data, representing the so-called normal period 1961–90. Mean temperatures for January, July and the year are -7.6, 10.7 and 1.1 °C. For the same period of time, annual precipitation averages 857 mm, of which 45% is snow (Swedish Meteorological and Hydrological Institute).

Modern climate change (instrumental and proxy records)

Like the situation in many other northern regions worldwide, the climate in this part of the Scandes has improved during the past 100 years, as expressed by records from Storlien/Visjövalen meteorological station (see above), with data from the early 20th century. For the period June –

August and December–February, significant linear trends, of + 1.5 and 1.4°C, respectively, were recorded. Summer warming was most prominent during the first four decades of the 20th century, with a broad peak in the late 1930s (Figs. 2, 3). Thereafter, the temperatures have prevailed at a relatively high level, although with a large variability on the scale of years and short periods of years. Winter temperature has shown a more consistent warming trend since the early 20th century. However, the swings between single years have been larger than displayed by the summer temperature. Precipitation has increased by c. 15% since the early 20th century (Alexandersson 2006; Kullman 2007).

Proxy records of centennial climate change are provided by shrinking glaciers, earlier melt-out of alpine/subalpine snow patches and vanishing or reduced permafrost. In addition, snowmelt and birch leafing in the subalpine forest belt nowadays takes place about two weeks earlier than in the early 20th century (Kullman 2016). As a consequence of earlier and more complete snow-melt, the ground in alpine and subalpine areas in general is found to have dried out at earlier dates annually during the past century, with cascading ecological effects (Smith 1957; Wistrand 1962; Kullman 2004).

Plant cover

The study area provides a representative view of the subalpine biogeographic organization of the Swedish Scandes. A discrete subalpine belt with almost monospecific predominance of mountain birch (*Betula pubescens* ssp. *czerepanovii*) currently prevails between c. 700 and 900 m a.s.l. On the mountain here concerned, the upper distribution of closed birch forest stops at a broad front along a topographic discontinuity in the form of a “knee”, 840 m.a.s.l., representing transition from concavity to a flat terrace (Fig. 4). Solitary tree birches, minor groves and a few narrow wedges extend substantially higher, benefitting from local wind shelter. Large and late-thawing snow patches at high elevations provide more or less continuous supply of meltwater throughout the summer, which supports the well-developed birch forest belt below, also embracing extensive mires.

Scattered specimens of subordinate tree species prevail in the birch forest – *Sorbus aucuparia*, *Picea abies*, *Pinus sylvestris*, *Populus tremula* and *Alnus incana*. Except for *Sorbus*, which as a tree extends virtually as high as *Betula*, all other tree species have their respective treelines in the lower reaches of the birch belt.

The treeline is the limit for successful survival of the tree form. Henceforth, the treeline is narrowly defined for each species as the maximum elevation (m a.s.l.) of individuals with stems at least 2 m tall (cf. Miehle & Miehle 2000; Hofgaard et al. 2013; Kullman 2016a). Elevational treeline dynamics integrates climate-vegetation interactions on scales of decades to centuries and longer. Compared to other delimitations of the forest to alpine tundra transition, this treeline definition provides the most clear-cut ecological expression of prevailing climate conditions, particularly apt for adequate comparisons in space and time (Fagre et al. 2003; Nagy 2006; Kullman 2010).

The ground cover vegetation in the birch forest and up to the top of the mountain is since long ago affected by summer grazing and trampling by reindeer (*Rangifer tarandus*), which since the early Holocene constitute an integral part of this environment (Fig. 4). An expression of this situation is that in the Sami tradition, the study mountain is named “Reindeer Mountain” (Sw. Renfjället). Past human usage is indicated by the finding of an iron arrow head, which recently melted out from a late-lying snow patch, and probably it was lost in connection with reindeer hunt about 1000 years ago (Öberg & Kullman 2011). A Sami dwelling site prevailed until the early 20th century close

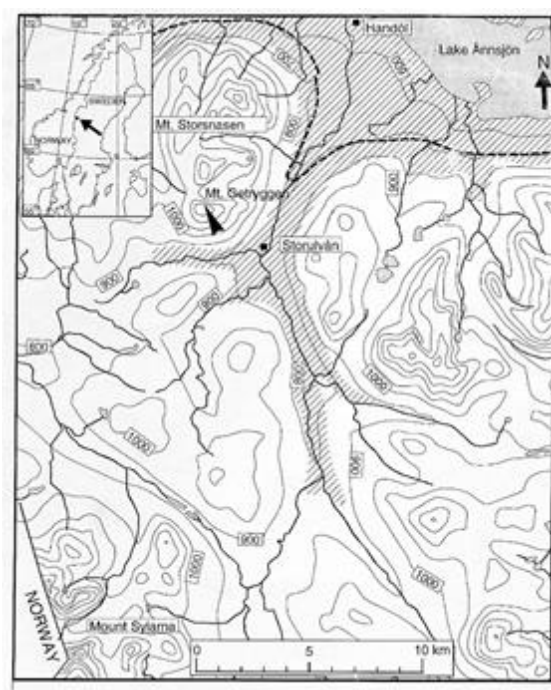


Figure 1 Location map, showing the position of Mt. Getryggen (arrow) in the Handölan Valley, northern Sweden.

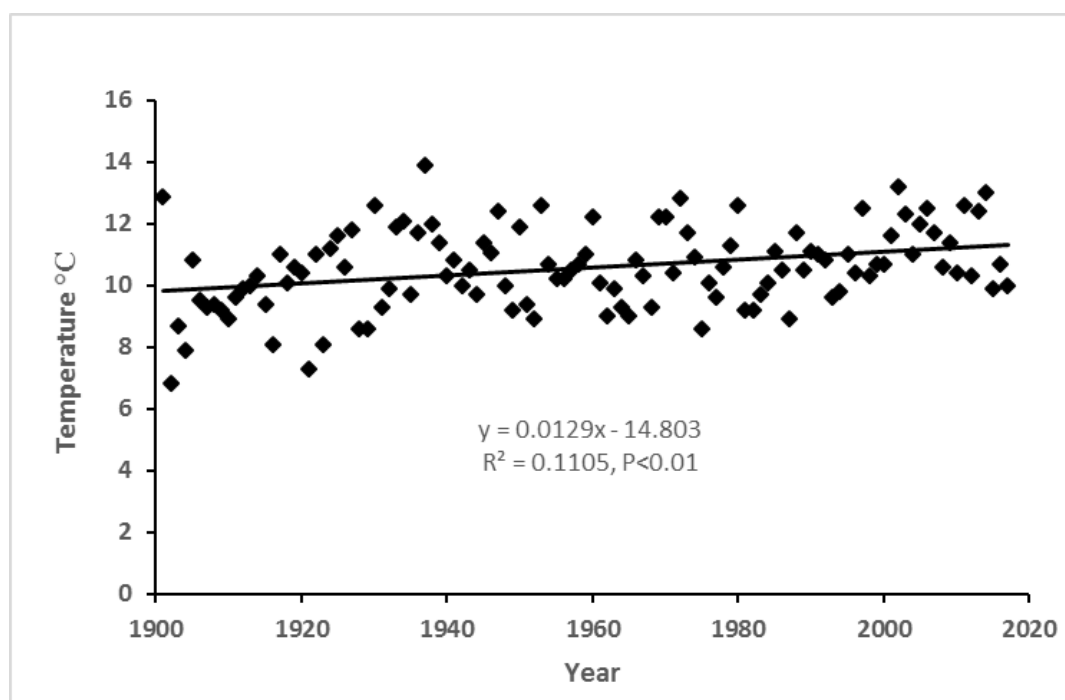


Figure 2 Annual records (1901-2017) of June-August temperature at Storlien/Visjövalen meteorological station.

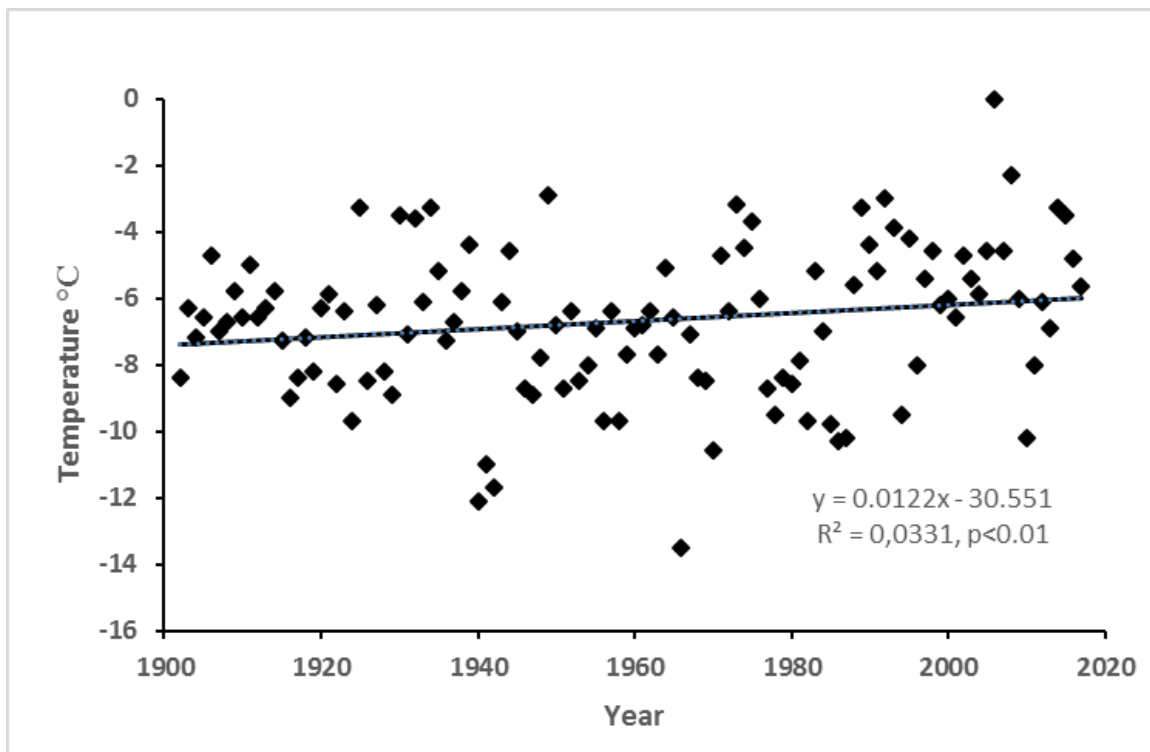


Figure 3 Annual records (1901-2017) of December-February temperature at Storlien/Visjövalen meteorological station.



Figure 4 The south-facing slope of Mt. Getryggen. Continuous birch forest stops beneath the distinct terrace around 840 m a.s.l., while small groves and solitary trees extend to much higher elevations. The arrow indicates the position of a recovered megafossil birch, i.e. the birch treeline of the early Holocene (cf. Fig. 6). Photo: 2010 -09-10.

to the valley floor on the southeast facing flank of the mountain. Associated activities caused some local thinning of the birch forest, although leaving the treeline ecotone virtually unaffected.

Since the early 20th century, reindeer numbers have increased steadily in this region (Kullman 2016a), which has to be taken into account in connection with evaluation of recent vegetation dynamics in these mountains. Aside of Sami utilization, human disturbance to the plant cover is considered to be negligible (Virtanen et al. 2003), although this mountain is currently frequently used by tourists, both summer and winter.

Holocene arboreal history

The course of present-day vegetation and treeline evolution integrates modern climate change and variability with vegetation structures and patterns reflecting climate and environmental change prevailing during earlier epochs of the Holocene. Therefore, a short historical overview may be motivated, as a basis for interpretation of the obtained results in perspective.

For long, vegetation history has been synonymous with pollen analysis. However, that approach has been proven to provide an imperfect and incomplete view of Holocene treeline elevation, composition and structure (Kullman 2002, 2008, 2017b; Elven et al. 2013). A more qualitatively accurate view in these respects is provided by analyses of megafossil tree remains, preserved in peats and under glacial ice (Kullman 2013, 2017b). It appears that all of our principal treeline trees were present in northern and western Scandinavia at early deglaciated nunataks already during the Late-Glacial, high above (500–700m) current treeline positions. The relatively highest elevations of tree growth were obtained 11500–9000 cal. yr BP, forced by higher than present orbitally driven summer solar irradiance and accordingly summer temperatures, about 3 °C, warmer than during the past few decades (Kullman 2017a,b). Examples of high-elevation tree growth during this period are provided by megafossils of *Pinus* and *Betula* (Figs. 5, 6). Remnants of a small birch tree were exposed by minor soil erosion close to the wind-swept peak of the mountain, 1355 m a.s.l. (Fig. 6). This is 310 m higher than the birch treeline of the present day (Kullman & Öberg 2009). The site coincides with the upper limit of *Vaccinium myrtillus* and features of podzolization in the soil. Tentatively, this implies that, in general, the upper limit of *Vaccinium myrtillus* may be used as proxy for the maximum elevation of tree growth during the warmer-than-present early Holocene.

As evident from robust megafossil records, environmental conditions during the early Holocene also enabled the growth of warm-demanding broad-leaved trees (9500–7000 cal. yr BP), such as *Quercus robur*, *Corylus avellana*, *Ulmus glabra*, *Alnus glutinosa* and *Tilia cordata*, at relatively high subalpine elevations (the study area included), currently dominated by cool-adapted boreal species, foremost mountain birch, spruce and pine (Kullman 1998b,c, 2008). Megafossil analyses provide substantially earlier records of presence of the thermophiles than interpreted by local and regional pollen analyses (Hafsten 1992; Giesecke 2005). This discrepancy highlights a more general methodological problem in vegetation history (Kullman 2017b).

Apparently, the early Holocene high-elevation forests contained a richer tree flora than today. In particular *Alnus incana* constituted a prominent member of the early subalpine ecosystems. *Picea abies*, for long erroneously considered as a late-Holocene immigrant to the Scandes (e.g. Huntley & Birks 1983), prevailed at high elevations during the early Holocene, also on Mt. Getryggen (Fig. 7). Subsequently, gradual cooling was initiated and maintained throughout much of the

Holocene, which forced regression of the dominating pine treeline ecotone and the warmth-demanding trees. As a further consequence of this Neoglacial environmental change, the present-day character of the treeline ecotone gradually evolved. The result was the current zonation pattern, characterized with a distinct upper subalpine birch forest belt and montane spruce/pine forests below. Apparently, the subalpine birch forest belt was initiated in the wake of a distinct cooling episode around 8200 cal. yr BP (Kullman 2013). This course of climate and associated regressive tree cover evolution reached a Holocene nadir by the late 19th century, culminating with the Little Ice Age of the past 700 years or so (Grove 1988).

Substantial warming of the past 100 years represents a fundamental break in the Holocene course of climate and biogeographic evolution (Kullman 2003; Kullman & Kjällgren 2006; Kullman & Öberg 2009). Recent treeline rise of *Betula* and *Pinus* have locally reached levels higher than any time during the past 5000–7000 years (Kullman 2013, 2017a). In fact, temperature reconstructions from the southern Swedish Scandes indicate a long-term cooling trend over the past 1000 years prior the recent warm phase (Kullman 2015c; Fuentes et al. 2017).

Notably, present-day climate and biotic change, as focused in this paper, take start from a natural bottom level, representing “ice age-near” climatic conditions and climatically depauperized ecosystems (cf. Auger & Payette 2010). It is important to consider, however, that treeline rise over the past 100 years has not been an overall monotonic course of change. A severe, although transient, climatic set back during the late 1980s caused extensive tree and sapling mortality at treelines in the study region (Kullman 1989). This experience is fundamental to the current discourse concerning anticipated future climate change and landscape evolution.

METHODS

Positional treeline shift

Treeline shift was elucidated along broad elevational belt transects, centred upslope of the treeline positions given by Smith (1920) and resurveyed by Kullman (1979) and Kullman & Öberg (2009). A recent treeline survey of three of the mountain slopes was carried out in 2017, i.e. east, south and southwest-facing aspects, SITE 1–3, respectively. Each site embraces about 1 km in width. Trees beyond the treeline position by the mid- 1970s were positioned (GPS) and tallied. Some specimens had been photographed at earlier occasions, which enabled rephoto analysis and clear-cut evidence of the overall character of change or stability.

The accuracy of Smith’s tree-line records, with virtually the same definition as the one used here, was assessed and confirmed by boring birches at 2 m above ground level (Kullman 1979). Tree rings were counted in the laboratory, using a stereomicroscope.

Experimental studies

Based on regional studies of centennial treeline change of mountain birch and spruce, it appeared that positional treeline progression has to a high degree relied on phenotypic plasticity rather than processes related to the regenerative niche (Kullman 1979, 1986a, 2010,). In order to shed some further light on this aspect, long-term experimental studies were initiated on Mt. Getryggen in the late 1970s and early 1980s. Early life history stages were specifically studied, e.g. seed quality, seed bank, germination in the field, establishment, and early-life survival. Details and results of these studies (until 1992) are given by Kullman (1984, 1986, 1993). The latest survey was carried out during the autumn 2013 and is reported below.



Figure 5 Megafossil remains of a pine tree, recently exposed by wind erosion. The position is 1250 m a.s.l., which is 515 m higher than the present-day treeline in this slope. Radiocarbon dating yielded 10 520 cal. yr BP. Photo: 2003-09-01. Source: Kullman & Kjällgren (2006).



Figure 6 Erosion scar (1355 m a.s. l.) close to the peak of Mt. Getryggen, which has exposed wood remnants of birch, dated 9370 cal. yr BP. The site is indicated by an arrow in Figure 4. Photo: 2012-09-12.



Figure 7 An extensive spruce krummholz individual on the south-west facing flank of the mountain, 995 m a.s.l. Megafossil wood remains were dug out in the center of the formation and dated 6860 cal. yr BP (Beta-474250). Photo: 2012-07-31.

Annual records of birch germinability were tested on seed collected in a stand 775 m a.s.l. on the south-facing slope of Mt. Getryggen. Percentage viable seeds were tested in the laboratory (cf. Kullman 1984). The possibility of a birch seed bank was elucidated by the burial of see lot of 5000 seeds in the lower part of the A-horizon, 5 cm below the soil surface. Viability was tested intermittently until 2013.

A sowing experiment was initiated in the autumn of 1980. Seeds of local provenance with 15 % germinability were sown on mineral soil in three contrasting habitats where the ground cover had been removed; – *Birch forest*, 775 m a.s.l., *Snow Bed*, 825 m a.s.l. and *Tree-limit*, 930 m a.s.l. The number of living seedlings was surveyed annually 1980-2013.

A transplantation experiment was initiated in 1978. For that purpose, naturally established seedlings of virtually uniform size and age, c. 4.5 cm tall and 3 yr old were planted in three contrasting habitats 820-830 m a.s.l., where the original vegetation had been removed. These habitats were *Windswept crest*, *Moderate snow bed* and *Extreme Snow bed*.

Further nuances to the interpretation of results obtained by the observed treeline dynamics of dominant native species were gained from the outcome of a small-scale trial with planted native *Pinus sylvestris* and some exotic tree species in the mid part of the birch belt in a sparse and snow-poor *Empetrum*-lichen heath, situated on the east-facing slope of Mt. Getryggen, 800 m a.s.l. (Kullman 1985). Planting was carried out in the early summer of 1980, and comprised 0.5- 0.8 m tall saplings of the following species, *Picea abies*, *Picea omorika*, *Picea pungens*, *Picea engelmannii* and *Larix sibirica*. All plants were produced in the nursery

of *Arboretum Norr* in Umeå and were provided by Dr. C.G. Thögersen. Survival, height growth and injuries have been monitored annually up to 2017.

RESULTS

SITE 1. East-facing slope of Mt. Getryggen

Birch treeline

Smith (1920) measured the treeline of mountain birch to be at 810 m a.s.l., a value which was confirmed as reasonable by boring an old-looking tree 2 m above the ground level at this specific elevation (Fig. 8) (Kullman 1979). By the mid-1970s, the treeline had reached 920 m a.s.l. (Fig. 9) (Kullman 1979) and in 2007 it was positioned at 940 m a.s.l. (Kullman & Öberg 2009). The most recent assessment was in 2017, when 945 m a.s.l. was attained by the advancing treeline (Fig. 10). Thus, over the past 100 years, the treeline has shifted 135 m upslope. This continual course of change is paralleled with increased ramification and foliation of birches growing in the treeline advance zone (Fig. 11).

Treeline rise relative to the position prevailing in 1915 seems to have been accomplished predominantly by phenotypic plasticity of old-established polycormic specimens, i.e. transformation from prostrate to erect tree form. Judging from the presence/absence of stools with multiple stems, recently established specimens are rare in the zone where the treeline advanced during the past hundred years (Fig. 10).

Below the treeline, substantial in growth of birch has taken place in topographic concavities, where previously too much late-lying snow precluded tree growth. This phenomenon is highlighted for a site on the



Figure 8 This birch, growing at 810 m a.s.l. represents the treeline around 1915, as evident from dendroecological analysis and field records (Smith 1920). Photo: 2003-07-20.



Figure 9 A. In the mid-1970s, a solitary birch tree, 920 m a.s.l., with a recently broken top marked the treeline. Photo: 1978-08-15. B. The same tree has recovered substantially up to the present day. Photo: 2017-08-15.



Figure 10 A. The new and higher treeline, 945 m a.s.l., attained after 2007. Photo: 2017-08-15. B. An extensive and multi-stemmed stool of stems from the same root indicate that this is a decidedly old-established specimen. Photo: 2017-08-15.

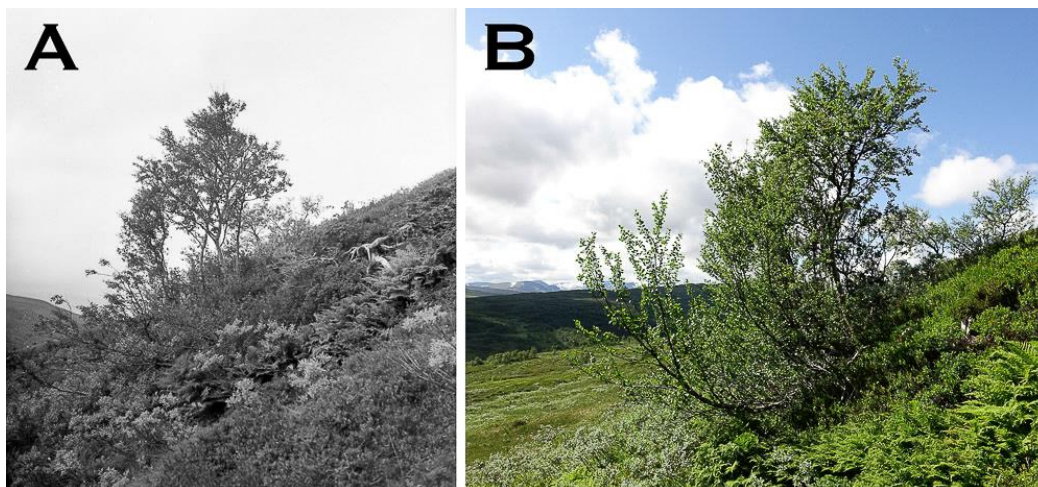


Figure 11 A. Polycormic birch copse growing 890 m a.s.l., i.e. 80 m atop of the position held by the early 20th century. The largest stem initiated rapid height growth in the early-1940s. Photo: 1973-06-28. B. During the past 3-4 decades, this specimen has been affected by heavy snow pressure and over the same time foliage has increased. Photo: 2017-08-03.

lower east-facing slope of Mt. Getryggen (Figs. 12, 13). An age structure study revealed that by the early 20th century, a sparse cover of low-growing birches prevailed at the bottom of the depression. A peak of instatement of new stems occurred in the 1930s. Intermittent observations show that until the late 1980s, these birches staggered as low growing shrubs (<0.5 m tall). Subsequently and up to the present day, stem density and height have increased substantially, without perceivable stem mortality. By 2017 the height of the stand was 4.3 ± 1.02 m, to be compared with 0.12 ± 0.03 m in 1980. A more detailed account of the evolution of birch growth at this site is given by Kullman (2016c).

Spruce treeline

Spruce occurs infrequently as clonal groups in the birch forest belt on this slope. Radiocarbon dates of subfossil wood preserved underneath the clones indicate that presence of spruce is an ancient feature here, with its roots in the mid- Holocene or earlier (Figs. 14, 15) (Kullman 2001). Dendroecological analysis indicated that by the early 20th century the treeline was positioned 730 m a.s.l. in the form of a multi-millennial old specimen (Fig. 14) (Kullman 1996). Present-day treeline is at 830 m a.s.l. Thus, during the past 100 years, the treeline has advanced by 100 m, as a consequence of increased height increment of ancient krummholz individuals, existing prior to the 20th century (Fig. 16). Seed regeneration has been extremely sparse during this period of time.

Pine treeline

During the past 100 years, the treeline of pine has risen from 700 to 775 m a.s.l., i.e. 75 m in elevation, as manifested by tree-sized pines, younger than 80 years, growing above the early-20th century treeline (Fig. 17, 18). In one case an upshifted pine of this category produced offspring during the early 21st century (Fig. 19). Seed regeneration and elevational pine expansion is largely confined to open habitats, such as mire margins and sparse birch forest. Hereabouts, young pines have continually increased in size and vigor up to the present day.

SITE 2. South-facing slope of Mt. Getryggen

Birch treeline

Smith (1920) measured the treeline of mountain birch to be at 830 m a.s.l., a value which was confirmed by Kullman (1979), by means of boring an old-looking and still living tree, 2 m above ground level (Fig. 20). No such old trees were confirmed at higher elevations. This aspect was further tested in 2017, when 21 trees, at approximately the same elevations, were bored by the same premises. It turned out that 15 of 21 trees were older than 100 years at the boring stem position, which means that they were 2 m or higher in 1915. Older trees were looked for at higher elevations, but no one was found. These results further strengthen Smith's estimate.

In 1951, Kilander (1955) recorded the treeline at 906 m a.s.l. Buried wood remains, associated with an extant tree stem (Fig. 21) at virtually the same elevation, are dated 4770 cal. yr BP (Öberg & Kullman 2012). Moreover, (Smith 1920) noticed prostrate birches 920 m a.s.l. and Kilander (1955) found a 1.5 m high thicket 920 m a.s.l. and 1 m shrubs at 950 m a.s.l. Thus paleoecological and sub-recent data suggest that a pool of prostrate birches existed high above the treeline prevailing by the early 20th century. Birches within this category may be the result of phenotypic regression of prior tree-sized birches, in response to Neoglacial cooling of the past 3000 years or so and survival in that state up to the present day (Kullman 2013). Taken together, these

circumstances support the contention that modern treeline rise is mainly accomplished by phenotypic progression of birches contained in a pool of old-established relict krummholz birches growing above the treeline of the early 20th century.

By the mid-1970s, the treeline had reached 930 m a.s.l. (Kullman 1979) (Fig. 22) and in 2007 it was still positioned at the same elevation (Kullman & Öberg 2009). The most recent assessment was in 2017, when 1045 m a.s.l. was reached by the advancing treeline in the form of a slender and youngish looking specimen (Fig. 23). The evolution of this specimen has been followed over a period of 37 years, from tiny sapling, severely browsed by hare or reindeer, to current tree form (Figs. 23, 24).

Over the past 100 years, the treeline has shifted 215 m upslope. The most recent phase of this continual course of this change is depicted in a series of photos (Figs. 25-27).

As depicted above, treeline rise relative to the position prevailing by the mid-1970s, has been accomplished to some extent by quite newly established individuals. This contrasts with treeline rise during earlier periods of the 20th century, when plastic phenotypic responses of old-established multi-stemmed specimens seem to have been the rule (Öberg & Kullman 2012).

Conspicuously, many trees in the treeline advance zone have increased their foliation over the past few decades (Fig. 25). These specimens have frequently suffered from winter browsing by hare (*Lepus timidus*). Despite heavy damage to twigs and buds, birches often survive this brutal treatment, which may decide growth form at the mature stage (Fig. 26).

Strictly locally in this slope, the upper boundary of closed forest has advanced upslope to 900 m a.s.l. in the form of a narrow wedge, which is associated with the main melt water stream from late-lying snow patches in the alpine region (Fig. 27). The present forest limit position is to be compared with 840 (1949) and 840 m a.s.l. (1978), given by Kilander (1955) and Kullman (1979), respectively.

During the first decade of the 21st century, young seedlings of birch, spruce and pine were observed at the rim of vanishing snow patches, virtually up to the peak of the concerned mountain (Fig. 28). At the present day, most of these seem to be extirpated (cf. Kullman 2014 and updates).

Spruce treeline

Spruce is currently a truly rare tree in this slope, dwindling in the dense birch forest. Some of today's uppermost trees existed as low-growing krummholz by the early 20th century. At that time, the treeline was at 770 m a.s.l. (Fig. 29) (Kullman 1986). Thereafter, it has advanced by means of accelerated height increment of old-established krummholz spruces to 820 m a.s.l. (Fig. 30). This implies treeline rise by 45 m over the past 100 years, although stability and consolidation since the mid-1970s. A few solitary seed-generated tree spruces have established between the treeline of the early 20th century and the present treeline, 810 and 815 m a.s.l., respectively (Fig. 31).

Pine treeline

A solitary and fast-growing pine has established at a mire margin in the lower slope, 740 m a.s.l. (Fig. 32). Large subfossil wood remnants of tree-sized pine, at the same elevation, with >200 tree rings, indicate that this specimen, represents the minimum elevation of the early-20th century treeline (Fig. 33). Thus, virtually no treeline rise during the past 100 years is manifested here, although pine has locally reclaimed its mediaeval position, from which it was depressed by Little Ice Age cooling (cf. Kullman 2015) or cutting by the Sami population, formerly



Figure 12 A. In the early 1980s, this topographic depression, 795 m a.s.l., in the birch forest was totally devoid of trees, although prostrate specimens lingered in the ground cover. Large masses of late-lying snow restricted their growth to trees. Photo: 1980-09-07. B. Up to the present day, the snow cover has tended to melt increasingly early, and as a consequence, birch vegetation has proliferated, with trees more than 4 m tall. Photo: 2017-08-07.



Figure 13 The same view as depicted in Fig. 12, showing its character as a snow-accumulating site. The new birch population has benefitted from snow retraction at the lower margin of the huge snow drift. The birch stand at the opposite and relatively snow-poor side of the depression is virtually unchanged or has somewhat declined in density over the same period of time. Photo: 2016-05-02

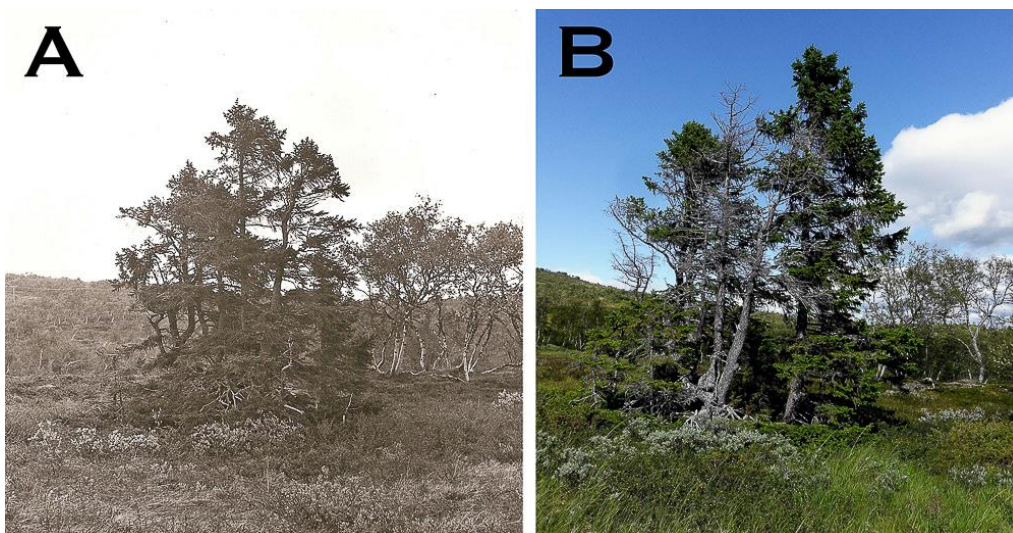


Figure 14 A. The spruce treeline, 730 m a.s.l. as it was in the early 20th century and until the mid-1970s. This specimen is radiocarbon-dated 5905 cal. yr BP (Kullman 2001). The oldest living stems are more than 400 years old. Photo: 1973-06-28. B. During the past few decades, the vitality has perceptibly declined and some of the major stems have died. No seedlings or saplings have appeared in the neighbourhood. Photo: 2017-08-14.



Figure 15 This specimen, 770 m a.s.l. further attests to the long-term stability of spruce distribution on this slope. Wood remnants buried in the soil indicate that this spruce existed 5650 cal. yr BP. Tree size was attained well after 1915 and thus this spruce was part of the treeline rise process during the past 100 years. The spruce is legally protected as a nature memory (Sw. naturminne) and is named Old Pompe, to the memory of a legendary dog. Photo: 2011-08-31.



Figure 16 The new and raised treeline of spruce is manifested by this specimen, 830 m a.s.l. Stout basal trunks show that the spruce existed at this spot as a low-growing shrub by the early 20th century. Tree size was attained in the mid-1970s, when the highest stems measured 2.2 m. At the present day, this is still the treeline and the stems have reached a height of 3.5 m. Photo: 2017-08-15

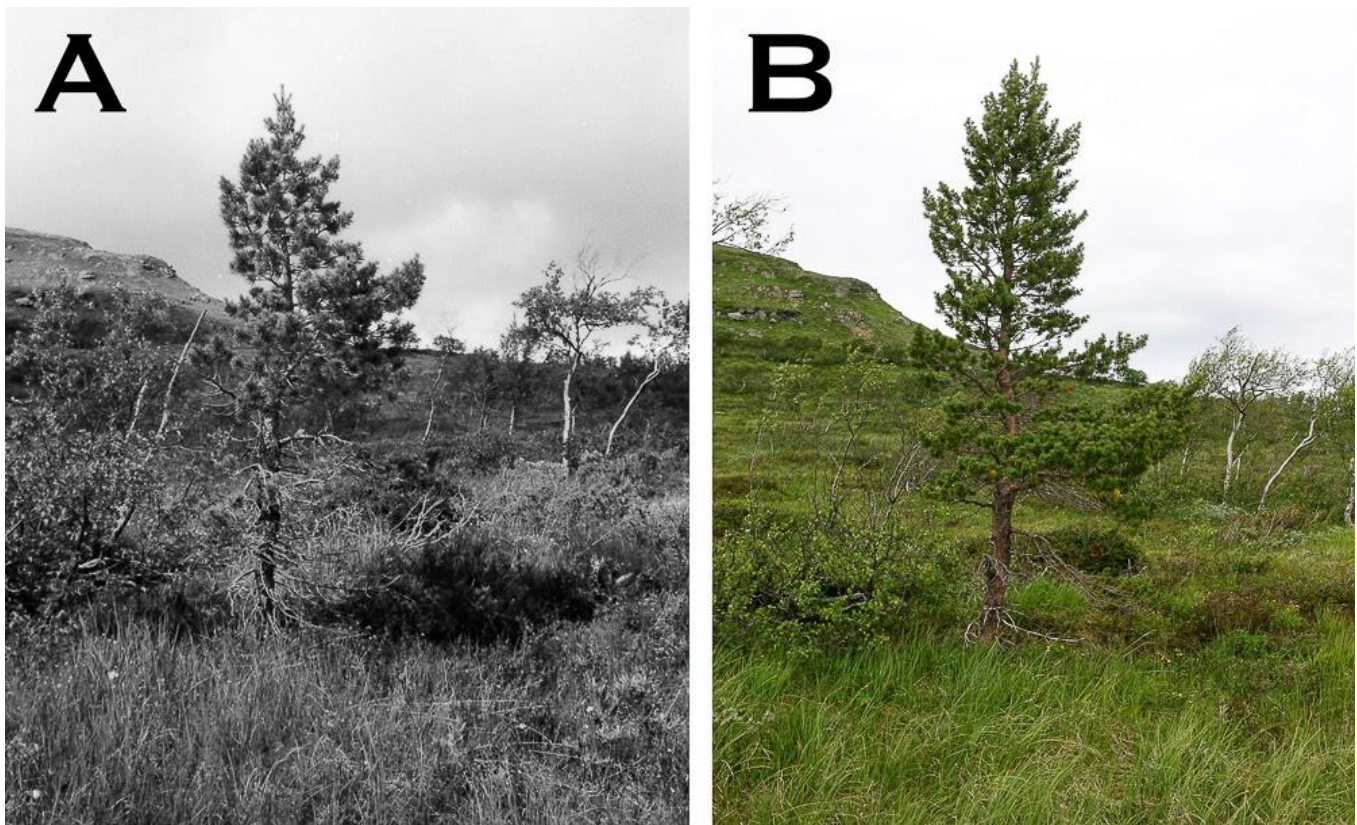


Figure 17 The present-day treeline, 775 m a.s.l., characteristically established in an open habitat, such as a mire margin. The tree became established in the mid-1950s. A. Photo: 2004-07-26, B. Photo: 2017-08-15.

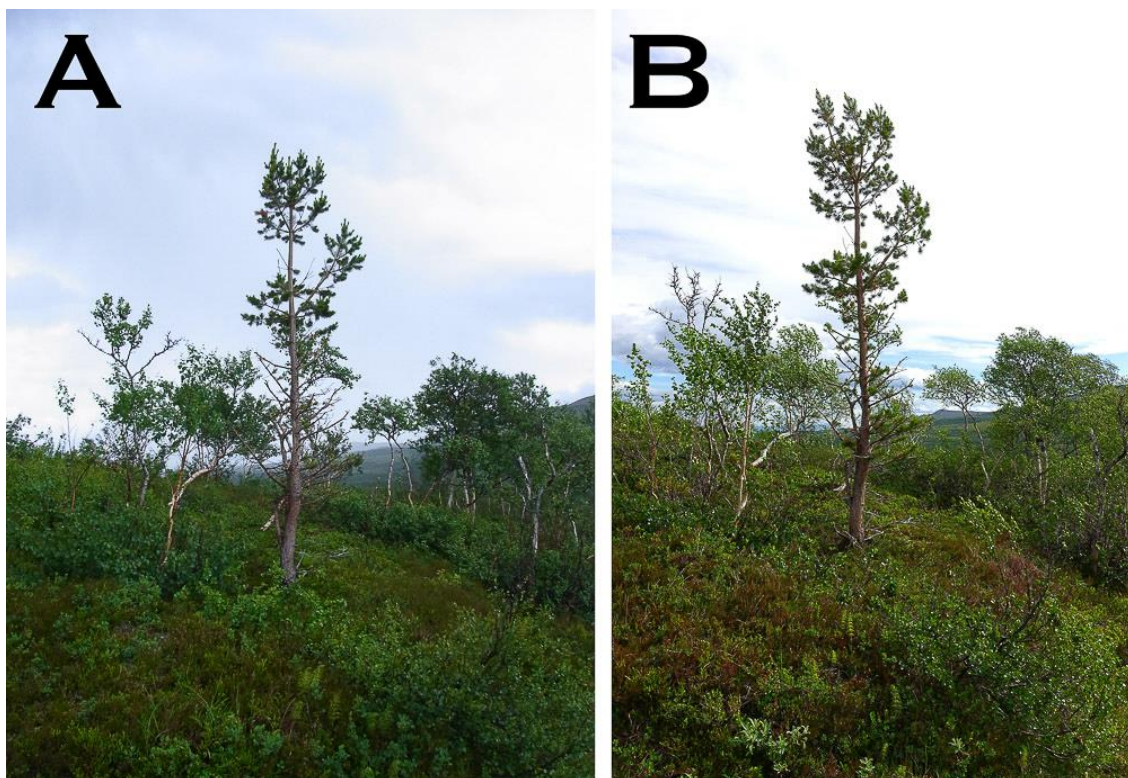


Figure 18 Pine, 770 m a.s.l., which is part of the elevational expansion process and penetration into open spaces at increasingly higher elevations in the birch forest belt. A. Photo: 2012-07-31. B. Photo: 2016-06-30.

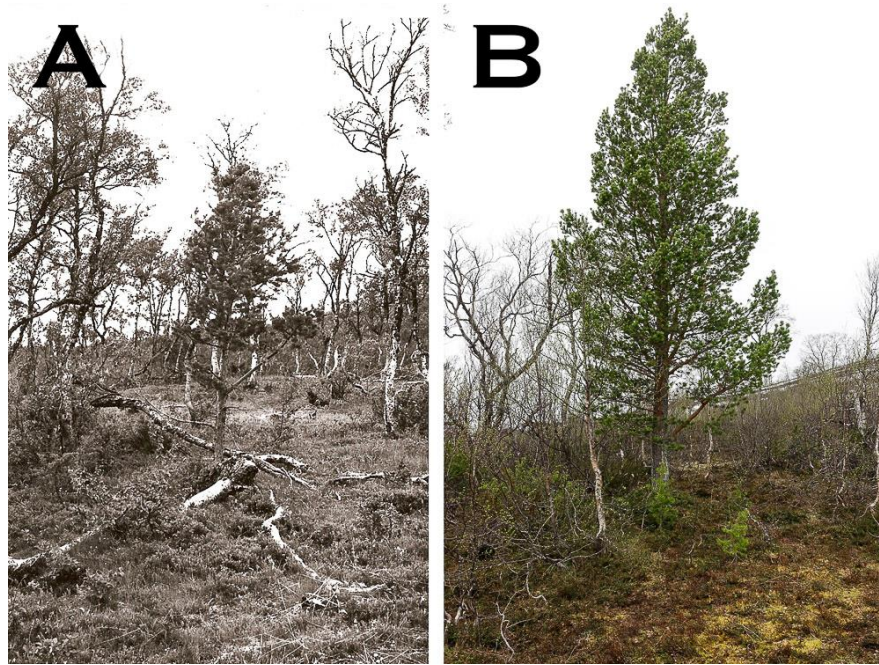


Figure 19 A. Solitary pine, 750 m a.s.l., established in the early-1940s and growing 50 m above the treeline of the early-20 century. Around 1990, this pine was 3.4 m high. Photo:1991-07-12. B. Until the present day, this pine has gained vitality and a size of 5.5 m. Photo: 2017-06-10. During the past 10 years or so, the pine has produced offspring within a radius of c. 10 m.



Figure 20 A. Old-growth birch, 830 m a.s.l., representing the treeline position around 1915. Photo: 1974-06-07. B. The same tree as it appears today. On major branch has been lost. Photo: 2017-08-08.

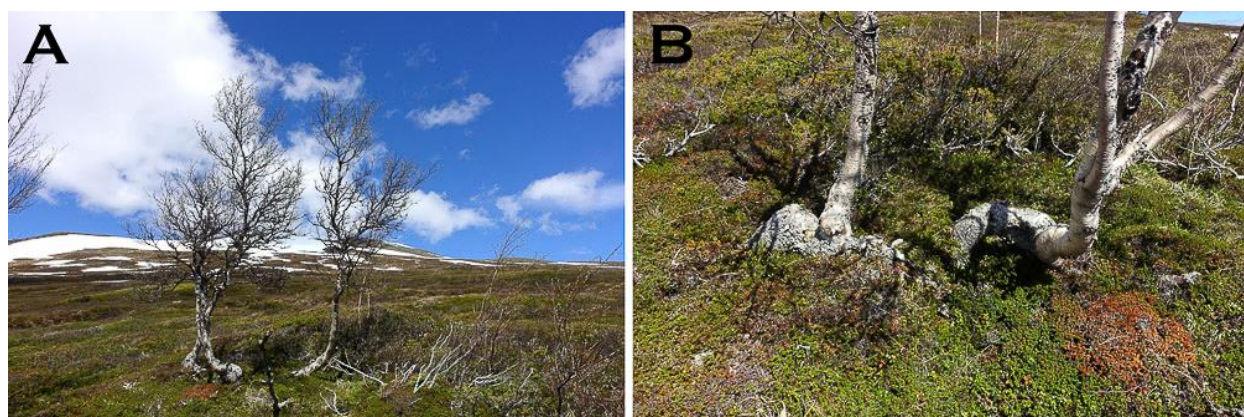


Figure 21 A. Birch tree, 905 m a.s.l., which marks the treeline position by the early 1950s. This specimen like many others alike existed in a more low-growing form much earlier. B. Radiocarbon-dated wood remnants in the upper soil and associated with living stems yielded a date of 4770 cal. yr BP (Source: Öberg & Kullman 2012).



Figure 22 A. By the mid-1970s, the treeline had advanced 100 m in elevation, to 930 m a.s.l., as represented by this tree. Photo: 1979-08-08. B. An up-to-date version of the same tree displays crown expansion and increased foliation. Photo: 2017-08-08.



Figure 23 A. The new and most recent treeline position is manifested by this small tree, 1045 m a.s.l. The evolution of this specimen has been followed from its early seedling stage in 1980 (Fig. 24) to the present tree-size mode. Photo: 2017-08-03. B. Basal part of the birch depicted in A. Single-stemmed specimens of this kind are generally interpreted as seed-generated during some recent decades. Photo: 2016-09-29.

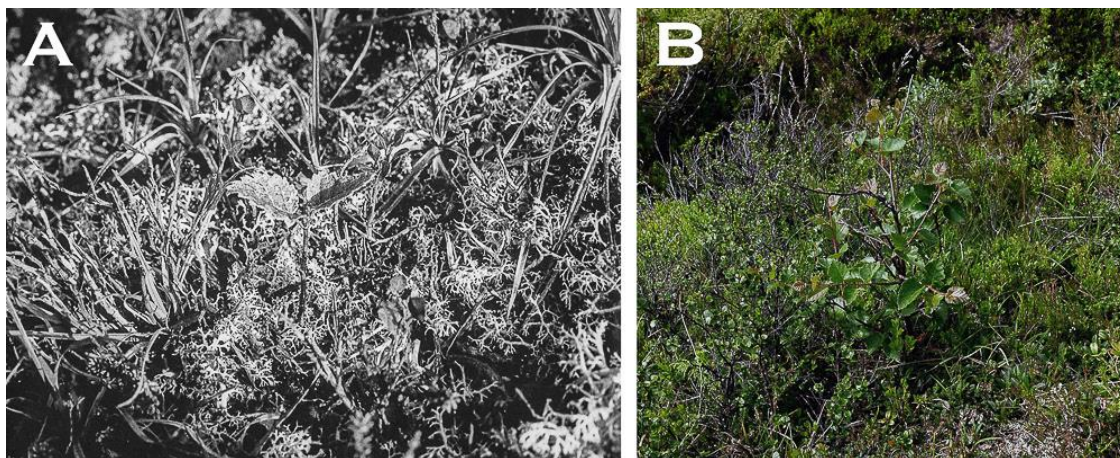


Figure 24 Early stages in the evolution of the treeline birch depicted in Fig. 23. A. A 5 cm high sapling in undisturbed vegetation of lichens and sedges. Photo: 1980-07-28. B. Heavy browsing by reindeer or hare has checked the height growth (now 40 cm high) and promoted evolution of multiple shoots. Photo: 1988-07-18.

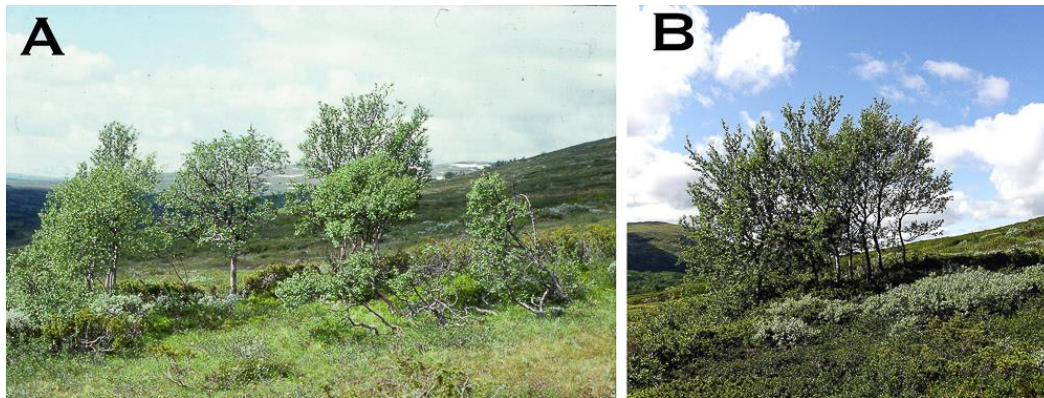


Figure 25 A. Birch copse, 880 m a.s.l., i.e. 50 m above the treeline position in the early- 20th century. Photo: 1978-08-09. B. The same birches as they manifest 39 years later, when increased foliation and rapid height increment (3.5 to 5.5 m) may be gleaned. Photo: 2017-08-03.

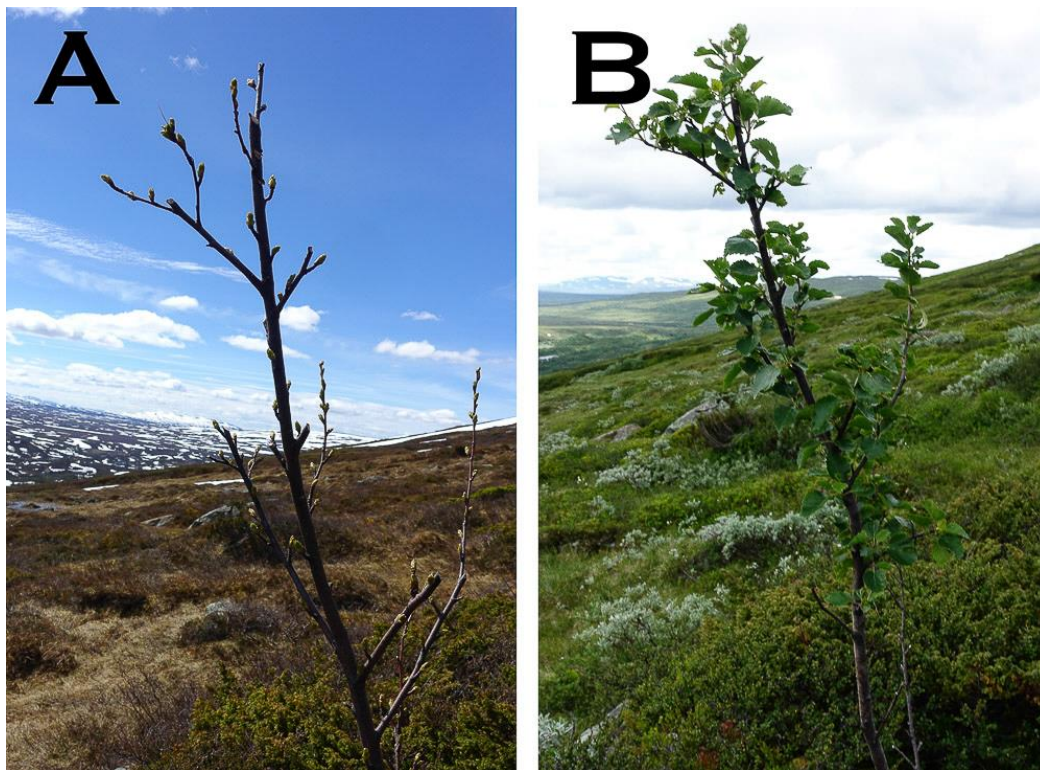


Figure 26 Young birch tree in the upper treeline advance zone, 965 m a.s.l. A. In the early summer, it displayed signs of heavy browsing by hare. B. As evident later in the same summer, it survived this treatment with a more compact crown and foliation, which may impact its future growth form. Photo: 2017-08-03.

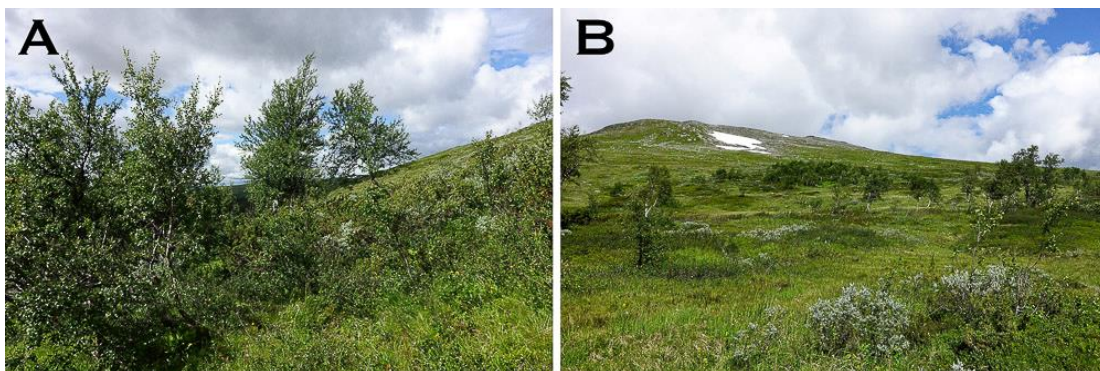


Figure 27 A. A wedge of closed forest protruding upslope to 905 m a.s.l. Photo: 2017-08-09. B. The same forest from below, 835 m a.s.l., i.e. right at the treeline position by the early-20th century. Birch clustering here relates to a steady supply of meltwater from the snow patch higher upslope. Photo: 2017-08-08.



Figure 28 Increasingly recent melt-out of snow patches has conditioned the evolution of moss mats (*Polytrichastrum sexangulare*) in the alpine region (here 1205 m a.s.l.), where in addition, scattered birch seedlings have become established in spots where the cover of mosses has been grazed by lemmings (*Lemmus lemmus*). Photo: 2003-07-13.



Figure 29 Spruce representing the treeline position by the early 20th century, 770 m a.s.l. Photo: 2017-08-14.



Figure 30 Old-growth spruce, 820 m a.s.l., which developed from a low shrub in the early-20th century to an erect tree by the mid-1970s. During the past few decades, the foliation has increased and the treeline seems to be stabilized at this elevation. Photo: 2017-08-14.



Figure 31 Quite unusually today, young and fast-growing seed-generated spruce trees have emerged in sparse birch forest close to the treeline. 810 m a.s.l. Photo: 2017-06-17.

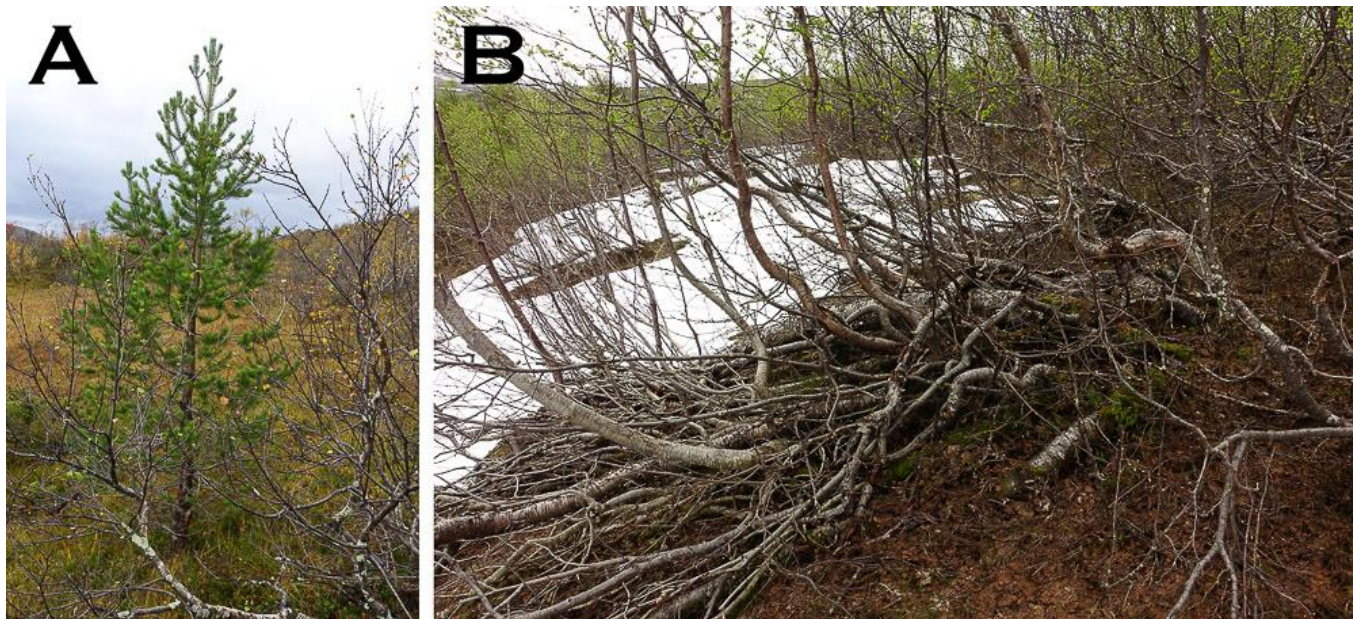


Figure 32 A. Present-day pine treeline, 740 m a.s.l., in the form of a 3.5 m high individual, established in the early-1980s. The site is a mire margin. Photo: 2016-09-23. B. Dense birch forest around the pine treeline (750 m a.s.l.), in combination with snow retention into the summer, counteracts pine establishment in this part of the slope. Photo: 2017-06-17.



Figure 33 Megafossil pine tree remnant, 740 m a.s.l. Radiocarbon-dating yielded 465 cal. yr BP (Beta-446537). Photo: 2016-09-23.

dwelling here in the neighborhood. Establishment of pine in this slope is largely prohibited by densified birch forest stand around the pine treeline. A few widely scattered pine saplings have emerged in the lower reaches of the alpine tundra (Fig. 34).

Grey alder treeline

Today Grey alder (*Alnus incana*) is a rare tree in the subalpine birch belt (Kullman 1992, 2018), which contrasts with the situation prevailing in the first part of the Holocene (cf. Kullman 2013). In this specific slope, clonally perpetuating relict individuals occur in the subalpine birch belt, nearly as high in elevation as the uppermost birches (Kullman 1992). Radiocarbon-dated wood remnants indicate that one such multi-stemmed tree-sized and still living specimen (885 m a.s.l.) existed already 4400 cal. yr BP. It remained as a low-growing shrub until the late 1990s. Thereafter, it has grown in height, to reach 3 m in 2017 (Fig. 35). Tree-sized alders displaying more than 100 year rings 2 m above ground-level exist 755 m a.s.l. and indicate tentatively by comparison with the present position that the treeline has advanced 135 m over the past 100 years.

By the early 21st century, young seedlings and saplings were observed at the fringe of receding snow patches high above current treeline of both alder and birch (Fig. 36). Many of these have succumbed during recent years, of prolonged seasonal snow cover duration (cf. Kullman 2014).

SITE 3. South-west facing slope of Mt. Getryggen

Birch treeline

This slope is exposed to strong westerly winds, which cause a poor snow and a sparse tree cover. Just a few birches prevail in the lower slope. Smith (1920) did not record any birch treeline at all, although (Kilander 1955), mentions from 1949 a 0.2 m tall shrub, heavily injured by frost 920 m a.s.l. Today, the treeline is at 945 m a.s.l. and is formed by widely scattered youngish trees (Fig. 37). A few living older trees exist at 840 m a.s.l. which reasonably mark the treeline by the early-20th century (Fig. 38). This implies treeline rise by 105 m during the past 100 years. Megafossil studies show that birch trees grew quite frequently here between 9600 to 3600 cal. yr BP (Kullman 1994) (Fig. 39).

Spruce treeline

As depicted above, still existing clonal krummholz-mats of *Picea abies* have prevailed here (about 1000 m a.s.l.) since at least 6860 cal. yr BP (Fig. 7). In a few cases they have produced leaders (>2 m tall) in recent years (Fig. 40). Thus, by definition, one may discern the emergence of a current spruce treeline, 1000 m a.s.l. in this slope, which is about 160 m above the valley floor. The latter figure may be tentatively used as a minimum reference with the recent treeline position, thereby suggesting secular treeline rise by 160 m. Except for this ancient individual, no other spruces exist on this slope. This specimen further attests to the general pattern of early-Holocene presence of *Picea abies* in the Swedish Scandes (Kullman 2001, 2008).

Table 1 Total treeline upshifts (m) 1915-2017 at the tree investigated transects on Mt. Getryggen (SITE 1-3)

Species/Site	SITE 1	SITE 2	SITE 3
Betula	135	215	105
Picea	100	45	160
Pinus	75	10	no value
Alnus	no value	135	no value

Summary of recent treeline upshifts

A summary of treeline advances for all three studies transects is given in Table 1.

Experimental studies

Annual birch seed germinability has been followed since 1972 and up to the present day (Fig. 41). Germination occurred all years, with a peak (c. 60%) for some years around 2002, followed by a downturn to more modest conditions during subsequent years (20-40 %).

The sowing experiment in contrasting subalpine habitats yielded initially quite high germination rates, although mortality increased rapidly and by the mid-1980s the initial cohort was virtually depleted in all three habitats. After 2001 all seedlings had died. Virtually the same course of change was recorded for the cohort of transplanted saplings. In that case the last few survivors persisted in 2004.

The seed bank experiment yielded steadily lower germination percentages with annual tests. Still after 11 years germinability yielded 4% (Kullman 1993), but after 1999 no viability has been recorded.

The experimental trial with exotic tree species has been successful with respect to survival and growth. Tested species have survived to the present day with 75-100 %, which contrasts with the control cohort of native *Pinus sylvestris*, which was entirely extirpated (frost drought) by 2003. With respect to growth, *Picea engelmannii* and *Larix sibirica* have been most successful and have attained maximum heights of 3.5 and 5 m, respectively (Fig. 42).

DISCUSSION

Substantial treeline rise over the past 100 years, relating to the climate warming after the Little Ice Age, characterizes birch and spruce on all three aspects of the study mountain. Treeline stands of these species display a conspicuous lack of dead individuals, which is compatible with quite recent stand rejuvenation and sustained favorable growth conditions for trees and subalpine/alpine vegetation (Kullman 2010; Sundqvist et al. 2008).

Pine has advanced on SITE 1 and 2, while grey alder shifted upslope on SITE 2 only. For all species, the extent of upshift varied substantially between the sites (Table 1). This is an experience also from prior more extensive studies concerning all species focused in this study (Kullman & Öberg 2009). The reason was found to be local topoclimatic conditions, enabling treeline responses to manifest in subdued form in most parts of the landscape. Although the largest current upshifts display the most clear-cut relationship with climate change, they appear quite infrequently in the treeline landscape. Spatially idiosyncratic responses could imply that even in a hypothetical case of dramatic future climate warming, large expanses of the alpine landscape may remain untreed, as inferred for the warmest part of the Holocene. i.e. 10 500-9000 cal. yr BP (Öberg & Kullman 2011; Kullman 2013). This implies that modelling results, purporting extensive and pending forest encroachment on the alpine tundra (e.g. Kellomäki et al. 1997; Moen et al. 2004) are not validated by recent observations (cf. Holtmeier 2005; Hofgaard et al. 2013). At odds with results from other regionally extensive monitoring studies in the Swedish Scandes over the period 2003-2012 (Hedenäs et al. 2016), treeline progression in the concerned area has continued over this period of time. This discrepancy may relate to treeline definition incongruencies with different sensitivities to climate change.

In contrast to birch, treeline rises of other species are manifested by relatively low densities of new trees atop of the treeline prevailing by the early 20th century. This is particularly valid for pine, which is the



Figure 34 Young pine sapling, 0.6 m tall, growing in alpine tundra 895 m a.s.l. Dead twigs indicate repeated winter desiccation, when passing the maximum depth of the snow cover. Photo: 2017-08-08.

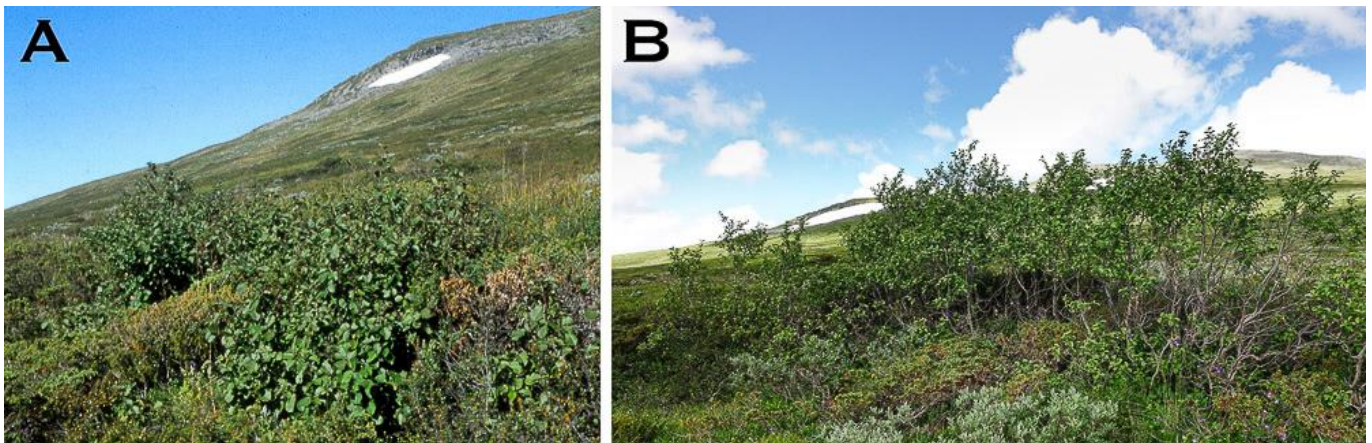


Figure 35 A. Clonally reproducing multi-stemmed shrub of *Alnus incana*, maximum 1.2 m high, 890 m a.s.l. Photo: 1998-07-22. B. Up to the present day, the entire stand has attained a height of about 3 m. Photo: 2017-08-03.



Figure 36 Young sapling of *Alnus incana* which has germinated in a moss mat at the fringe of a receding snow patch, 1060 m a.s.l. Photo: 2004- 08-02.



Figure 37 Raised treeline by 105 m, manifested by conspicuously young birch trees, 945 m a.s.l. Photo: 2011-04-30.



Figure 38 The treeline position around 1915 is marked by this old-established tree, 840 m a.s.l. Photo: 2011-04-30.



Figure 39 Megafossil wood debris of birch, exposed in an eroding fen, 1000 m a.s.l. Radiocarbon dating yielded 9600 cal. yr BP. Source: (Kullman, 1994)



Figure 40 This ancient krummholz spruce, 1000 m a.s.l. (see Fig. 7), has produced some leaders 2-2.3 m tall during the past few years. Thereby, they announce treeline rise, where no tree-sized spruces existed during the past 100 years. Photo: 2012- 07-31.

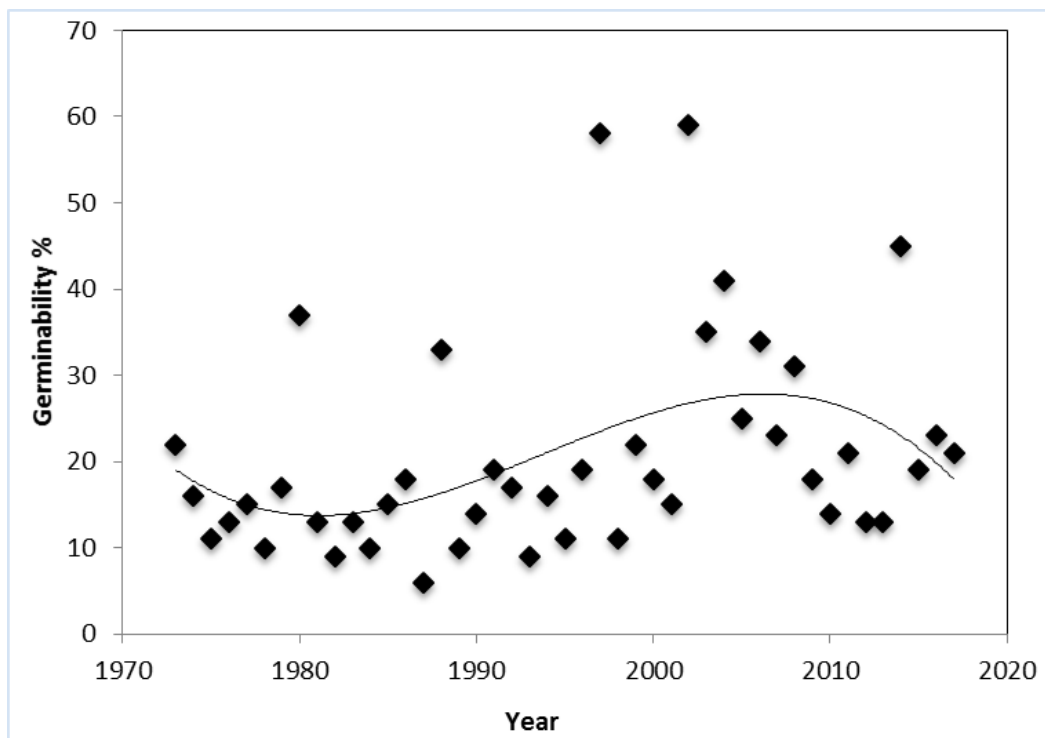


Figure 41 Annual tests of birch seed viability from trees on the south-facing slope of Mt. Getryggen, 775 m a.s.l.

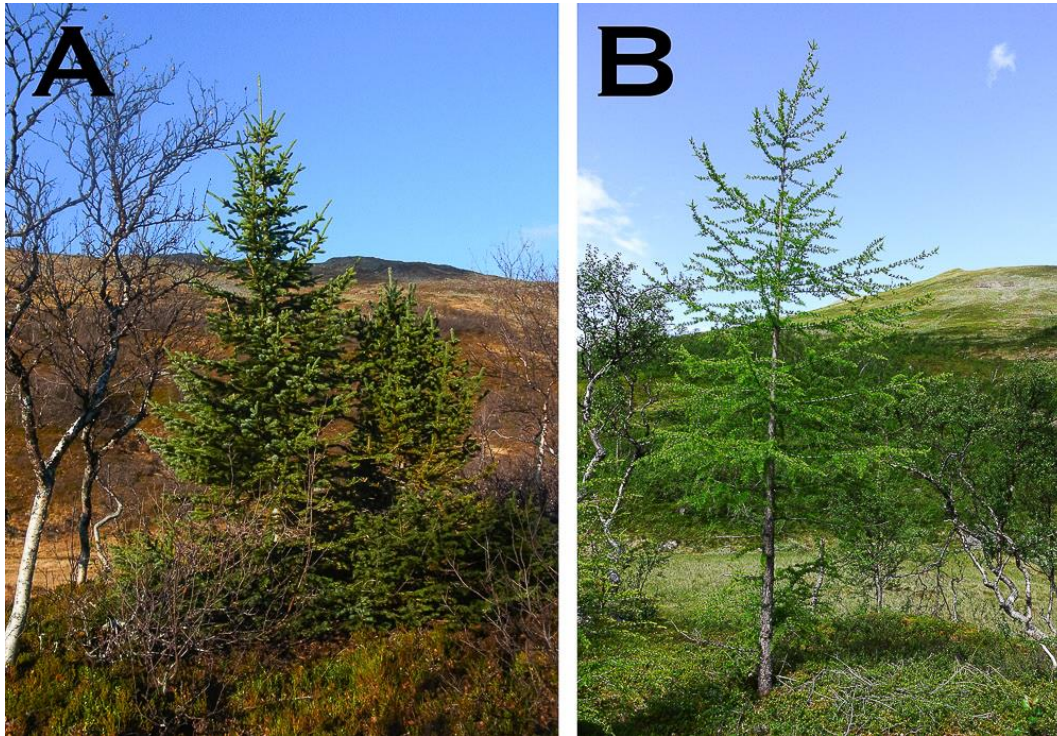


Figure 42 A. *Picea engelmannii* is one of the most successful exotic species tested in the mountain birch forest. Photo: 2014-10-16. B. Also *Larix sibirica* has developed well during the past few decades. Photo: 2016-07-03.

species with the lowest treeline, commonly encased in the dense birch forest filter, which restricts its potential to spread (Kullman 2016b). In contrast to extensive treeline rises, a common pattern for all studied species is that forest encroachment on the alpine tundra is patchy and largely negligible. Recent surges of tree species saplings into exceptionally high positions (Kullman 2004, 2007a,b) appears to be a transient phenomenon as mortality in these cohorts has been substantial during the past few decades (Kullman 2014).

The most extensive treeline advance was displayed at SITE 1 by birch; 215 m. This implies a rate of 21.5 m per decade, which is double the rate as an average for different taxonomic groups worldwide (Chen et al. 2011; Aakala et al. 2014). Recent treeline advance with this magnitude is an inter-regionally recurrent pattern along the Swedish Scandes. Analogously high values have been obtained for birch and other tree species in different regions from south to north along six degrees latitude (Kullman & Öberg 2009; Öberg & Kullman 2012; Kullman 2015a,b, 2016a,b, 2018). This geographically common response pattern, at odds with other studies (e.g. Dalen & Hofgaard 2005), indicates that climate change during the past 100 years is the ultimate driver of treeline change. This contention is further strengthened by the fact that treeline rise by more than 200 m corresponds quite well with recorded secular warming (1915-2017) by 1.5 °C and a temperature lapse rate of 0.6 °C per 100 m altitude (Laaksonen 1976). Moreover, the present results provide little support (cf. Kullman 2015b) of generalizations that treeline birch population dynamics is primarily driven by reindeer grazing, as purported by Van Bogaert et al. (2011).

Birch treeline rise by maximum 215 m implies, in perspective of the regional Holocene birch treeline history (Kullman 2013), that recent advance has reached an elevation unprecedented during the past 5600 years. With respect to *Pinus* in the southern Swedish Scandes, the corresponding figure is about 7000 years ago (Kullman 2016a). In view of the current discourse concerning future climate change, these early

dates of equal or higher-than-present treeline, could be interpreted in terms that current temperatures are unprecedented during the past 6000-7000 years. However, such an interpretation may be premature since the new trees above the old treeline are quite few and generally of small stature, as shown in this study. This implies that they may not leave any discernible imprint on the fossil record. Accordingly, similar episodes may have happened unrecorded in the past, which would make the recent upshift less unusual in an historical perspective. For example substantial local treeline upshifts have been recorded elsewhere in the southern Swedish Scandes about 2000 and 1000 year before today (Kullman 2013, 2015b).

As evident from SITE 2, birch treeline rise after 2007, appears to have been accomplished to some extent by rapid height growth of seed-regenerated monocormic birches. This contrasts with predominant phenotypic responses of old-growth polycormic krummholz specimens previously responsible for treeline shift prior to 2007 (cf. Kullman 2010; Öberg & Kullman 2012). Whether this new phenomenon bears any significant relation to recorded seed viability increase during the past 20 years is uncertain, since, according to ring counts, at least some specimens in the advance zone are older than peak germination around AD 2000. In addition, experimental studies, accounted for above, have evidenced poor establishment and survival rates of seedlings and small saplings during recent decades. Treeline rise has occurred contemporaneously with declining conditions for early growth and survival of experimental specimens. Thus climatic constraints to, those early life stages do not seem to have improved in recent years and may not restrict any advance. A critical growth phase, with respect to birch treeline performance, appears to relate to the average depth of the snow cover and the height of the warm boundary layer, when plants enter the early mature phase (cf. Körner 1998; Grace et al. 2002). Plants higher than that have good chances to survive and reach maturity, as evident by the progression of planted exotic tree species. These were clearly higher than the maximum snow depth when planted.

The strong reliance of vegetative regeneration of old-established specimens in connection with recent treeline performance of *Betula* and *Picea*, could imply a substantial degree of vegetation stability (Aerts et al. 2006; Auger & Payette 2010). Further upshifts of these treelines are restricted as the pool of krummholz specimens above the present treeline becomes depleted. Many candidate individuals have already attained tree size (Kullman 1993, 2013; Kullman & Öberg 2009).

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