

Treeline Ecotone Progression and Stability: Time Series Analysis of Individual Photographic Data 1973-2021 in the Swedish Scandes

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ABSTRACT

Positional and population change of the alpine treeline ecotone were studied at a site (isolated low-fell) in the Swedish Scandes. Methods included early-20th century records and subsequent re-visitations, including repeat photography, up to 2021. Substantial temperature rise (summer and winter) during the past 100 years, has left the elevational forest border virtually unchanged. However, the treelines, i.e. scattered solitary trees >2 m tall, of mountain birch (*Betula pubescens* ssp. *czerepanovii*) and Scots pine (*Pinus sylvestris*) have risen by maximum 70 and 65 m, respectively since the early 20th century, in contrast to inertia of Norway spruce (*Picea abies*). Hitherto, pine appears as the most successful species, particularly in the light of the relatively large numbers of new trees established around the elevated treeline and the proliferous regeneration in the treeline ecotone during the past few decades. Presumably, a subalpine pine belt may eventually replace the sparse birch belt in the snow-poor SE-facing slope, in accordance with regional tendencies. Climate warming has reduced the snow cover duration on the NE-facing slope, to the benefit of mountain birch. Possibly, closed birch stands will evolve here. The study mountain displays a spectrum of different local habitat types, with contrasting quantitative and qualitative responses to climate change, representative of prevailing regional treeline ecotone dynamics. Important and complex constraints to projections of treeline growth and rise, in response to alleged future climate warming, include geomorphology, herbivory and snow pack.

INTRODUCTION

A distinguished Swedish ecologist, Hugo Sjörs, stated that “the aim of ecology is to see what happens in nature” (Sjörs 1979). Accordingly, time is an essential dimension, particularly in cold-marginal landscape-ecological research and perception, which urges for long-term observational studies of individual and population responses (e.g. Däniker 1923; di Castri & Hadley 1985; Franklin 1987; Vale & Vale 1994; Webb 1996; Wolkovich et al. 2014). In that context, climate change with its real and imaginative consequences are signs in the time, with great public and scientific concern. With that perspective, climate models suggest that the proposed Post-Little Ice Age (15th to 19th century) climate warming may continue into the future (IPCC 2013). It remains an open question whether such a course of climate evolution

would mirror natural or anthropogenic recovery, or a combination of both, following the discontinuation of the Little Ice Age (Humlum et al. 2011; Akasofu 2010, 2021). Anyhow, the consequences for man and biota of future climate evolution (warming) are often projected in terms of more or less dramatic landscape-scale transformation by the end of the present century (Moen et al. 2004; ACIA 2005; Kaplan & New 2006; Kullman 2010a, 2019; Hagedorn et al. 2014; Kullman & Öberg 2021; Schickhoff et al. 2022). In that context, real-world data are urgently needed.

Up to the present day, after a century of rising summer and winter temperatures, climate and biotic variability in northern regions have shifted, largely within the frames of renowned natural Holocene variability (Bergman 2005; Kullman 2013; Paus & Haugland 2017; Ljungqvist 2017; Odland & Paus 2022). In that perspective, alpine treelines and treeline ecotones, in regions with insignificant human impact, have emerged as particularly suitable objects of sustained study with focus on past and recent environmental change (Tranquillini 1979; Kullman 1998; Smithson et al. 2002; Holtmeier 2009; Behringer 2010; Körner 2012).

Globally, treeline upshift is a common and basically climate-driven phenomenon (Holtmeier & Broll 2017), although modulated and constrained, to various degrees, by interrelated local factors, such as geomorphology, wind, snow cover, soil fertility, allelopathy, herbivory and human impacts (Kullman 1979; Hansen & di Castri 1992; Harsch et al. 2009; Leonelli et al. 2010; Elliott 2011; Dufour-Tremblay et al. 2012; Holtmeier 2012; Östlund et al. 2015; Alatalo & Ferrarini 2017; Hansson et al. 2021; Grigoriev et al. 2022; Fomin et al. 2022).

Along the entire Swedish Scandes, with relatively insignificant past and present human disturbance to the natural plant cover, treelines have advanced by more than 200 altitudinal meters during the past 100 years at optimal sites (Kullman & Öberg 2009; Kullman 2017a, 2021a). This process has locally brought tree growth back (foremost *Pinus sylvestris*) to the relatively high positions, that prevailed in the early Holocene, when temperatures in northern Europe are inferred to have been about 2-3 °C warmer than during the past few decades (Luoto et al. 2014; Välimäki et al. 2015; Paus & Haugland 2017; Kullman 2017a). These high treeline elevations refer to the treeline proper, i.e. the highest stations of solitary outpost individuals, at least 2 m tall. Treeline and glacier history converge to integrate climate change over decades and longer intervals and suggest that their recent changes may reflect significant and progressive turning points in the relatively cool and instable Neoglacial epoch (cf. Luckman 1994; Kullman 2003).

It is important to stress that most sites along the treeline display smaller upshifts than the obtained maximum values of >200 m, cited above (Kullman 1979, 1981; Kullman & Öberg 2009). From an analytical perspective it is particularly fruitful to compare treeline responses on sites with large and minor shift, respectively (Kullman 1979). Peripheral low-alpine fells form the lower end of such a continuum and often display a spectrum of different treeline habitat types.

To a large extent, dynamic treeline studies rely on imprecise remote sensing and unvalidated climate and ecological models, often with elusive range limit definitions (Kellomäki et al. 1997; Moen et al. 2004; Kaplan & New 2006; Hofgaard et al. 2013; Frost & Epstein 2014; Mienna et al. 2022). Relatively little is known, based on direct *in situ* re-visitation studies of structural and

compositional changes and their climate controls within the treeline ecotone. The latter represents the transitional zone between the closed forest and the treeless alpine tundra. In particular, the balance of vegetative and sexual regeneration needs more attention (cf. Öberg & Kullman 2012). In that context, it has been argued that future change will largely rely on phenotypic plasticity (Kullman 1993; Macias-Fauria et al. (2012). The efficiency of that mode gains historical support from the performance of mountain birch and spruce during the past 100 years of predominant climate warming (Kullman 1979, 1986). Documented multi-millennial longevity of the last-mentioned species, further strengthens such a contention (Öberg & Kullman 2011, 2012).

Concerning the forest limits, i.e. the upper boundary of closed forest stands, below the treeline, there are no indications, except for local local upshifts a few tens of metres, of significant advancement towards higher elevations in the Scandes (e.g. Öberg & Kullman 2012; Rannow 2013).

Commonly, the treeline ecotone in the Scandes is a mosaic of solitary trees, small groves and open patches with alpine tundra, mostly dwarf-shrub heath and mire. Prevailing tree species are mountain birch (*Betula pubescens* ssp. *czerepanovii*, Norway spruce (*Picea abies*) and Scots pine (*Pinus sylvestris*). As a rule, mountain birch forms a distinct subalpine belt above the mixed coniferous forest (Kjällgren & Kullman 2002).

On low-alpine fells (this study), without an alpine relief, at the eastern and southern fringes of the Scandes Mountains, the treeline ecotone is depressed in altitude and tree species zonation manifests in compressed form, due to strong exposure. This feature is an expression of the so-called “Gipfelphänomen” and relates to various interrelated topoclimatic constraints to tree growth, e.g. wind, snow cover, convex topography, soil depth and moisture (Scharfetter 1938; Holtmeier 2009). These mountains display a variety of microhabitats (toposequences), representative of the treeline ecotone in wider geographical context; snow cover, wind, insolation, moisture and herbivory. These circumstances, within a limited area and a homogenous climate, in addition to logistic facilitation, make them suitable objects, as natural experiments in general treeline ecology.

An important constraint to tree establishment and survival in these habitats is so called winter desiccation. This phenomenon is a complex action of temperature, wind, snow cover and transpiration, when the water supply is blocked by frozen ground (Holtmeier 1974; Tranquillini 1979; Kullman 1993, 2007a). In general, over the past 10-15 years, this stressor has become alleviated in concert with climate improvement (Kullman 2007; Kullman & Öberg 2021).

The existence of these low fells is often related to climate cooling and “alpinization” during the Little Ice Age since the 14th century (Payette et al. 1985; Kullman 2012, 2015b, 2017a). Typically, they are characterized by small treeless caps, exposed to wind from all directions and a thin and early disappearing snow cover. The ground layer flora used to be a mixture of species with alpine and boreal affinities, respectively. Characteristically, they and form an “archipelago” in a matrix of predominant closed coniferous boreal forest at the eastern and southern and fringes of the Scandes. In most cases these summits rise only 50-100 m above the treeline (Wistrand 1962). This situation implies that they potentially receive plant propagules of most

appearing tree species in the region, i.e. seed limitation should not constrain treeline rise (Kilander 1955). Thus, their dynamics in the recent past may provide some ideas as to the general performance of treeline ecotones and their biodiversity in response to possible future climate change and associated tree layer emergence (e.g. Dumais et al. 2014).

Some prior studies have witnessed upward encroachment and densification of tree vegetation in concert with climate improvement during the past 100 years in these kinds of habitats (Wistrand 1962, 1965, 1981; Engelman & Zackrisson 1980; Kullman 1991b, 2020; Aakala et al. 2014). However, few studies rely on direct comparison of historic and recent observations, (but see Aas 1969; Kullman 1979, 2017a, 2019). The latter aspect is addressed specifically in the present paper, which is an open-ended study, analyzing arboreal change at the level of individuals since the mid-1970s on an isolated low-alpine mountain surrounded by closed boreal coniferous forest.

This paper is the latest in a series of case studies accounting for structural and compositional change in treeline ecotone during the recent phase of Post-Little-Age climate recovery and warming era (Kullman 2012, 2014 a, b, 2015a, 2017a, b, 2019, 2020a, b, 2021a, b, 2022; Kullman & Öberg 2018, 2021). Hopefully, the results may serve as challenging baselines for future studies of climate-mediated treeline dynamics and the generation of evidence-based ecological models of landscape transformation as climate changes (cf. Larsen 1988; Peters 1992). In fact, the study mountain is part of a larger area with the most robustly documented past and recent treeline ecotonal changes in the Scandes and in a context of Holocene records.

STUDY AREA

Mount Middagsvalen (summit 880 m a.s.l., 64° 08.590' N; 13° 03.556' E) is an isolated low-fell at the eastern fringe of the Swedish Scandes, in the county of Jämtland (Fig.1).

Praealpine spruce forest and a narrow discontinuous subalpine birch forest belt encircle the mountain (Fig. 2). The tree species zonation pattern is compressed, in comparison with higher mountains at the same latitude. The birch treeline, in particular on the south-facing slope, is diffuse and clearly depressed in elevation. Apparently, this feature results from insignificant of melt water from snow-covered terrain at higher elevations and ensuing late summer drought (Ljungner 1944; Kullman 2012, 2019). The ground layer plant cover is dwarf-shrub heath, with predominant *Betula nana*, *Empetrum hermaphroditum*, *Vaccinium myrtillus*, *Phyllodoce caerulea*, *Kalmia procumbens*, *Arctous alpina*, *Avenella flexuosa*, *Pedicularis lapponica* and *Diapensia lapponica*. The north-facing slope is moister, due to presence of banks of late-lying snow cover, which support conspicuous abundance of *Vaccinium myrtillus*.

The upper limit of ± closed mountain taiga stands (Kullman 2005) is at 760 and 790 m a.s.l. on the NE and SE-facing slope, respectively.

The tree cover has suffered extensively from winter browsing of moose (*Alces alces* L.) and to a lesser degree reindeer (*Rangifer tarandus*) during the entire study period. Young saplings and trees, in particular *Pinus sylvestris*, are heavily affected in this way (Fig.19). No traces of fire scars on living trees or soil charcoal were found. The closed forest on the lower north-east facing slope bears signs of sparse selective logging of large pine trees.

The local climate, here represented by the nearest official climate station Storlien/Visjövalen, 642 m a.s.l., 50 km to the northwest), provides mean annual temperatures (1991-2020). The temperatures for January, July and the year are -4.5, 12.3 and 2.1 °C. Annual precipitation amounts to c. 1000 mm/year, presumably somewhat less at the study site.

Long-term temperature trends (1901-2021) for summer and winter are presented in Figure 3. Warming has occurred by 1.6 and 1.5 °C, respectively. A conspicuous dip is perceivable over about four decades after the 1930s (Alexandersson et al. 1995). Particularly low winter temperatures characterized the 1980s. In consequence, praealpine coniferous forests and treeline ecotones suffered substantial stand-level dieback (Kullman 1988, 1989, 1991a, 1996; Kullman & Högberg 1989). The subsequent arboreal recovery from this episode is the main focus of this study.

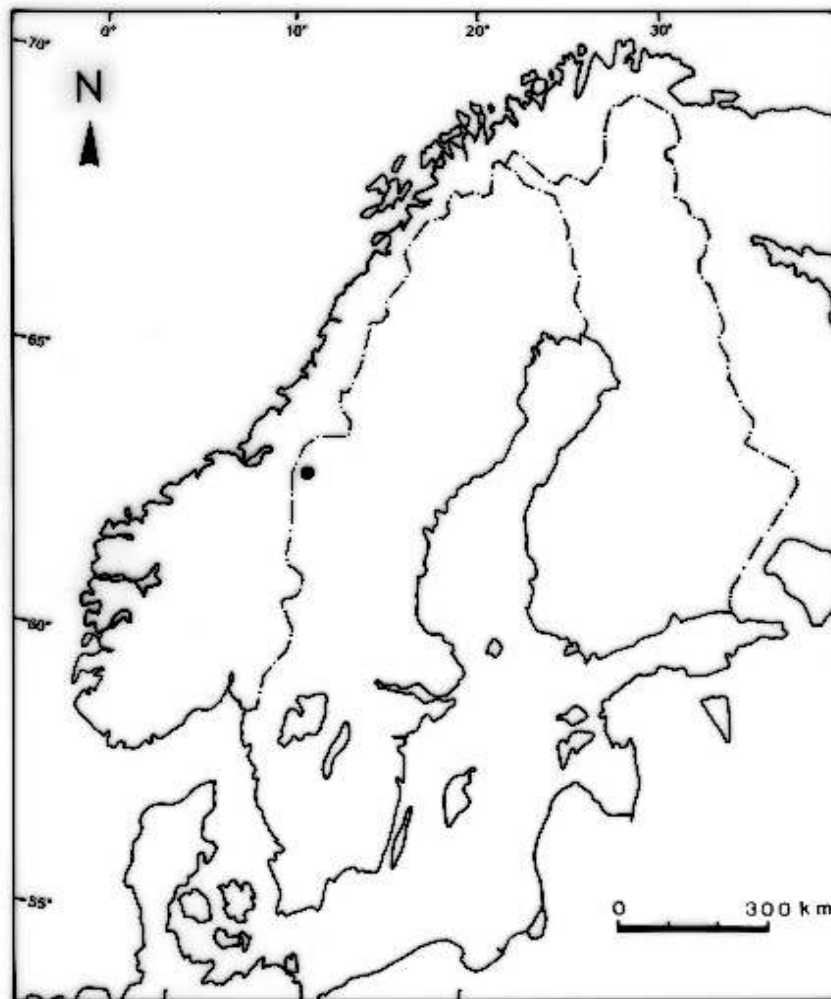


Figure 1. Map showing the study site (plot) in Sweden

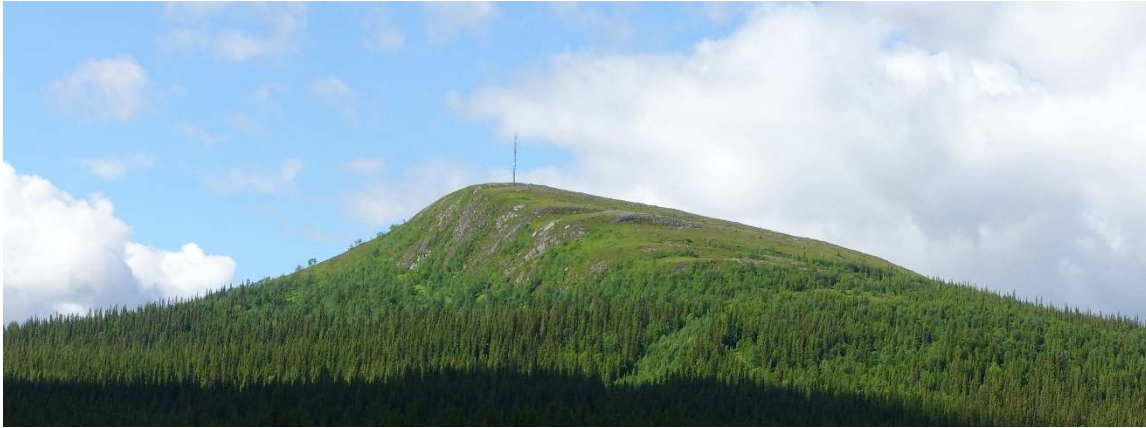


Figure 2. Mount Middagsvalen (880 m a.s.l.), displaying the east- and north-facing slopes, with surrounding spruce and mountain birch forest. 2016-07-04

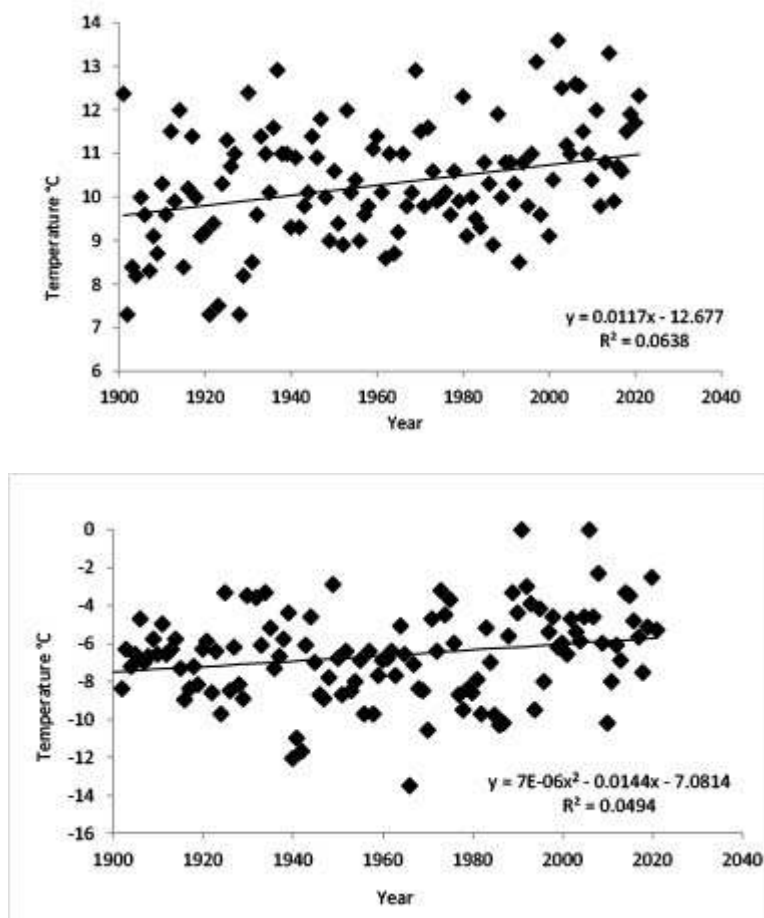


Figure 3. Mean annual regional air temperatures recorded at Storlien/Visjövalen/Storvallen meteorological station, 1901-2021. Upper. June-August. Lower. December-February. Source: Swedish Meteorological and Hydrological Institute

METHODS

The study is based on repeat photography, a method well suited to study of structural change in semi-open and climate-sensitive landscapes, e.g. treeline ecotones (Webb 1996; Luckman et al. 1999; Moiseev & Shiyatov 2003; Munroe 2003; Zier & Baker 2006; Webb et al. 2010). Since

1973 and intermittently onwards, a representative sample of trees growing in the treeline ecotone has been photographed from virtually the same position. The results are here displayed for the dominant tree species, captured on the southeast- and northeast-facing slopes, respectively. In 2021, all pine saplings >0.3 m high were tallied with respect to height and age. Saplings shorter than 2 m were aged by counting branch whorls and adding 2 years to account for the difference between the seed point and lowest whorl. Some large saplings were sawn off at the stem/root junction and the tree rings were counted on stem sections, taken as close to the ground level as low as practicable possible.

The study comprised two transects (300x300 m) running towards NE and SE, respectively from the summit and downslope to the upper limit of closed forest. For all tree species, the treeline (definition above) was determined. In addition, all specimens >0.3 m high, growing in the SE-facing transect (820-880 m a.s.l.) were recorded 1973 and 2021, respectively. In 1973, the surveyed transects were permanently marked with bamboo sticks in corners. Three of these could be recovered in 2021, which enabled reconstruction of the border of the entire plot and accurate resampling of the number of saplings.

Positional treeline positions (m a.s.l.) were determined by a GPS navigator (Garmin 60 CS). Repeatedly checked against elevation figures given by modern topographical maps. In some rare cases, a difference of maximum 5 m in relation to earlier records by barometric altimeters (Thommen system) was discerned (Kullman 1979).

RESULTS

General overview

The general physiognomy of the treeline ecotone has not changed perceivably during the past 100 years. As evidenced by repeat photographs, changes are in the finer details; growth and establishment of widely spaced individuals of previously common tree species in the region. The position of the border between closed forest (mountain taiga) and the treeline ecotone has remained virtually unchanged. The detailed results are presented by commented photographs, separately for the NE- and SE transect (Figs. 4-21).

Treeline positions of all three tree species are significantly lower compared to adjacent higher mountains in the region (cf. Kullman & Öberg 2009). The tree species zonation is substantially compressed, with only minor differences between species. This pattern contrasts with the modal regional arrangement, with *Betula* forming the highest treeline, followed in order of *Picea* and *Pinus* (cf. Kjällgren & Kullman 2002). Over the period 1915 to 2021, treelines of birch, pine and spruce have shifted upslope. Positional treeline changes are depicted below, separately for the NE and SE-facing transect (Table 1).

The largest treeline leap by birch (70 m) is manifested in the NE-facing slope, where it has now ascended to its highest position on the entire mountain. This circumstance is paralleled by the large growth in population within this study plot. A majority of extant birch trees is estimated to represent old-established multi-stemmed clones, some of which have attained tree-size during the past few decades, although some newly established specimens appear to prevail. The treeline of birch has responded by 25 m upshift in the south-east facing transect (Table 1). Over the same period of time, population density has changed just marginally (Table 2),

Pine has shifted upslope by 65 m over the past 100 years (SE-facing transect), in most cases by germination and growth of new individuals. Treeline advance is reflected by substantial population increase since the mid-1970s, particularly within the SE-facing transect. In addition to most extant trees, a large proportion (65 %) of pine saplings showed signs of being browsed by moose or reindeer (Fig. 18).

Spruce has advanced least of the concerned species, i.e. by a few tens of meters since 1915, on the NE-facing slope. Here, between 1973 and 2021, the treeline retreated by 10 m, due to the impact of snow loading damage of the treeline marker (Table 1). The inferior success of *Picea* is seen also from its relatively sparse and virtually stable sapling population numbers within both transects.

Table.1. Treeline positions (m a.s.l.) and elevational shifts 1915 to 2021 in the NE-facing and SE-facing transect, respectively. Source; Kullman & Öberg 2009, updated

SPECIES/ASPECT	1915	1973	2021
Betula/NE	800	825	870
Betula/SE	830	830	855
Pinus/NE	785	785	825
Pinus/SE	790	810	855
Picea/NE	805	835	825
Picea/SE	825	825	825

Table 2. Population densities within the NE-facing and SE-facing transect, 1973 and 2021, respectively

SPECIES/ASPECT	1973	2021
Betula/NE	63	149
Betula/SE	44	35
Pinus/NE	15	20
Pinus/SE	21	121
Picea/NE	20	22
Picea/SE	25	28

Rephoto, NE-facing transect

Below, the evolution of the birch treeline ecotone is depicted by a sequence of photographs 1973 to 2021 (Fig. 4). In a relatively steep part of the slope, a huge late-lying snow drift has prevailed until quite recently. In this setting, birch has gradually established a sparse stand since the early 1970s. At that time only a few solitary tree-sized birches were present. Subsequent stand densification by slender and youngish trees and shrubs has taken place. This course of continual change has eventually shifted the treeline from 800 and 825 m a.s.l. in 1915 and 1973, respectively (Smith 1920; Kullman 1979), to 870 m a.s.l. in 2021 (Fig. 4). This implies. a total advance of 70 vertical meters during the past 100 years (Fig. 5).

The largest rise of the pine treeline in this transect amounts to 40 m (Fig. 9). The treeline of spruce has shifted least of all species and exclusively by phenotypic plasticity of old-growth individuals (Figs. 6-8).

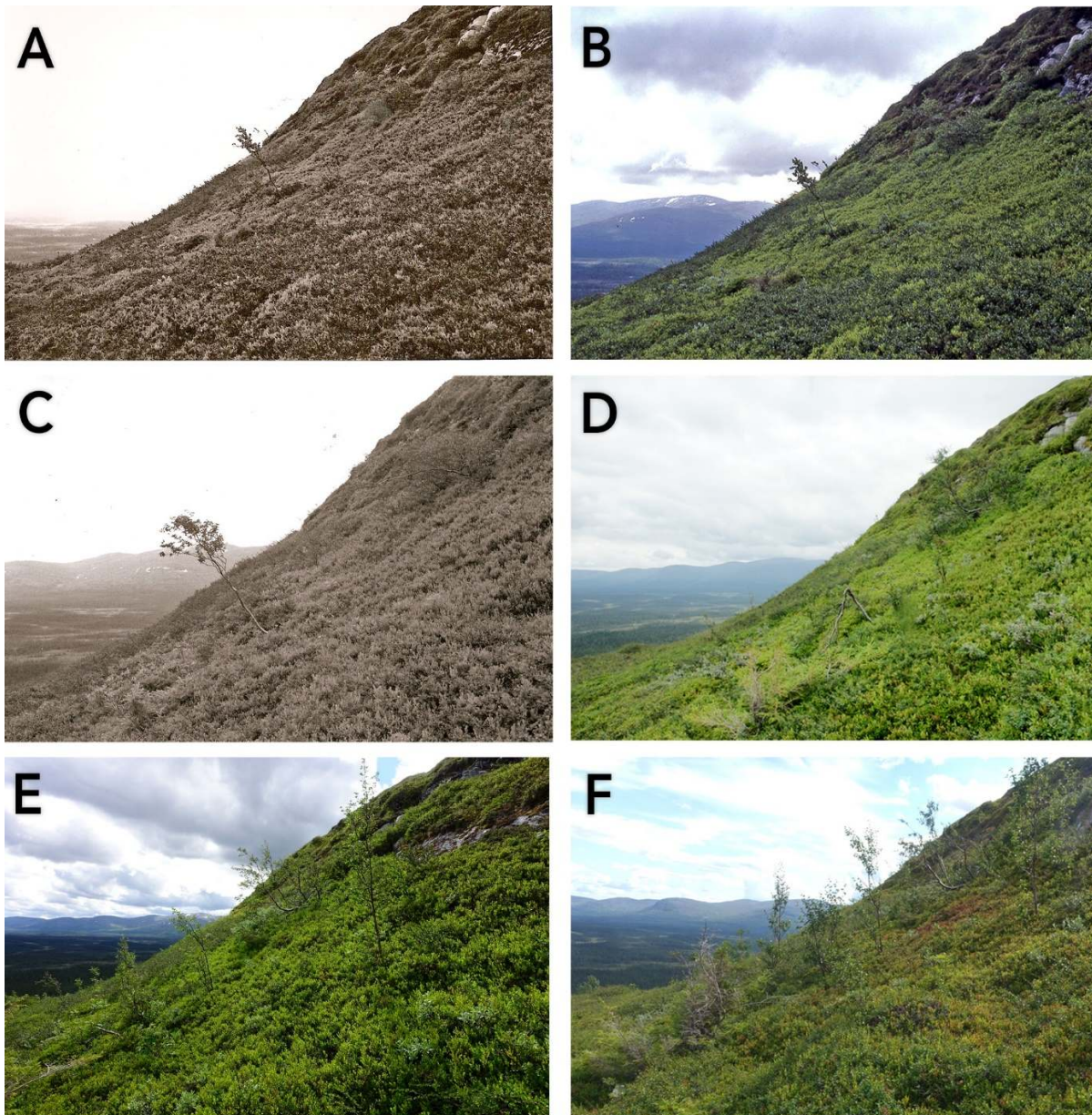


Figure 4. Progression of woody birch vegetation in the snow-rich NE-transect (825 m a.s.l.). A solitary birch tree grew in this subslope until 2009, when it suffered from snow breakage. At the same time, a sparse sapling population of predominantly recently seed-regenerated individuals showed up. Eventually, these have attained tree size and a sparse tree cover has emerged. A. 1973-07-01. B. 1991-07-11. C. 1999-07-05. D. 2009-08-09. E. 2016-07-04. F. 2021-08-05



Figure 5. The new and higher treeline of birch in the relatively snow rich NE-transect, 870 m a.s.l., which is 70 m higher than about 100 years ago, i.e. at the final stage of the Little Ice. Age. The basal part of the main trunk was at least 140 years old. 2021-08-05

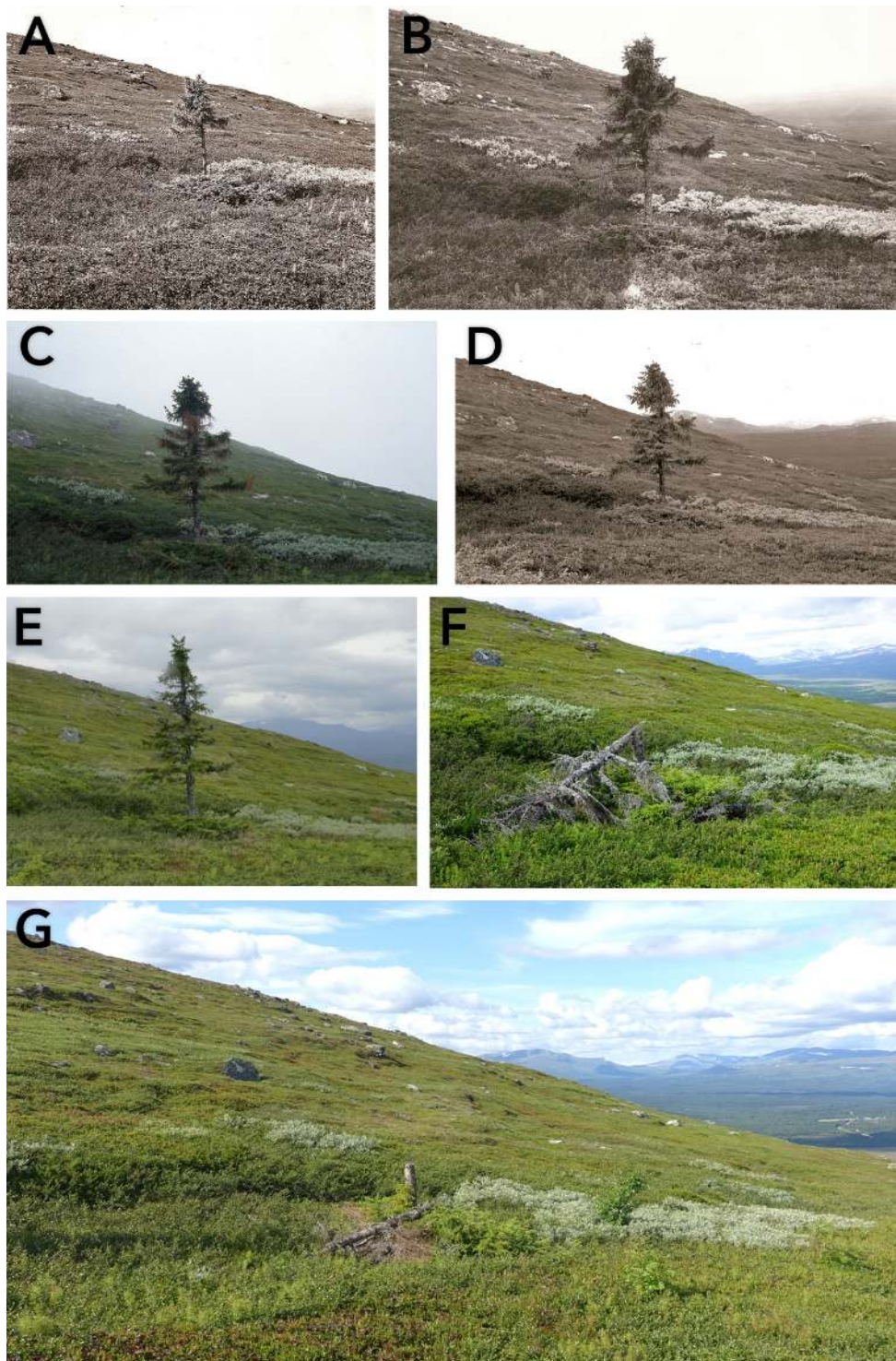


Figure 6. Long-term evolution of a treeline spruce (835 m a.s.l.), 1973-2021. The height of this spruce increased from 2.4 m 1973 to 3.6 m in 1986. Subsequently, the stem was broken by snow load, although individual life continued by prostrate layering stems. This spruce constituted the spruce treeline until its demise after 1986, which implicated subsequent treeline descent by 10 m (see Fig. 7). Tree rings in the main trunk show that this individual prevailed at this spot at least 200 years ago. A. 1973-07-01. B. 1991-08-18. C. 1994-08-03. D. 1999-07-05. E. 1986-07-20. F. 2016-07-04. G. 2021-08-05

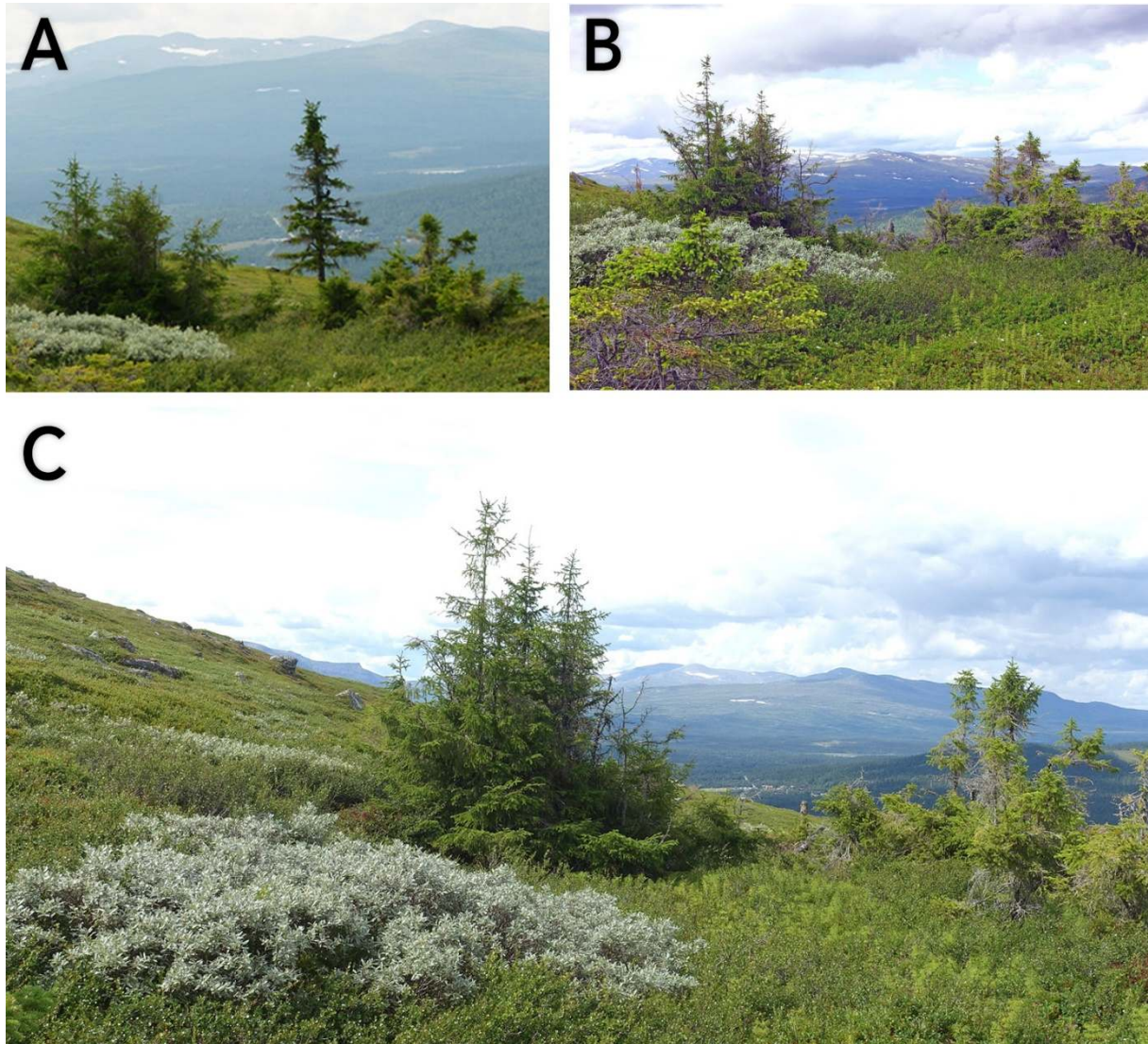


Figure 7. This clonal spruce represents the current treeline (825 m a.s.l.) after the breakage of the higher treeline marker (Fig. 6). Also in this case, a prior dominant stem (in the center) is broken by heavy snow accumulation. Surviving foliage and stems, to the left and right, have subsequently proliferated. The demised stem was, at the base, about 175 years old in 2009. A. 2009-08-09. B. 2016-07-04. C. 2021- 08-05



Figure 8. Spruce tree (825 m a.s.l.) in the NE-facing transect, growing 20 m higher than the treeline position by the early 20th century. This specimen is at least 145 years old at the stem/root junction. Apparently, it survived the final phase of the Little Ice Age as krummholz. Transformation to tree mode is consistent with subsequent climate warming. 2021-08-05



Figure 9. The current treeline of pine in the NE-facing transect, 825 m a.s.l. During the past 100 years, the treeline has risen by 40 m. This young and 2 m high specimen represents the most recent phase of the treeline advancement process. All of the elevational rise took place after the mid-1970s. 2021-08-05

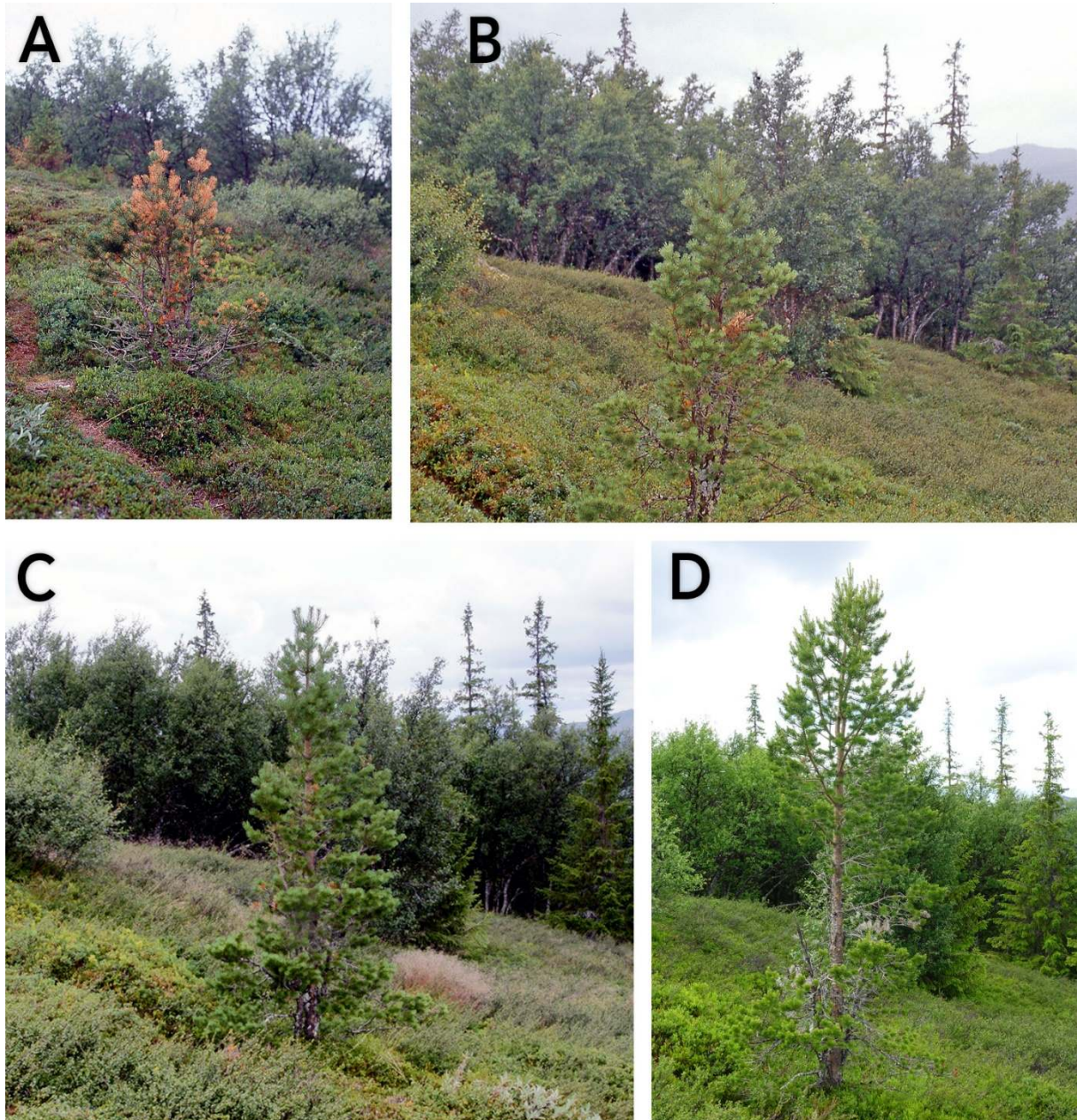


Figure 10. This pine, growing 5 m below today's treeline is part of the 40 m treeline rise during the past 100 years. Tree rings at the base indicate that this pine became established in the early 1940s. In 1973, the upper part of the canopy was heavily affected by frost desiccation. Subsequently, it has recovered perceptibly. A. 1973-07-01. B. 2005-08-16. C. 2009-08-09. D. 2021-08-05

Rephoto, SE-facing transect

Below, photographic evidence of arboreal change in the treeline ecotone is presented, separately for the concerned tree species in the SE-facing slope. Currently, treelines, of birch and pine attain the same elevation, 855 m a.s.l., while spruce stays at 825 m a.s.l. This implies rise by 30, 65 and 0 m respectively, since the early 20th century (Figs. 11-21). In the case of birch, treeline advance was exclusively accomplished by phenotypic plasticity, while pine

responded predominantly by establishment of new individuals and to some extent by enhanced height growth of old-established individuals.

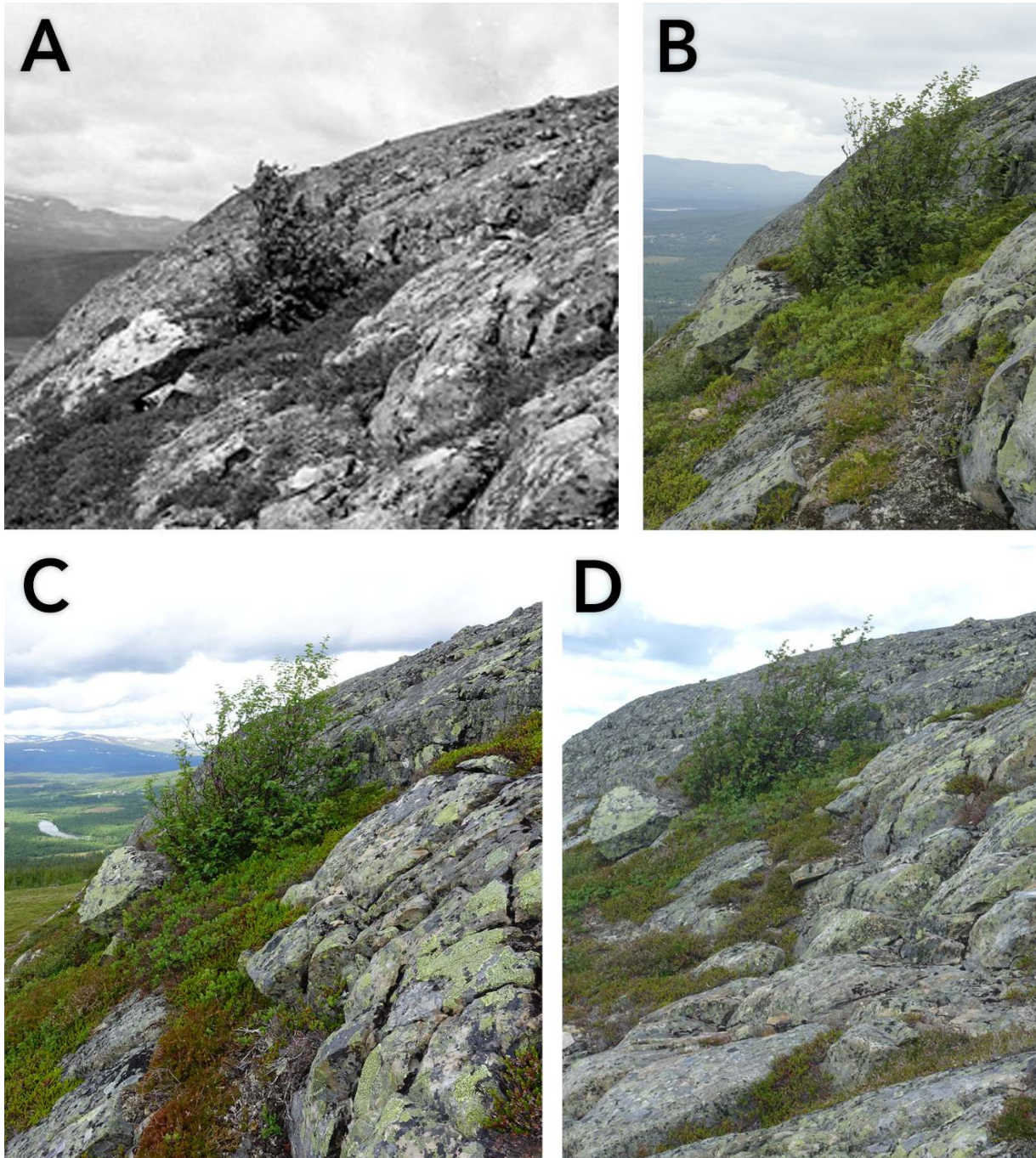


Figure 11. An old-established birch (855 m a.s.l.), growing at an exposed site with a thin soil cover. It transformed from krummholz to tree size during the past 100 years. Dendroecological study revealed that this specimen prevailed at this site by the 1780s or earlier. Height has increased from 1.7 m by 1973 to 2.5 m in 2021, and the number of stems emerging from the same root stock has proliferated. A. 1973-07-01. B. 2009-08-09. C. 2016-07-07. D. 2021-08-05.

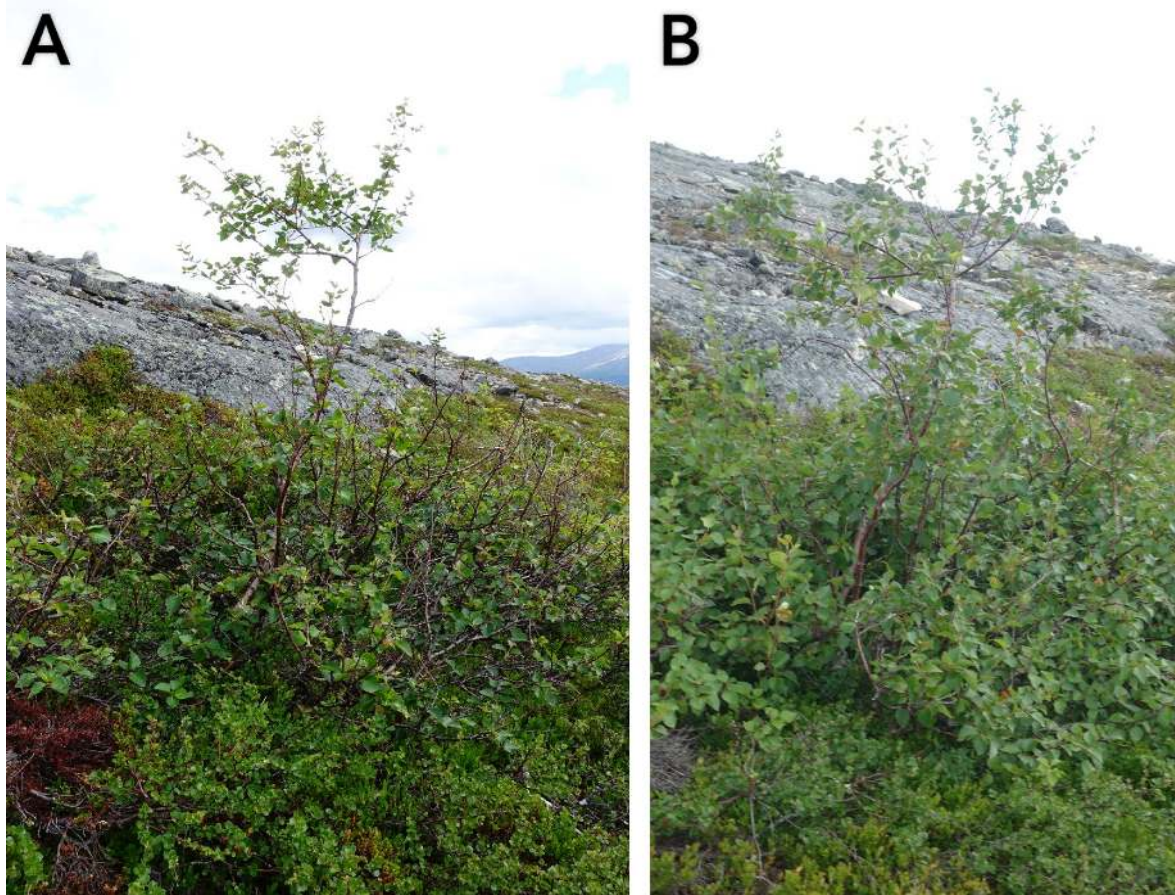


Figure 12. Treeline of mountain birch, representing rise by 25 m since the early 20th century and 5 m after 2016. 855 m a.s.l. Further upslope advances seem constrained by the rocky substrate. Tree rings in basal stem sections indicate this specimen existed as krummholz >150 years ago. A. 2016-07-07. B. 2021-08-05

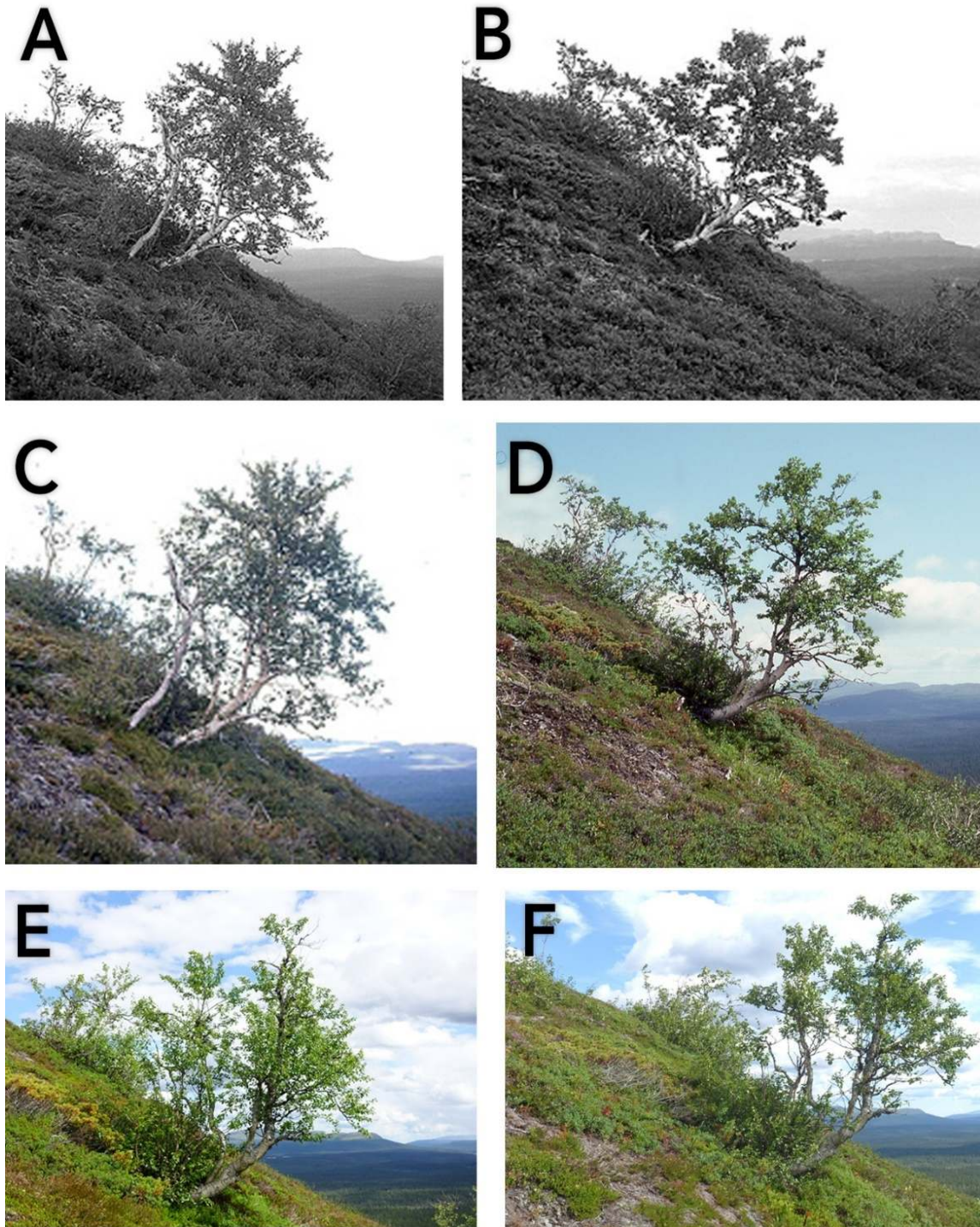


Figure 13. Old-growth birch marking the treeline position in 1915 and 1973 (825 m a.s.l.) Thereafter and up to the present day, its appearance has not changed perceivably. One initial stem has broken and is being replaced by basal shoots. The largest stem contained 156 annual rings at the base (1973), i.e. this individual was present long before the onset of the recent climate amelioration. Still, this birch prevails 15 m above the border of closed subalpine forest which appears to have remained fairly stable in position during the past 100 years of predominant climate amelioration. Note also the proliferation of the multi-stemmed birch copse in the background. A. 1973-07-01. B. 1977-08-02. C. 1986-07-20. D. 2009-08-09. E. 2016-07-07. F. 2021-08-05



Figure 14. Old-growth pine representing the pine treeline of the early-20th century, 790 m a.s.l., growing in a mixed forest stand of birch and spruce, 65 m below today's raised pine treeline within the SE-transect. This tree germinated during the 1720s. 1973-07-01

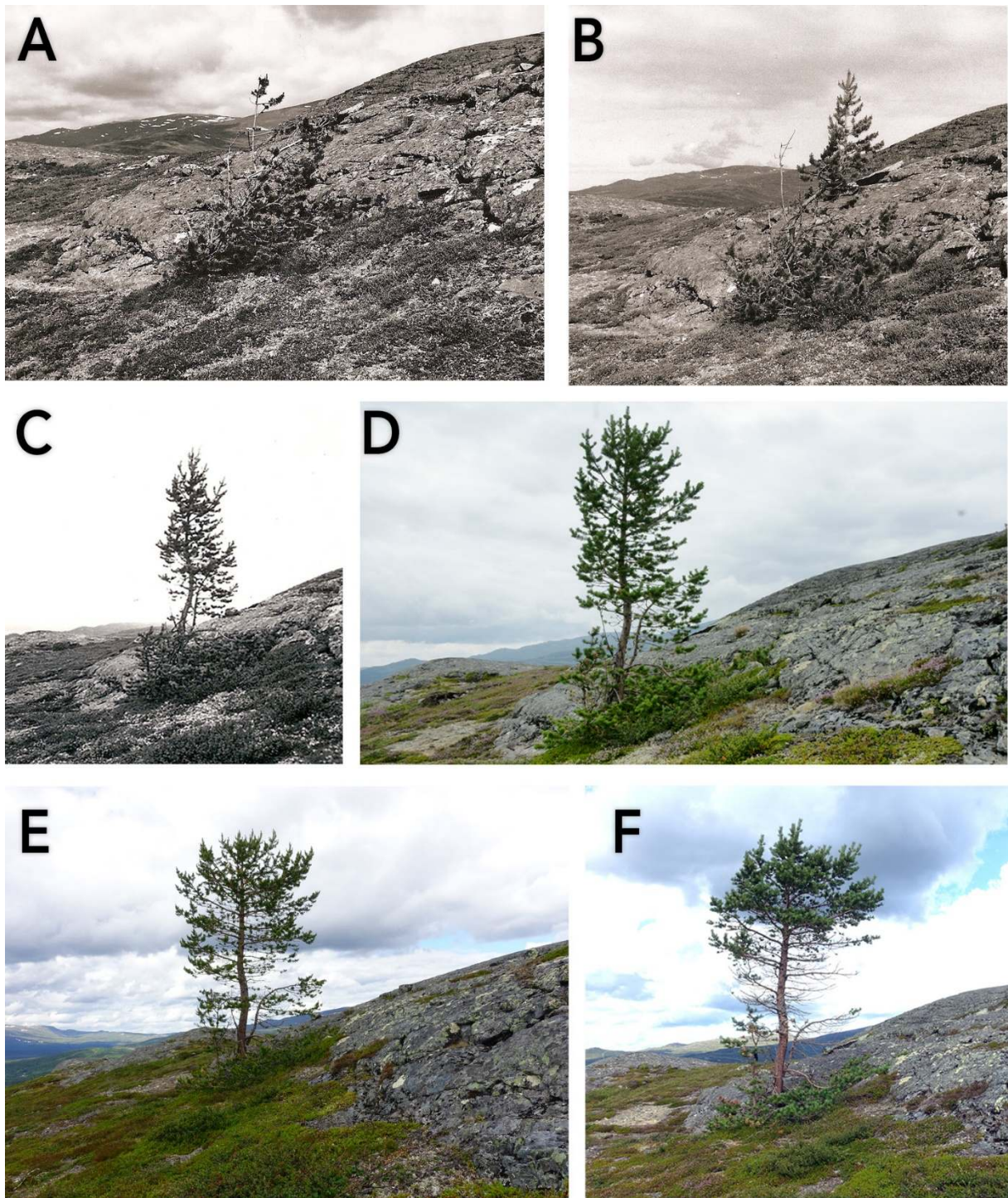


Figure 15. Progressive evolution from "krummholz" to erect tree size of a multi-stemmed pine in the treeline ecotone, 840 m a.s.l. In 1973, one of several prostrate and buried stems displayed 345 annual rings outside a rotten centre, indicating that this pine might have grown here already in the 16th century. This specimen prevails 50 m above the treeline as it was by the early 20th century. Further upslope advancement appears to be thwarted by prevalent naked bedrock. A. 1973-07-01. B. 1991-07-11. C. 1986-07-20. D. 2007-07-05. E. 2016-07-04. F. 2021-08-05

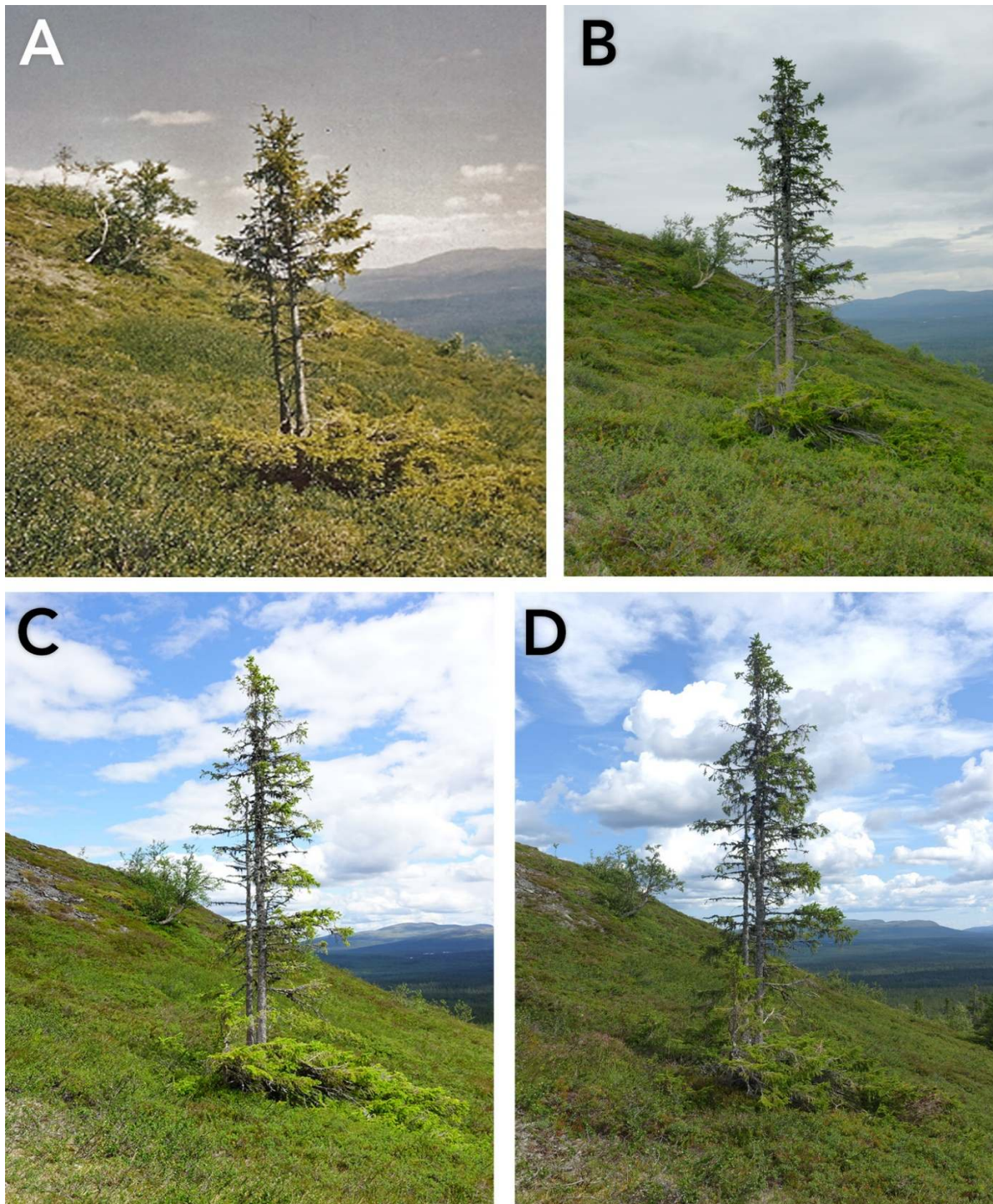


Figure 16. Progressive development of the current spruce treeline marker (825 m a.s.l.), 1973 to 2021. Over this interval, the height increased from 2.5 to 7.2 m. In addition, the ground cover of dwarf- shrubs, foremost *Betula nana* and *Vaccinium myrtillus* has become denser. Tree rings at the base of the largest stem show that this individual spruce grew at this spot at least 130 years prior to 1973. A. 1973-07-01. B. 2009-08-09. C. 2016-07-04. D. 2021-08-05

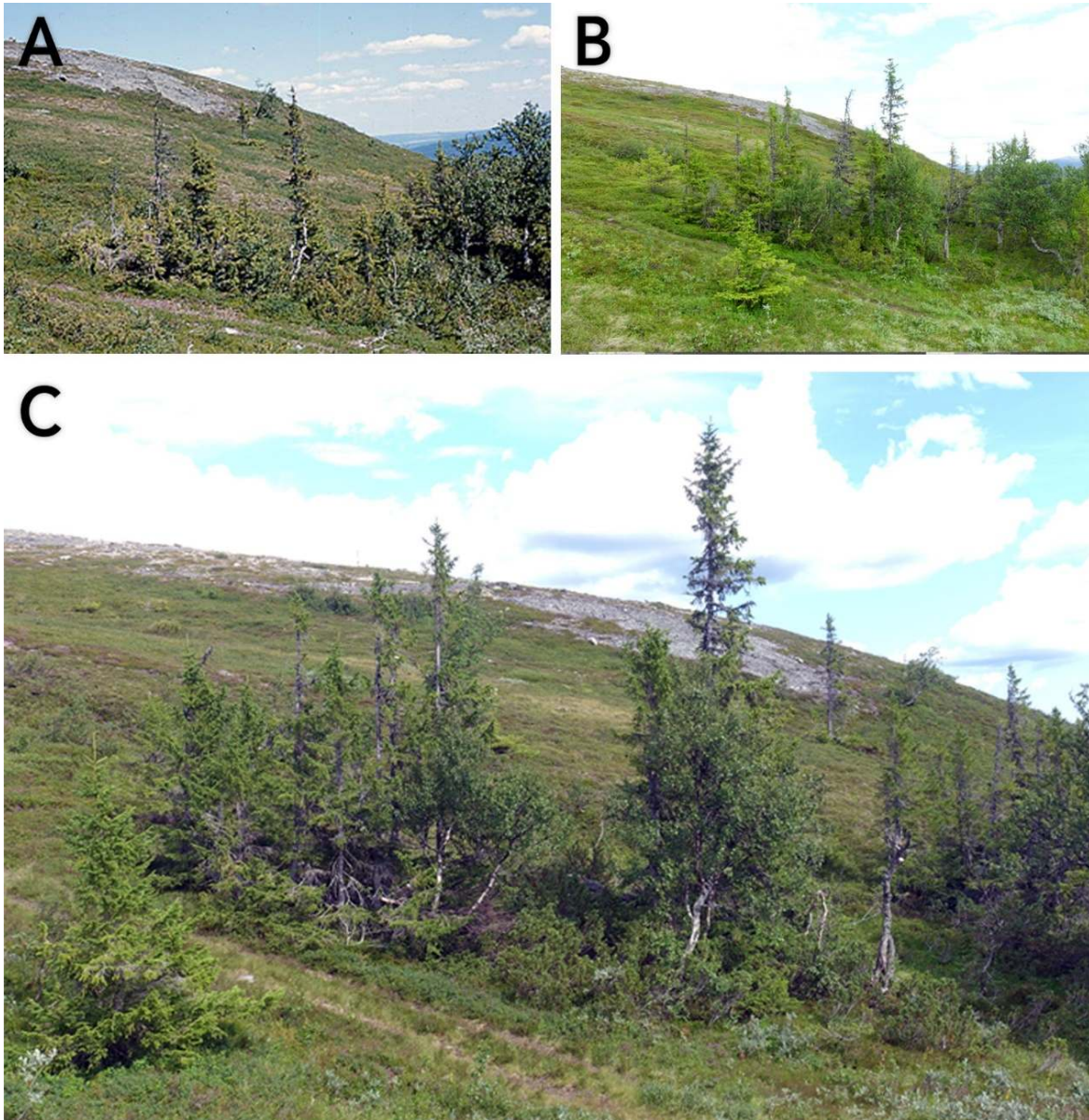


Figure 17. Multi-stemmed and old-established clonal spruce in treeline ecotone (825 m a.s.l.).
Since 1973, the canopy has expanded and has given rise to sparse offspring well outside of closed canopy. The highest stem was about 0.3 m high by the 1860s, which is a minimum age of the clone, which also contains birches of virtually the same age. A. 1973-07-01. B. 2016-07-04. C. 2021-8-05



Figure 18. The new and raised pine treeline in the SE-transect, 855 m a.s.l., which germinated in the late 1930s. This specimen is heavily browsed by moose in the winter. Based on extensive experience, it may survive and attain a more typical tree mode. A young sapling in the lower right-hand corner is likely to be offspring of this individual. 2021-08-05

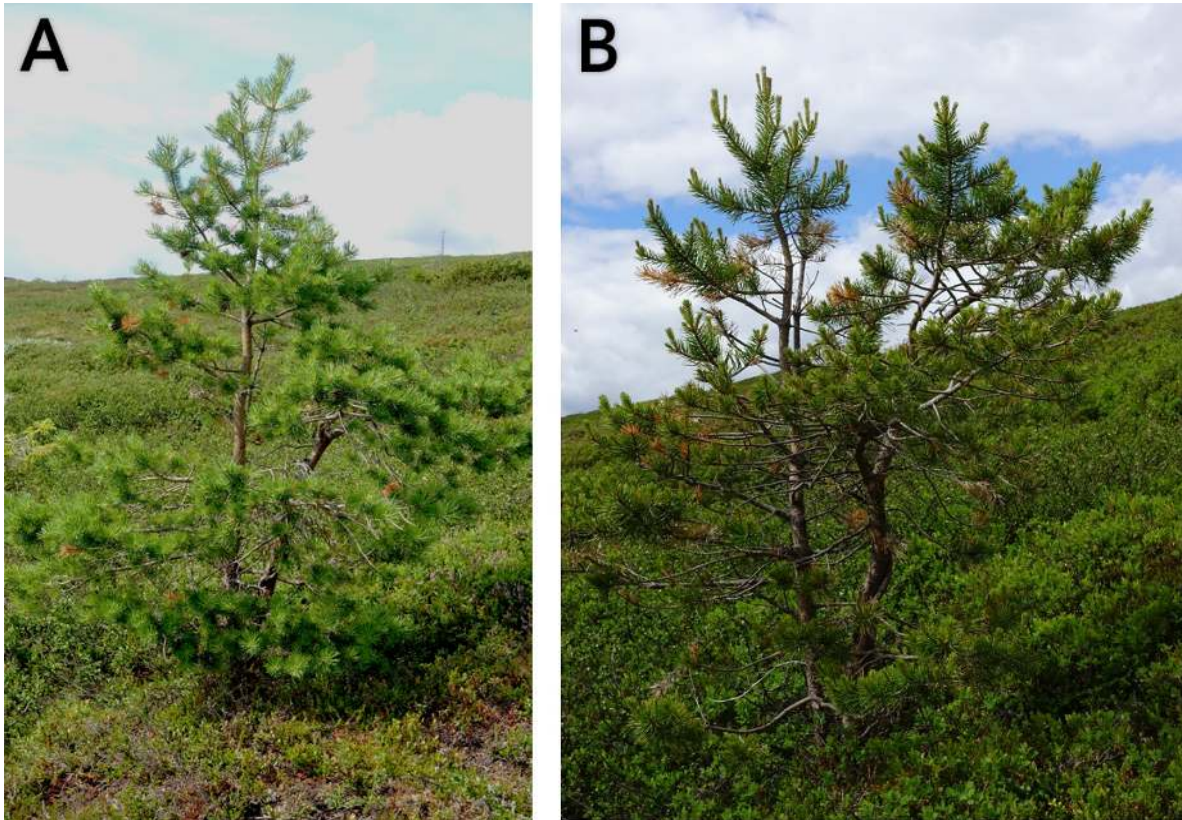


Figure 19. Young pine, growing in the treeline ecotone, somewhat below the new and raised tree line (820 m a.s.l.). Since 2016, the height has increased from 1.7 to 2.3 m. The age was estimated to 30 years (2021). A. 2016-07-04. B. 2021-08-05

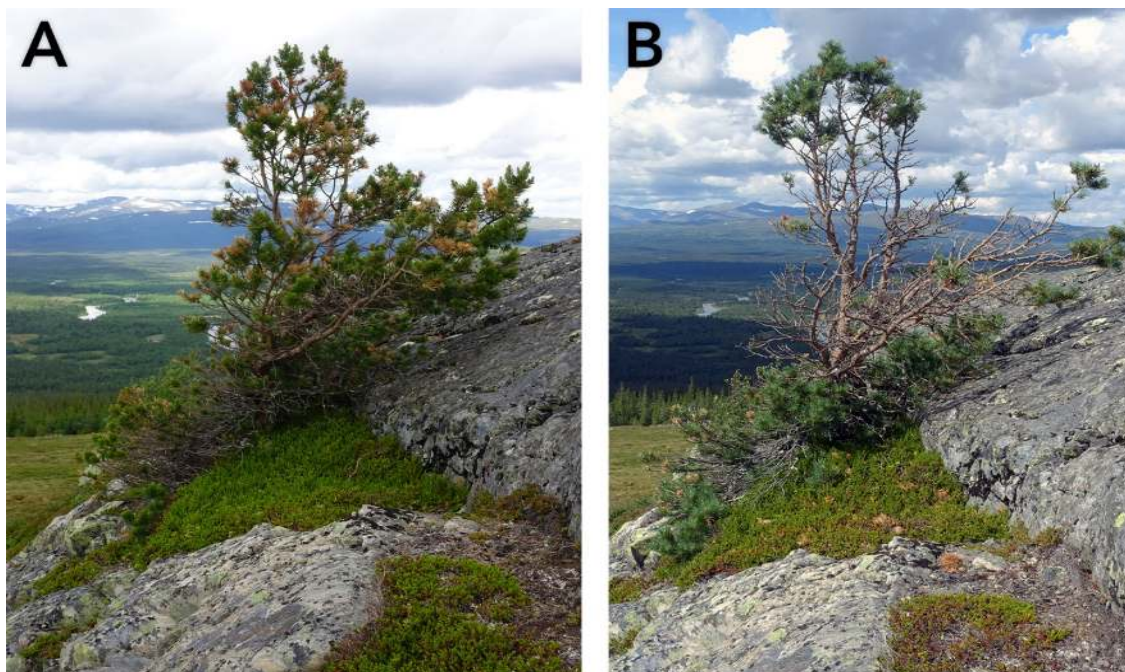


Figure 20. Current treeline of pine at an exposed site with a thin soil cover, 855 m a.s.l. Basal stems are 130 or more years of age (2016). Over the past 100 years, the treeline has advanced by 65 m. Recently, winter browsing by moose has reduced the foliage. A. 2016-07-04. B. 2021-08-05

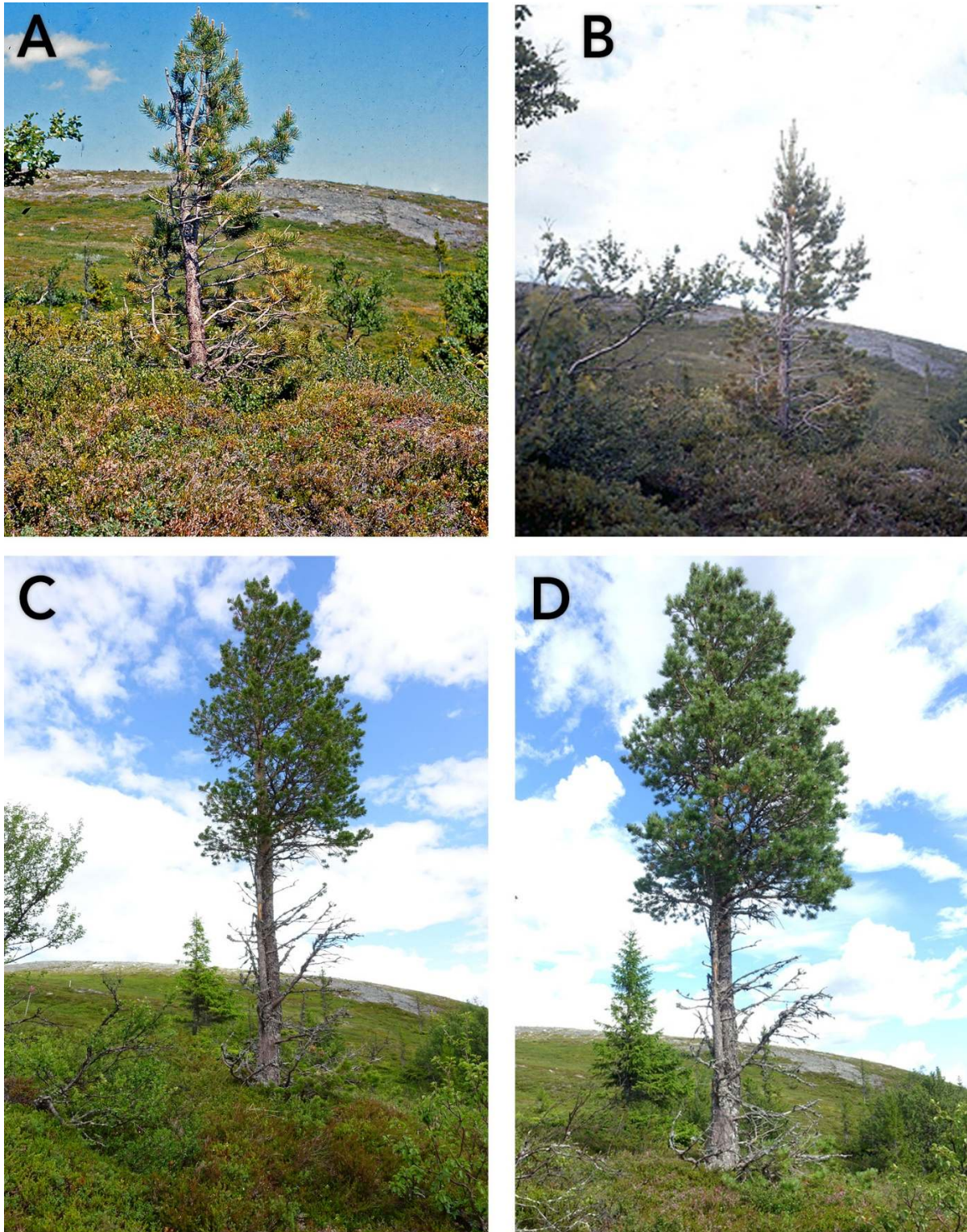


Figure 21. Young and recently seed-regenerated pine with rapid height growth, in the treeline ecotone (810 m a.s.l.). Over the period 1973-2021, this specimen has increased its height from 2.1 to 7.5 m and the canopy has expanded. Like many other specimens, the physiognomy is affected by browsing moose. A. 1973-07-01. B. 1977-08-02. C. 2016-07-04. D. 2021-08-05.

DISCUSSION

As evidenced by repeat photography at the local scale, arboreal changes in the treeline ecotone on a low-alpine fell comply with various modes of ongoing regional treeline dynamics over the past 100 years (Kullman & Öberg 2009). Recorded treeline positions and rises are much constrained by the low altitude of the mountain summit, just 10 m higher than the birch treeline, and the prevalence of thin soils and naked rock in combination.

The largest upshifts (pine and birch) are in the northeast transect, 65 and 70 m, respectively. The striking increase the pine sapling population (southeast transect) mirrors a more general pattern of population surge during the past few decades (Kullman & Öberg 2021). Spruce displays relatively modest treeline change of 30 vertical meters since the early 20th century and until the mid-1970s. Subsequently, its treeline descended in proximate response to snow load breakage of the treeline marker, although the individual spruce persisted as a low shrub. Also the birch treeline in this particular slope suffered from analogous physical disturbance, although without individual mortality and a depressed treeline. These experiences of snow load modulation of the treeline are consistent with reports of this as a chronic disturbance on low-fell regions in different parts of northern Fennoscandia (Hesselman 1912; Svedmark 1952; Autio & Colpaert 2005).

Conceivably, excessive snow accumulation has until quite recently precluded tree growth of birch and spruce strictly locally in the northeast slope. During the past 10-15 years or so, snow melt appears to have taken place progressively at an earlier time of the year, to the benefit of tree growth, which previously suffered from excessive snow cover duration. Improved conditions for birch are reflected also by significant population growth within the entire northeast transect (Table 2). Analogous local responses, i.e. establishment of new forest stands in prior snow rich environments are reported also from other parts of the Swedish Scandes and elsewhere (Kullman 1979, 2007b, 2021b; Zhou et al. 2022). Also the upshifts of pine are understandable in the light of earlier snow melt, as this species is poorly fitted to snow rich environments (Aas & Faarlund 2000; Kullman 2010b).

To a large extent, tree line advance of birch and spruce rely on phenotypic plasticity of old-established individuals. To a lesser extent, this also concerns pine, previously considered to lack the ability of layering and thereby survival as prostrate krummholz during harsh periods like the Little Ice Age (but see Kullman 2020).

Irrespective of regeneration mode, treeline advance and population growth in the treeline ecotone represent a return to a more advanced arboreal state, latest prevailing during the Medieval Climate Optimum (cf. Lamb 1982; Ljungqvist 2017) and predating the Little Ice Age climate cooling and ensuing vegetation retrogression. During the former interval, treelines in the concerned region and elsewhere in the North, were positioned as 100 m or more higher than today (Shiyatov 2003; Mazepa 2005; Kullman 2012, 2013, 2015b; Linderholm, Zhang, Gunnarson et al. 2014). The present-day treelines at the site, are in the lower range of this interval. Thus, we have good reasons to infer that the treeless alpine cap of this mountain is relatively young in a Holocene perspective. In that context, current progressive treeline performance, is leaving much of the treeline ecotone sparsely treed. Like other records, the forest border is virtually unchanged in position since the early 20th century (Kullman 1979). Obtained aspects of change and stability appear to be well within the frames of natural

variability and conforms to ongoing modest climate-mediated conversion of the forest-alpine tundra ecotone (Kullman 2019). Given the prolific regeneration of pine in the treeline ecotone and the new and higher treeline (SE-slope), it may be reasonable to assume the sparse subalpine birch forest belt may become replaced by a subalpine belt of predominant pine. Tendencies in that direction are recorded from the southernmost Swedish Scandes (Kullman 2014a, 2019). In the snow rich NE-facing slope, stands of birch forest may evolve, in the case of further climate warming and more earlier seasonal melt-out of the snow cover. However, alarmistic model predictions of a pending major transformation of alpine tundra in the Swedish Scandes to subalpine forest (e.g. Moen et al. 2004; Bernes 2007) are little supported by the current and other real-world observations (cf. Willis et al. 2010; Hofgaard et al. 2013; Kullman 2019). Even if we knew each and every detail in future climate development, complex interactions between regional climate and local factors, as highlighted in this study, make detailed and realistic projections into the future virtually impossible. However, time and continuous unprejudiced monitoring of robust baseline observational data may shed more light on this issue (e.g. Kullman 2014a).

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