



(REVIEW ARTICLE)



Subalpine "pinification": Early signs of a pending and distinct biogeographic shift in the Swedish Scandes: Review and updates

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International Journal of Science and Research Archive, 2023, 10(02), 402–432

Publication history: Received on 13 October 2023; revised on 21 November 2023; accepted on 24 November 2023

Article DOI: <https://doi.org/10.30574/ijrsra.2023.10.2.0958>

Abstract

This study focuses, by *in situ* records and long-term observations, on recent (post-Little Ice Age), arboreal change in a mountain birch dominated (*Betula pubescens* ssp. *czerepanovii*) valley in the Swedish Scandes. During the early Holocene thermal optimum and up to the onset of the mid-Holocene Neoglaciation, Scots pine (*Pinus sylvestris*) dominated the tree cover of this valley and formed the treeline ecotone adjacent to the early alpine tundra. Subsequently, and consistent with progressive cooling until the late 19th century, prevailing pine stands demised and opened for landscape-level expansion of birch and spruce (*Picea abies*). A short and distinct break in that process took place by the Medieval Climate warming phase, about 1000-800 years before present. Subsequently, during pre-industrial time, temperatures reached their lowest levels of the entire post-glacial period. This was the so-called Little Ice Age, which ended the long-term Holocene cooling. That cold-climate epoqe was broken by the late-19th and early 20th century. Thereafter and up to the present-day, temperatures in the study region (summer and winter) have increased by slightly less than 2 °C. As a consequence, treelines of all species have advanced by a maximum of more than 200 altitudinal meters. Pine displays the most persistent expansion, particularly over the past few decades. "Falangist" occurrences appear in the pure birch forest, tens of kilometers and hundreds of meters, respectively, beyond and above the outposts by the early 20th century. Occasionally, scattered young pine trees now grow close to the birch forest limit and somewhat above. In particular, at sites where pine stands demised during the Little Ice Age, c. AD. 1300-1850, prolific regeneration and insignificant winter mortality are recorded over the past 15 years. In comparison, birch and spruce provide no analogous signs of recent expansion. It may be hypothesized that unabated climate warming and corresponding arboreal progression will profoundly transform the plant cover of this valley, and others alike, into the same pine-dominated state that prevailed during the early Holocene. In other words, a new biogeographic zonation pattern may be on the rise, with pine back as the dominant subalpine species. This option is focused by continued monitoring.

Keywords: Tree line ecotone; Subalpine forest; *Pinus sylvestris*; Climate change; Regeneration; Permanent plots; Re-photography

1. Introduction

Treelines and adjacent subalpine forests, are among the most temperature-sensitive biological transition, with respect to position and structure/composition (Smithson et al. 2002; Paulsen & Körner 2014; Camarero et al. 2015; Lu et al. 2022). Consequently, these elements in the mountain landscape serve well in the forefront of biogeographic climate change impact assessment and early detection (Holtmeier 1974; Kullman 1979, 1981, 1998, 2002a, 2021h; Smith et al. 2009; Gaire et al. 2014; Körner 2021; Vinós 2022).

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World-wide, treelines have commonly and to various degree and pace extended their elevational ranges, primarily in response to rising temperatures over the past 100 years or so (Aas 1969; Kullman 1979, 1981, 1986b, 2003; Kullman & Öberg 2009; Harsch et al. 2009; Shiyatov & Mazepa 2015; Lu et al. 2021; Grigoriev et al. 2022; Hansson et al. 2021, 2023). Aside of climate variability, treeline positions are mediated by local conditions, e.g. slope, aspect, geomorphology, soil conditions, herbivory and human impacts, which constrain full elevational responses to climate change (e.g. Kullman 1979; Elliott 2011; Holtmeier & Broll 2012; Cudlin et al. 2017; Crofts & Brown 2020; Frei et al. 2023).

In principle, treelines integrate effects of climate change and variability, foremost temperature (all seasons), over relatively long periods of time. Maybe a truism, but it needs to be stated that our present age and the future can be understood only by an historical perspective on the nature and its dynamics (Hill & Redford 1986; Lamb 1995; Reichholf (2008). In other words, time is an essential aspect of ecological analysis and comprehension, particularly in range-margin situations (Franklin 1987; Veblen & Lorenz 1991; Gitzen et al. 2012; Wolkovich et al. 2014; Kullman & Öberg 2022b). Therefore, it is needed, for a proper analysis of treeline change in a context of recent and future climate variation, to consider that during the early-Holocene thermal optimum (10 000-5000 cal. a BP), the high mountains of the Swedish Scandes were patchily clad with tree groves at high elevations, where no trees can exist at the present day. Predominantly pine (*Pinus sylvestris*), then grew in stands high above (500-700 altitudinal meters) present-day treelines and with a boreal forest flora and fauna. Preferentially, trees occupied empty glacier niches, which underscores the favorable climate of the time (Kullman 2008, 2013, 2021a; Luoto et al. 2014; Väiliranta et al. 2015; Paus & Haugland 2016; Helmens et al. 2018; Kullman & Öberg 2020). These circumstances, illustrated by Figures 1-3, favour the option that alleged future anthropogenic climate warming (IPCC 2021), although apparently overstated (cf. Vinós 2023), may eventually accomplish a virtually analogous and progressive biogeographic shift in the same direction (cf. Svenning & Sandel 2013; Fisher et al. 2018). Such a course of change, may imply reduction of the subalpine birch forest belt to the favour of pine-dominated tree stands, reappearing close to their highest postglacial positions, although questioned by some researchers (Holtmeier 2005; Young et al. 2011). These progressive projections gained early support from historical data and observations of enhanced regeneration in northern Fennoscandia during the 1920s-1940s (Hustich 1940, 1948, 1958; Blüthgen 1942, 1960; Erkamo 1956; Sirén 1961). They contrasted with the traditional view that northern pine forests were continually regressing due to prevailing cold climate and associated infrequent regeneration (e.g. Renvall 1912; Hagem 1917).

This study highlights a conspicuous novel phenomenon of enhanced pine reproduction and growth close to the treeline in northern Fennoscandia, that appears to be more distinct than the pulse of the early 20th century (Kullman 2015, 2016a, 2018, 2019b; Kullman & Öberg 2021).

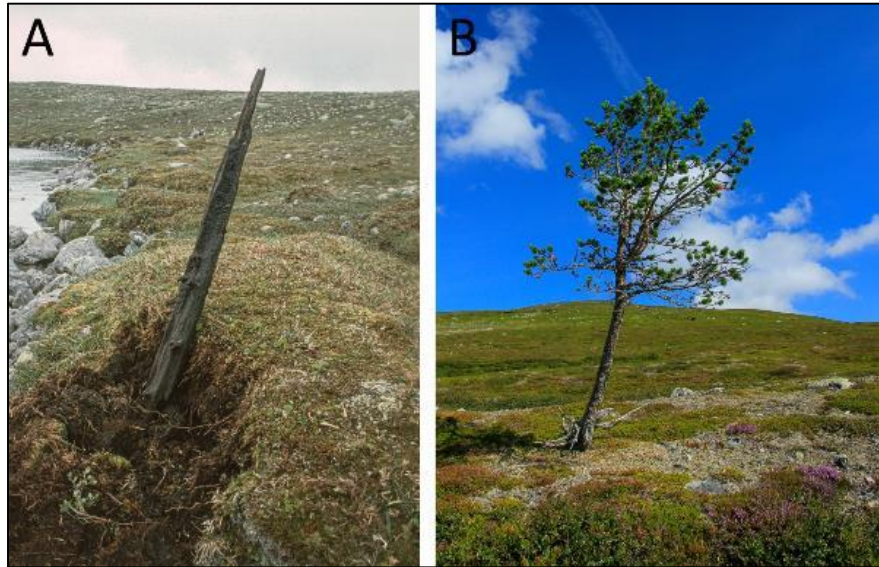
History rarely repeats itself. In the present context, however, it is important to consider the ecological effects of the global Medieval Climate Optimum (AD 800-1300), as well as the subsequent Little Ice Age event (AD 1300-1850). The last-mentioned relatively cold episode prevailed, with short warmer reversals, prior to the current warming phase. The Little Ice Age caused extensive regression of cold-marginal tree stands and human societal stress world-wide (Bauer 1958; Proctor et al. 1980; Payette et al 1985; Shiyatov 2003; MacDonald 2010; Kullman 2015; Ljungqvist 2017). This event constitutes a pertinent baseline perspective and background for evaluation of the progressive subalpine/alpine landscape evolution over the past 100 years or so (Lamb 1995; Grove 2004; Ljungqvist 2017; Kullman & Öberg 2009, 2021, 2022a).

As stressed by Anderson et al. (2009), new data based on accurate and precise retrospective approaches (species identification and growing sites) have prompted the paleoecological society to rethink the late-glacial and early postglacial high-elevation landscape, its biotic components, structure and drivers, as well as conventional methods of paleoecological research (Kullman 2008, 2017b; Parducci et al. 2012; Kullman & Öberg 2020; Paus 2021; Nota et al. 2022).

These new insights and inferences are briefly accounted for below. Accordingly, and subsequent to the early-Holocene thermal optimum (10 000-9500 cal. a BP), the structure and composition of the treeline ecotone gradually transformed (mainly retrogression), culminating with the Neoglacial climate cooling (Kumar 2011). That epoch was enhanced about 6000-5000 cal. a BP. It was driving boreal ecosystem regression, with short reversals, up to the late 19th century (Smith 1920; Bergman et al. 2005; Kullman 1995, 2013, 2021b; Ljungqvist 2017; Kullman & Öberg 2020; Paus & Haugland 2016; Paus 2021; Paus et al. 2023) (Fig. 3). Apparently, the subsequent modern climate warming (20th century and onwards) and associated progressive ecological responses started from a deep environmental nadir, which had imposed a heavy stress on the northern landscape and society.

The main intention of the research presented in this paper is primarily to add detail and to develop the conception and understanding of the natural Scandinavian subalpine world and its evolution. Hopefully, this narrative, based on factual

observations may avoid adding fuel to an overheated and alarmistic discourse of anthropogenic and catastrophic future climate change (cf. Körner & Hiltbrunner 2021; Vinós 2023).



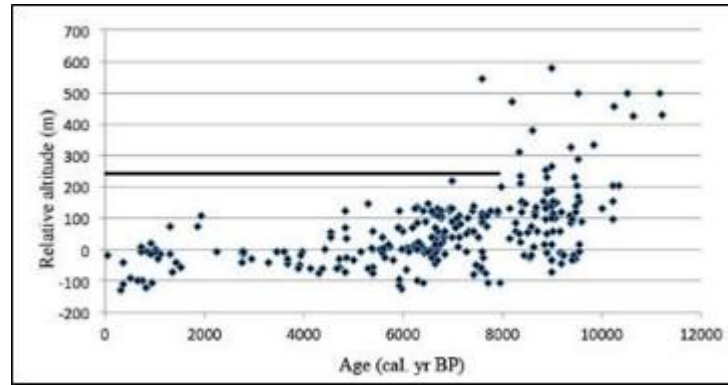
Photos: A. 2002-08-15. B. 2013-07-28.

Figure 1 A. Megafossil pine (*Pinus sylvestris*) trunk, unearthed from the rim of a small alpine lake 1180 m a.s.l., which is 205 m higher than the present-day (early 21st century) pine treeline. Radiocarbon-dating yielded 10 390 cal. a BP. Mt. Storvätteshåga (Province of Dalarna). B. Today's treeline (975 m a.s.l.) in the same slope is marked by a single tiny tree, growing at an exposed, snow-poor and intensively reindeer grazed site. It represents treeline rise by 140 m since the early 20th century. Source: Kullman (2004, 2017a)



Photo: 2017-07-07

Figure 2 The largest pine (*Pinus sylvestris*) treeline upshift documented in the Swedish Scandes during the past 100 years (225 altitudinal meters) is recorded at Mt. Molnet (Province of Dalarna), 1100 m a.s.l., which is also the highest known present elevation of pine treeline in the Swedish Scandes. This elevation may be higher than any time during the past 7000 years or so, indicating that climate warming over the past 100 years is an unusual episode, although not necessarily unique (Fig. 3). Source: Kullman (2013, 2017a).



Source: Kullman (2013)

Figure 3 Composite of all radiocarbon-dated pine megafossils (intercept values) obtained from the mountains of the provinces Dalarna, Jämtland and southern Lapland, in the Swedish Scandes. Each dating (quadrat) is plotted relative to the treeline prevailing during the early 21st century (zero-level). The horizontal line indicates the extent of maximum regional treeline advance during the past 100 years

With the purpose to shed some light on possible future arboreal evolution in the high mountains, it may be relevant to focus on the current pine (*Pinus sylvestris*) treeline performance after the past century of climate warming. The choice of pine for this specific scrutiny is motivated by the fact that the genus *Pinus* is renowned as particularly invasive into open and exposed high-elevation landscapes, ultimately in response to temperature changes (Richardson & Rejmánek 2004). Accordingly, it has been argued that treeline populations of pine are likely to advance massively upslope in response to a proposed future warmer climate (Sormunen et al. 2011; Matías & Jump 2012; Bognounou et al. 2018). Based on long-term observational evidence, an initial phase of such a course of change may have been recently initiated in parts of the Swedish Scandes (Kullman 1981, 2017a; Kullman & Öberg 2021).

The general hypothesis to be tested by continued observational data gathering, is that progressively warmer summers and milder winters would promote enhanced high-mountain pine regeneration, survival and treeline rise (Kullman 2007, 2014a), but see Aakala et al. 2014 and Grigoriev et al. 2022.

Focusing on real-world observations in northern Fennoscandia, pine in particular displays a tendency of consistent elevational treeline advance and seed-generated infilling of sparse marginal stands during the past century. That course of change was particularly enhanced over the past few decades. This is the main focus of the present study, which provides updates and a meta-analysis of previous case studies. It highlights recent observations within a regional network of pine treeline monitoring (Kullman 1983, 2007, 2010, 2014a,b, 2016a,b, 2017a, 2018, 2019a,b, 2021b; Kullman & Öberg 2009, 2021, 2022a,b).

Recorded arboreal changes are richly documented by photographs, supporting their factual nature and character. Despite the tremendous current scientific focus on climate change and associated ecological changes, surprisingly few studies validate predictions of large-scale and profound biogeographic change by *in situ* observations over sufficiently long periods of time, i.e. at least the past 100 years.

A main intention of this paper is to provide a face of ongoing climate-driven subalpine landscape transformation in the Swedish Scandes. Much of the changes accounted for here are circumstantial in character, although based on regionally widespread and abundant observational data, with a time-depth providing a higher level of ecological significance than mainstream model outputs, often without a proper historical background of supporting empirical observational data (e.g. Moen et al. 2004; Kaplan & New 2006). Simplistically, these models assume upshift of the subalpine birch forest belt into the alpine tundra. Alternatively, however, the subalpine birch forest may become replaced by a subalpine pine belt, an option supported by recent observations (Kullman & Öberg 2021b, 2022a). Analogous inferences from western North America indicate future new patterns of tree species dominance in the treeline ecotone and novel treeline communities and ecosystems (Trant & Hermanutz 2014). An analogous option for the Swedish Scandes is the main focus of the present paper.

1.1. Study area

This study mainly concerns the treeline ecotone, i.e. the spatio-temporal mosaic and continuum between closed forest, scattered tree groves, solitary trees and open patches of alpine tundra in the southern Swedish Scandes, foremost the

provinces of Jämtland and Dalarna (Fig. 4). At the local subalpine stand level, the structure is highly variable in space. Responses to climate change and variability may differ significantly between nearby sites to one and the same climate change shift. Apparently, idiosyncratically modulated treeline shifts rely on a variable geomorphological structure and associated factors, such as wind and snow cover (Kullman 1979). Foremost, the dynamics of the alpine (upper) treeline is focused by this study. The *treeline* concept is strictly defined as the elevation (m a.s.l.) of the uppermost individual of a certain tree species, at least 2 m high.

Today, the generic arboreal zonation pattern in the Scandes comprises an upper subalpine birch forest belt (*Betula pubescens* ssp. *czerepanovii*). Downslope, this belt is fringed by boreal conifer groves and solitary trees, with spruce (*Picea abies*) and pine (*Pinus sylvestris*) treelines about 50 m and 100 m, respectively, below the birch treeline (Kullman 1981; Carlsson et al. 1999; Kjällgren & Kullman 2002; Kullman 2005a; Kuuluvainen et al. 2017). This entire transitional zone constitutes the *treeline ecotone*.

On the local scale, each mountain slope displays a structurally and compositionally unique treeline ecotone, which challenges a stringent distinction of a forest line, as a useful bioclimatic indicator (Kullman 2010; Grigoriev et al. 2022). The extant arrangement of this ecotone is the outcome of a long-term process, displaying more or less continuous arboreal change during the Holocene. Predominantly, regression prevailed, with respect to elevational position and stand density, ultimately driven by climate change, soil development and herbivory, in concert with species-specific ecologies and human impact (Kullman 2010, 2013, 2017a).

All sites, focused by this study, suffered substantial pine tree dieback and regeneration failure during the Little Ice Age. As a consequence, a general landscape pauperization and structural transformation of the living subalpine/alpine landscape took place (Kullman 1987, 2005c, 2015, 2019b). This was a pattern common to most of northern Scandinavia (Linderholm et al. 2002, 2014; Helama et al. 2020) and was followed by the modern phase of progressive climate and treeline evolution.

The ground cover within the treeline ecotone is largely composed of oligotrophic and sparse dwarf-shrub heaths, with *Vaccinium myrtillus*, *Empetrum hermaphroditum*, *Calluna vulgaris*, *Betula nana*, *Kalmia procumbens*, *Diapensia lapponica* and *Arctous alpina*. In addition, mires with sedges and bryophytes, in a mosaic with snowbed plant communities prevail (cf. Kilander 1955; Rafstedt 1984). The plant cover of the southernmost and most continental parts of the study area is dominated by reindeer lichens (*Cladonia* spp., *Flavocetraria nivalis*) (Andersson et al. 1978-1984).

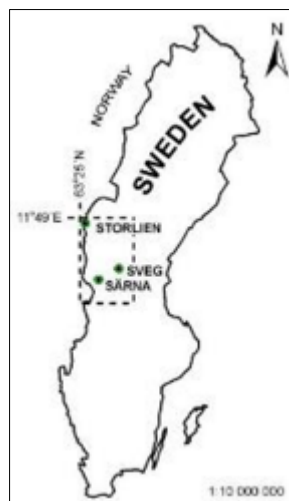


Figure 4 Study area in the southern Swedish Scandes

It is important to consider that reindeer is a natural biotic factor in high-mountain ecosystems and is constantly affecting the plant cover (Warenberg 1982). During the past century, reindeer grazing and trampling have conspicuously and increasingly impacted the ground cover; lichen-dominated plant communities in particular. Since reindeer do not normally feed on pine needles, their main effect is by trampling and grazing herbaceous plants, thereby creating gaps in the ground cover, suitable for seed germination and early growth of pine and other species. Moose (*Alces alces*) browses on pine saplings, locally with some disturbing impact on the population structure and its dynamics, particularly where pine is sparse on the landscape (Kullman & Öberg 2022b).

In one sense, the treeline ecotone and the upper boreal forest (*mountain taiga*) may be seen as a kind of a cultural landscape, since long coined by Sami reindeer hunting, which eventually transgressed into modern reindeer pastoralism (Kullman 2005a, 2016b; Eriksson et al. 2007; Josefsson et al. 2010; Rautio et al. 2016). In addition, over several past centuries, sedentary settlers have used subalpine plant cover resources, based on summer farms (Sw. *fäbodväsende*), for the purpose of livestock grazing, hay making and lichen harvesting (Josefsson et al. 2010; Kullman 2016). Presumably, the latter activities, largely discontinued after the 1940s, initially favored the abundance of the more fast-growing and disturbance tolerant mountain birch at the cost of pine, in particular (Kallio et al. 1971; Holtmeier 1974; Kullman 2017a, 2019b; Kullman & Öberg 2022a). In general, the treelines of all species, as narrowly defined here, is relatively little affected by human interference, referring the “Principle of Least Effort” (Shackleton & Prince 1992; Nygaard et al. 2022).

2. Method

Many explanations in the science of vegetation change only arise as a result of long-term sequential observations from the same fixed points in the landscape (e.g. Webb, Boyer & Turner 2010; Camarero et al. 2015; Lindenmayer et al. 2022). Field-based sustained ecological monitoring is needed to reduce the noise of short-term climatic and ecological disturbances, particularly since climate may eventually change (warmer or cooler) into the future (Gitzen et al. 2012; Sandvik & Odland 2014; Helmens et al. 2018; Helama et al. 2020). Accordingly, this study reports and analyzes arboreal changes within parts of a regional landscape-scale tree-line monitoring network of systematically distributed sites (c. 8000 km²), with elevational belt transect data over the treeline ecotone and extending back into the early 20th-century. Intermittent surveys have been carried out over the past five decades (Kullman 1979, 1981, 1986b, 2014a,b, 2017a; Kullman & Öberg 2009).

At a more local stand scale within a restricted mountain valley a system of 18 permanently marked observational plots (10 x10 m, 680-715 m a.s.l.), has been analyzed annually at the individual level (1972-2022) for pine demographic changes (Kullman 1993, 2007, 2014a,b, 2017a, 2018, 2019a). Each plot was centered on an old-growth pine tree, close to the treeline position of the early 20th century. These records are updated to 2022 by the present study.

In addition, the extent and character of arboreal change within the treeline ecotone are accomplished by rephotography of individual trees and surrounding local landscapes, from randomly distributed and permanently fixed points (Kullman 2014b, 2017a, 2019b), i.e. a kind of permanent plots (Bullock & Turner 2010; Townsend Peterson et al. 2022). This is a useful approach to provide holistic, unbiased and direct semi-quantitative and time-specific evidence of changes on individual and landscape scales, with an ability to account for unforeseen changes and impacts, e.g. mortality causes (Vale & Vale 1994; Webb, Boyer & Turner 2010; Kullman & Öberg 2022a, b). These records complement the landscape-scale records obtained by the permanent plots and other approaches.

Annual tests of pine seed viability (1974-2022) were performed on a composite sample from old-established trees within the 18 permanent plots located to the treeline ecotone (Kullman 2017a, updated). Cones were collected in the late winter each year. The laboratory testing procedure is described in Kullman (1984).

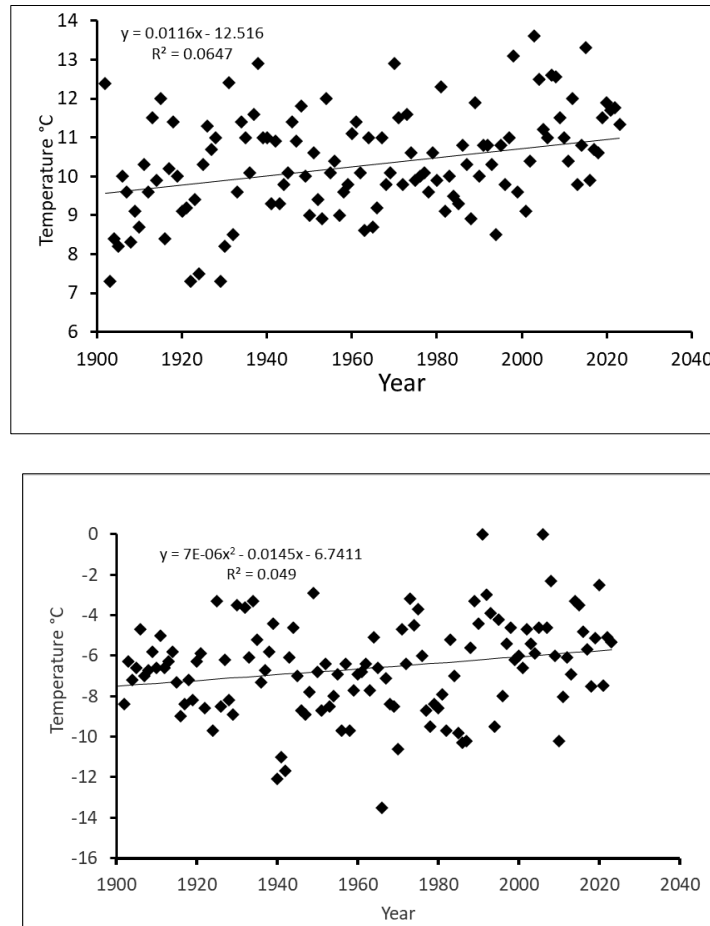
Altitudinal records are carried out by a GPS navigator (Garmin 60CS), with a precision of ± 5 m. Reported radiocarbon datings of megafossil wood were conducted by Beta Analytic Inc, Miami (USA). Calibration to calendar years are given by the intercept method (Reimer et al. 2009).

2.1. Recent climate and climate change

The present study focuses primarily on ecotonal treeline change during the past 100 years. As a background, instrumental temperature records (1901-2023) from an official and regionally representative weather station in the study area (Storlien/Visjövalen, 642 m a.s.l.) are provided for the summer and winter periods; June- August, December-February, respectively. (Fig. 5). Summer displays secular warming by 1.4 °C and winters by 1.9 °C. Both variables show strong inter-annual variation, not statistically, but ecologically significant. Notably, since about the year of 2000, few extremely cold winters have occurred. This pattern coincides with a cluster of warm summers, largely resembling or somewhat exceeding the high levels prevailing during the 1930s.

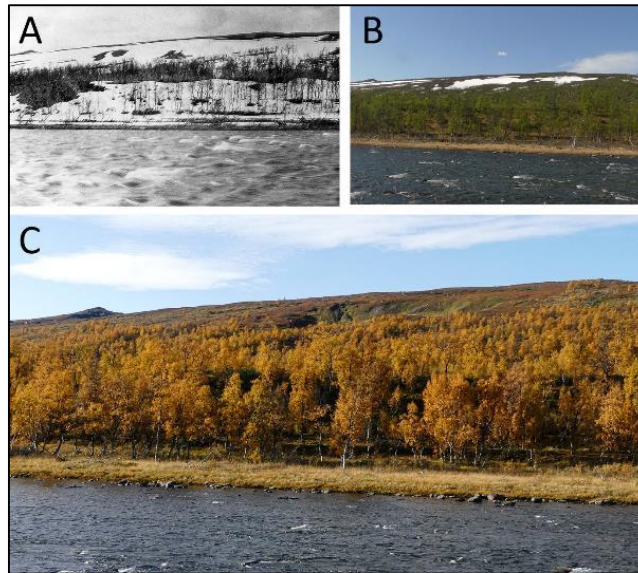
As stated by Smith (1920), periodical treeline life history phenomena provide particularly good indicators of the status of the subalpine/alpine plant cover in general. Accordingly, local phenological studies evidence earlier birch leafing/snow melt (two-three weeks), and delayed autumn discoloration/leaf fall (two-three weeks) over the past century (Kullman & Öberg 2022a). This implies that the growth period, bracketed by birch leafing and defoliation, has become at least one month longer during the past 100 years (Figs. 6-8). The pivotal role of growth season length in

connection with treeline dynamics has been particularly stressed by Hansson et al. (2023). Vanishing permafrost (cf. Kullman 2017a) is another indication of ameliorated ground temperature conditions in general, to the favor of high-elevation tree growth and plant performance in general (Kullman 2007, 2021g). An additional feature of secular climate change is provided by the performance of the small glacier (c. 0.2 ha) “Storsylglaciären” in the present study area. From a Holocene near-maximum by the end of the Little Ice Age, the glacier has shrunk substantially, and presumably, it may vanish within a few years (Fig. 9).



Source: Swedish Meteorological and Hydrological Institute

Figure 5 Mean annual regional air temperatures recorded at Storlien/Storvallen meteorological Station 1901-2023. Upper. June-August. Lower. December-February



Photos: A. 1914-06-11 (Harry Smith). B. 2023-06-12. C. 2023-09-23

Figure 6 Birch leafing and snow phenology over the past 100 years. A. By the early 20th century, just prior to the onset of the modern warming phase, snow cover in the lower subalpine birch belt persisted patchily well into late June, accompanied with relatively late birch leafing (Smith 1920). B. Annual monitoring since 1977, has provided a view of much earlier birch leafing and snow melt, with virtually the same landscape appearance as the one depicted here. This implies an early-season phenological extension of the growth period by two-three weeks. C. During the concerned period of time, autumn coloration has been delayed by 2-3 weeks. Mt. Lillulvåfjället (province of Jämtland), east-facing slope, from 740 m a.s.l.



Photos: A. 1997-07-15. B. 2023-07-13.

Figure 7 Matched pair of photographs showing earlier subalpine snowmelt today relative to the late 1990s. Mt. Storsnasen (province of Jämtland), 710 m a.s.l. The age structure of the birch forest grove in this minor slope indicates that tree growth was initiated by the 1930-1940s



Photo: 2023-09-22

Figure 8 The same subalpine birch stand as depicted in Figure 7, showing leaf discoloration 2-3 weeks later than in the early 20th century

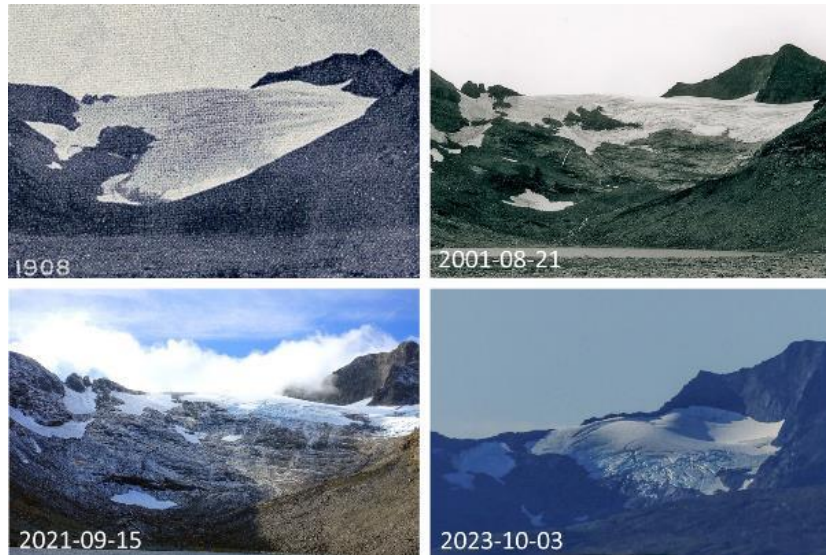


Figure 9 Photographic record of the continual recession of (1908-2023) of the glacier “Storsylglaciären” in the Sylarna Massif (highest summit 1761 m a.s.l.). During the past few years, a crack in the ice (*Bergschrund*) has manifested close to the upper margin and a deep depression has become evident further downslope. The lower front is currently actively disintegrating

3. Results

3.1. Recent regional pine treeline dynamics

An observation study of elevational pine treeline (definition as above) change was conducted at 60 systematically distributed sites over an area of about 8000 km² in the southern Swedish Scandes. The interval 1915 to 2016 was embraced by this analysis (Kullman 2017a). The average rise was about 80 m in altitude, with large inter-site variability and no case of treeline retraction. The largest upshift was 225 altitudinal meters (Fig. 2). The latter maximum figure is virtually the same as obtained for treelines of other common species, *Picea abies* and *Betula pubescens* ssp. *czerepanovii* along the entire Swedish Scandes (Kullman 2021c), which argues for a common background of climate change as the ultimate cause.

In order to add more detail, a study focusing on regional pine treeline change (1915-1975) in the same area of the southern Swedish Scandes highlighted that a majority of new and elevated treeline markers became established during the period 1946-1950 (Kullman 1981). This pattern somewhat post-dates the thermal peak by the late 1930s and virtually coincides with the highest peak of pine radial growth of the prior >300 years (Kullman 1987; Linderholm 2002; Linderholm et al. 2014). These circumstances further speak in favor of a regionally common external cause, obviously climate warming and a longer growth period.

Treeline rise of *Betula* and *Picea* was quite rapid following the warm 1930s, but has virtually stagnated during the past few decades (Kullman & Öberg 2009; Kullman 2021d), while pine has performed relatively more actively and progressively up to the present day (Kullman 2021b, c). Evergreen pine appears to have specifically benefitted from the substantially prolonged growing season (cf. Holtmeier 1974; Oksanen & Virtanen 1995). This difference may represent species-specific regeneration modes, with birch and spruce largely relying on vegetative regeneration. That option short-cuts regeneration stages and allows more swift responses to climate improvement, based on a bank of old-established krummholz individuals prevailing above the former treeline. This source is currently largely depleted since the majority of such specimens has already attained tree-size. At the same time seed regeneration of these two species has virtually ceased at and beyond their respective treelines (Kullman 2021d, e).

In contrast to spruce and birch (cf. Öberg & Kullman 2011), pine virtually lacks the ability of near “eternal” individual life by layering. Therefore, treeline rise is dependent upon a protracted process of establishment, requiring favorable climatic conditions during a sequence of years. This circumstance tends to delay its elevational treeline response to the ever-changing mountain climate with its particularly large and haphazard inter-annual variability (Hustich 1947; Pohtila 1980; Massa 1988; Alexandersson & Eriksson 1989). In addition, the light-demanding pine, with its treeline generally located in the lower birch forest belt, appears to have been initially hampered by the relatively rapid

phenotypical responses of preestablished old-growth mountain birches (Öberg & Kullman 2012). Emerging dense and durable birch stands (Kullman 1976), restricted initially the establishment and growth of pine, and still largely hinders pine to spread and attain its potential climate limit and abundance on the subalpine landscape (Blüthgen 1960; Kullman 2021b). Nevertheless, solitary pine trees have recently expanded more than 10 km into birch-dominated mountain valleys (Kullman 2021b), where it has established in open habitats, such as mires and river-side escarpments with an unstable and sparse vegetation cover (Figs. 10-12). In particular, the latter habitat type appears as an important landscape corridor, displaying records of treeline movements, both early advance and delayed retraction, in response to climate improvement and deterioration, respectively (Kullman 2016a, 2017c; Kullman & Öberg 2018). Further advancement into this valley is heralded by the appearance of young, healthy and fast-growing pine saplings further 6 km to the south of the pine depicted by Figure 10. Pine progression is favored by the ability of saplings to recover from more or less total defoliation by frost desiccation (Fig.15).



Photos: A. 2013-09-28. B. 2023-08-18

Figure 10 A. Young pine tree, which has extended the treeline 12 km deeper into the birch-dominated Handölan Valley since the early 1970s. It germinated by the late 1930s or early 1940s. Mt. Tjallingklumpen (Province of Jämtland), 800 m a.s.l. Since 2013, the pine has grown by size and foliation



Photo: 2023-09-18

Figure 11 Solitary pine tree growing isolated in sparse birch forest (840 m a.s.l.), representing treeline rise by 130 m over the past 100 years. Mt. Laptentjakke (Province of Jämtland)



Figure 12 Pine treeline rise by 140 altitudinal meters since the early 20th century, finished by the growth of a tiny sapling (830 m a.s.l.) to tree-size over the period 2007-2023. The time lapse photo series displays a remarkable recovery potential following severe needle mortality in response to winter desiccation. The site is a south-facing river escarpment of a west-east trending tributary (Norder-Tvärån) to the Handölan River

Apparently, lack of seed and competition with birch, may be important constraints to more widespread and abundant establishment of pine at higher elevations (cf. Shiyatov 2003; Juntunen & Neuvonen 2006; Holtmeier 2009; Kullman 2010, 2019b; 2021b; Kharuk et al. 2022).

Nevertheless, the balance of circumstances outlined above may imply that much of the current birch forest belt may be potential pine or mixed pine/birch forest and will gradually transform into that direction, given that the current warming phase prevails (Kullman 2021b).

Notably, the present results display a geographical pattern, with the extent of treeline rise increasing significantly, with large inter-site variations, towards the south in the study region (Fig. 13). Initiated in the 1930s, the process of upshift prevailed consistently up to the present day. In the southernmost part of the study region, with its relatively sparse and narrow birch belt, the new and higher pine treeline has locally reached the same elevation as the treeline of the mountain birch, and even “leap-frogged” over it (Kullman 2017a). Continuation and geographical extension of that process northwards along the entire Scandes implies that the treeline landscape may be on the brink of transformation into a biogeographic zonation pattern resembling the state prevailing by the warm and dry early Holocene. During that period the treeline ecotone was patchily positioned substantially higher (500-700 altitudinal meters) than today and displayed a mixture of pine, birch, spruce and larch. Summer temperatures are inferred to have been at least 3 °C higher than at present (Kullman 2013; Kullman & Öberg 2015, 2020; Paus 2021; Paus & Haugland 2016). This optional course of future climate and ecological change is discussed in more general form by Macias-Fauria et al. (2012).

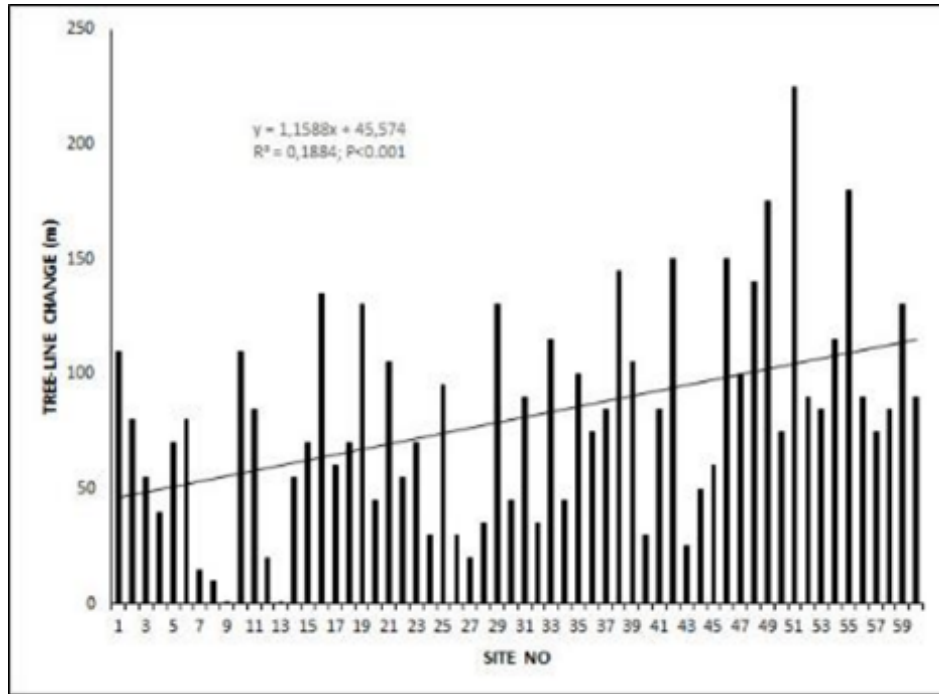
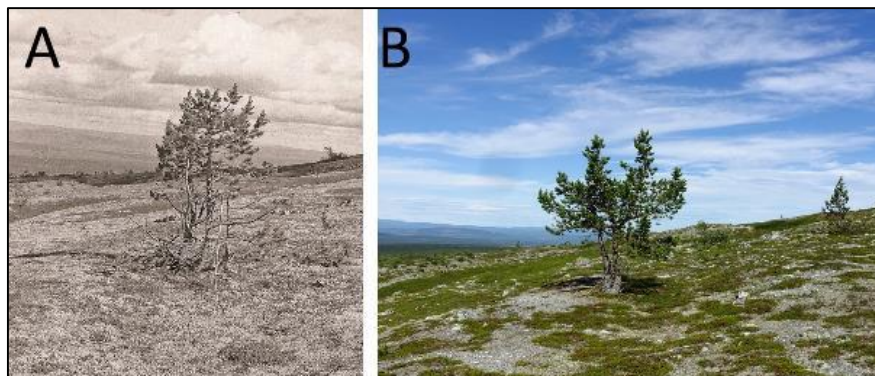


Figure 13 Extent of pine treeline upshift (1915-2016), displaying a geographically rising trend, 230 km north to south in the study region. Notably, the inter-site variation is quite large. Site numbers refer to Kullman (2017, Table 1)

Reindeer grazing and trampling are aspects of particular interest in connection with recent treeline change (Fig. 14). Semi-domestic reindeer herds have increased substantially in the study area over the past 100 years, coincident with climate warming and treeline rise by 200 altitudinal meters or more (Virtanen et al. 2003; Kullman & Öberg 2009; Kullman 2017a). Low-alpine heaths were strongly overgrazed and denuded during the first decades of the 20th century, which prompted deliberate radical decimation of the herds (Smith 1920). In addition, during the late 19th- and early 20th century, low-alpine lichen grounds were extensively utilized by the settled farming population for gathering of winter lichen fodder for the livestock. This combined use is reported to have caused substantial devastation and a perceptible change of the landscape appearance (Kullman 1975, 1979).

Thus, already by the onset of the modern climate amelioration more than 100 years ago, exposed and snow-poor low alpine heaths may have displayed a sparse state, facilitating pine establishment and early growth later on. These circumstances raise the question as to the causality regarding the drivers of treeline change in general and concerning pine in particular (climate versus reindeer action), a complex issue discussed more in detail below.



Photos: A. 1974-08-22. B. 2017-08-11

Figure 14 A. Pine tree within the treeline ecotone (940 m a.l.s.), growing in dense carpets of reindeer lichens (*Cladonia* spp. and *Flavocetraria nivalis*). B. After the mid-1970s, semi-domesticated reindeer started to utilize this area, which substantially reduced the lichen cover and favoured expansion of *Empetrum*-clones. Scattered new pine trees have emerged on the landscape. Source: Kullman (1989a)

It is increasingly acknowledged, although counter-intuitively, that modest action by reindeer may have a positive impact on pine and birch regeneration/growth and consequent treeline rise, by reducing the barrier to establishment executed by dense carpets of reindeer lichens and by increasing nutrient cycling and soil temperature (cf. Moir & Huckaby 1994; Sedia & Ehrenfeld 2003; Cairns & Moen 2004; Raunio et al. 2008; Tømmervik et al. 2004, 2009). This option contrasts with the view purported e.g. by Van Bogaert et al. (2011), claiming an overall negative impact of reindeer on tree seedling survival in the treeline ecotone, although critically discussed on data from virtually the same area (Kullman 2021f). Strictly locally, however, where free-roaming reindeer are restricted and concentrated by fences, negative effect on tree establishment may occur (e.g. Höglund & Eriksson 1973; Kullman 2017a).

Since the abundance of terricolous lichens in the low-alpine heaths with a thin snow cover, increases towards the south in the study area, in accord with rising climatic continentality and decreasing soil fertility (Raab & Vedin 1995), it seems plausible that the pine-promoting impact of reindeer action has been particularly large in this region. Hereabouts, lichen heaths were a prominent feature of the treeline landscape by the early 20th century, followed by recession up to the present day (Sernander 1899; Samuelsson 1917; Lundqvist 1944, 1951; Allard et al. 1998; Kullman 1989a, 1997), coincident with relatively large treeline upshifts (Fig. 13). This aspect is particularly evident at sites with an initially sparse birch forest belt, where pine trees exclusively grow on exposed and snow-poor crests, where intensive reindeer grazing takes place in winter and spring, which has reduced the lichen cover, as described by Allard et al. 1998 (Figs.15-17). In these situations, birch is conspicuously receding and giving way to pine (Fig. 18).



Photo: 2013-07-24

Figure 15 Scattered pine trees, which became established in the 1930s and later. They have surpassed the birch belt and are on the brink of forming a new sparse subalpine pine belt above. Mt. Ö. Barfredhågna (Province of Dalarna), 870-880 m a.s.l. Source: Kullman (2014b)



Photo: 2006-05-01

Figure 16 A characteristic feature of the ecology of treeline pine and is its association with a sparse snow cover, both in time and space. Young pines manage to establish on wind-exposed sites in the upper part of the treeline ecotone, despite (or thanks to) the attraction to reindeer, as here evident from abundant footprints in the snow. Mt. Stådjan (Province of Dalarna), 975 m a.s.l.



Photo: 2022-09-14

Figure 17 Characteristic appearance of ground cover where pine has established abundantly during the past few decades. As a rule, variable proportions of *Empetrum hermaphroditum*, *Calluna vulgaris* and *Betula nana* constitute the sparse dwarf-scrub matrix. Interspersed patches with fragments of lichen thalli indicate a former denser reindeer lichen cover, reduced by reindeer action. Typically, pine avoids the highest and most exposed positions in the micro-topography. Mt. Storsnasen, 670 m a.s.l.



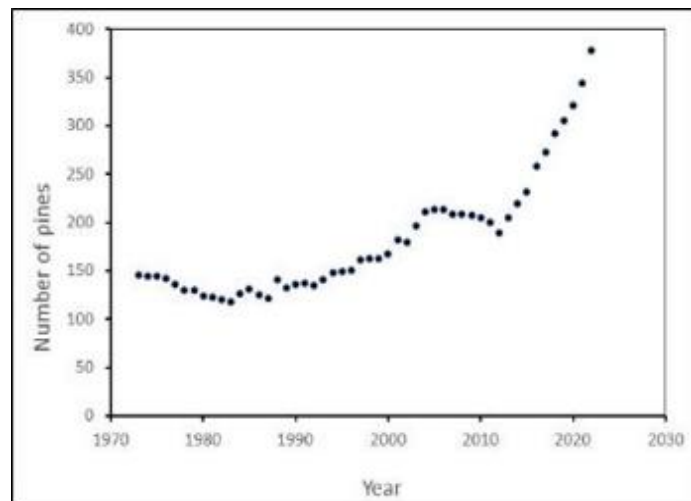
Photo: 2023-08-12

Figure 18 In some districts with a poor and early melting snow cover, pine progression is paralleled and possibly facilitated by birch regression Mt. Barfredhågna 860 m a.s.l

3.2. Local stand-level treeline processes

3.2.1. Permanent plots

During the period 1973-2023, demographic processes were monitored annually within a system of permanent plots located to the pine treeline ecotone in the Handölan Valley, province of Jämtland (Kullman 1983, 1993, 2007, 2014a; Kullman & Öberg 2022). In addition, some nearby outlier forest groves have been investigated with respect to static age structures (Kullman 1986a, 2005c; Kullman & Öberg 2021), showing a first distinct peak of regeneration by the mid-20th century, which is somewhat later than the warming peak by the late 1930s. This kind of delayed response may rely on ground-cover dynamics (cf. Zackrisson et al. 1995), and the need for a relatively long period of coincident favorable summer and winter conditions to achieve successful pine regeneration and growth to tree-size. The latter preconditions, in particular the winter period, were not present for some decades after the 1930s (Fig. 5).



Source: Kullman & Öberg (2022a)

Figure 19 Evolution of pine demography, as number of living pines, annually surveyed within 18 permanent plots (10x10 m) over the period 1973-2022

Initially, during a period of relatively cold winters (early 1970s to late 1980s), the density of young saplings at and above the treeline was low and many individuals were in a poor condition, following repeated winter desiccation injuries (Kullman 1981, 1983, 2014a). Accordingly, the total number of living specimens decreased gradually up to a nadir by the late 1980s. Thereafter, a steady rise has taken place, mainly a consequence of increased recruitment and insignificant winter mortality (desiccation) (Kullman 2014a). In particular, from 2010 and onwards, the composite population pine and seed viability have increased prolifically (Figs. 19, 20). This distinct phase of pine progression in the treeline ecotone seems to rely ultimately on a period of relatively high summer and winter temperatures, which may have been conducive to recruitment, growth and survival.

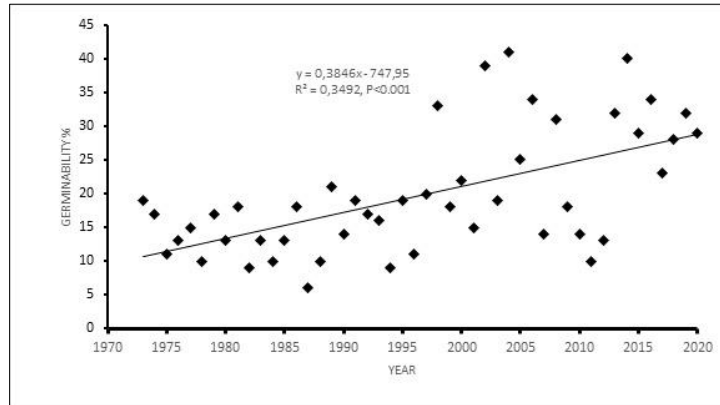
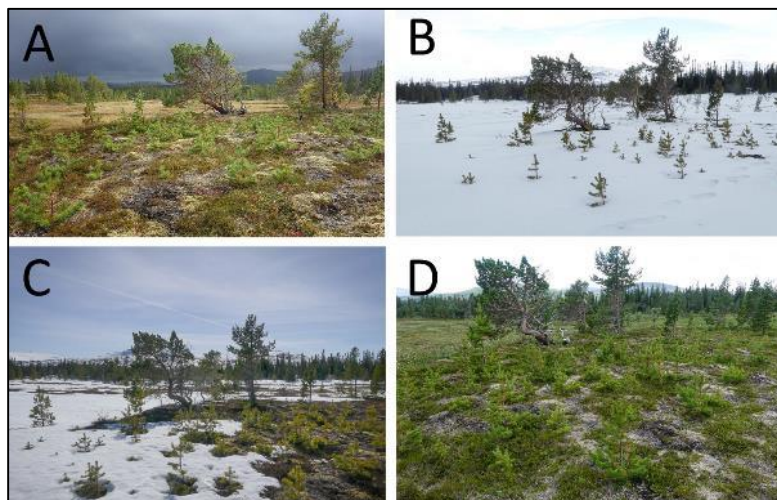


Figure 20 Annual records (1973-2022) of pine seed viability from pines growing in the treeline ecotone. Source: Kullman & Öberg (2022a)

Below, we highlight, by representative images, this quite remarkable happening, which may have a bearing on the future evolution of the treeline ecotone, given that climate warming continues unabated. This option is a subject of continuous monitoring. Caution is needed however, since a majority of extant saplings is still protruding just above the snow surface. In that state, they may face extensive extirpation risk due to short episodes of winter desiccation and cold-conditioned fine root mortality (Jalkanen 1985; Kullman 2007; Camarero et al. 2023).



Photos: A. 2022-09-29. B. 2023-04-11. C. 2023-04-18. D. 2023-07-11

Figure 21 Prolific pine regeneration at an exposed sites within the treeline ecotone (680 m a. s.l.), where dense tree stands were gradually exterminated during the Little Ice Age. The tree-sized and “knee-formed” mature pine in A germinated in the late 17th century and attained a height of >2 m by the mid-20th century. Winter views of the stand are depicted in B and C. D. The sapling population passed the winter hazard (2022/2023) without needle desiccation and produced long terminal shoots in 2023. The ground cover is affected by cryoturbation and is dominated by *Calluna vulgaris*, *Empetrum hermaphroditum*, *Racomitrium lanuginosum* and fragments of reindeer lichen thalli. Mt. Storsnasen (Province of Jämtland)

The extent of recent upsurge in pine reproduction in the treeline ecotone is conspicuous and has never been reported at the same density, growth and vitality in Fennoscandian treeline literature (cf. Kallio et al. 1971). Predominantly, dense sapling populations (30 000-50 000 individuals/ha) have emerged centrifugally in the near-vicinity of old-growth treeline pines during the past 15-20 years (Figs. 21-23) In many cases, these putative mother trees were the last survivors and seed-bearers of extensive stands which demised during the Little Ice Age (Fig. 24) (Kullman 1987; Kullman & Öberg 2021).



Photo: 2022-11-11.

Figure 22 The forest stand in the background is largely the result of the 20th century climatic amelioration. A prior stand of full-size trees here prior to the Little Ice Age, as evidenced by scattered radiocarbon-dated stumps in the foreground. During the past 15 years, massive pine regeneration has reclaimed the area lost during the Little Ice Age. Currently, the ground cover is dominated by *Calluna vulgaris*. Mt. Storsnasen (Province of Jämtland), 670 m a.s.l.
Source: Kullman & Öberg (2021)



Photo: 2023-06-27

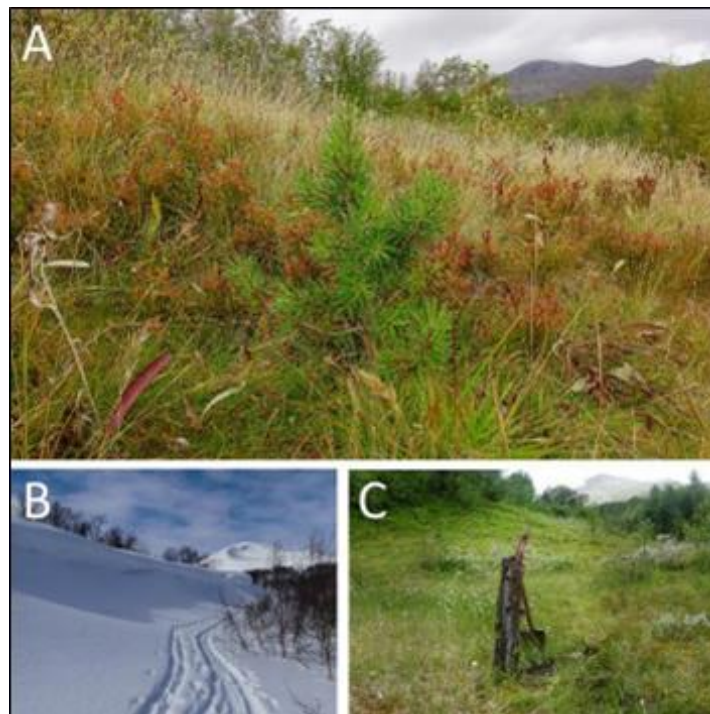
Figure 23 Treeline pine established during the warm 1930s. Over the past 10-15 years it has continuously produced dense offspring of still healthy saplings. Hereabouts, pine regains territory held by the Medieval Climate Anomaly and lost during the subsequent Little Ice Age. Mt. Täljstensvalen (Province of Jämtland), 735 m a.s.l



Photo: 2023-06-15.

Figure 24 By the early 20th century and until 2005, this tree, which became established in the mid-17th century, manifested the pine treeline in the Handölan Valley, 705 m a.s.l. It was downed by a winter storm in 2005. Shortly prior to that, it produced offspring, some of which are more than 2 m tall today. Source: Kullman 1987; Kullman & Öberg 2021

A new and striking phenomenon is that scattered pine “long-fliers” are currently becoming established in subalpine and alpine snow-patch vegetation (Kullman & Öberg 2022a) (Fig. 25). However, no altitudinal rise of closed pine forest is recorded for the past 100 years (Kullman 2014a,b, 2016a, 2021b), although old-established outpost stands have densified, particularly in recent past decades. In the southernmost Swedish Scandes, pine progression is paralleled and facilitated by birch demise (Fig. 18).

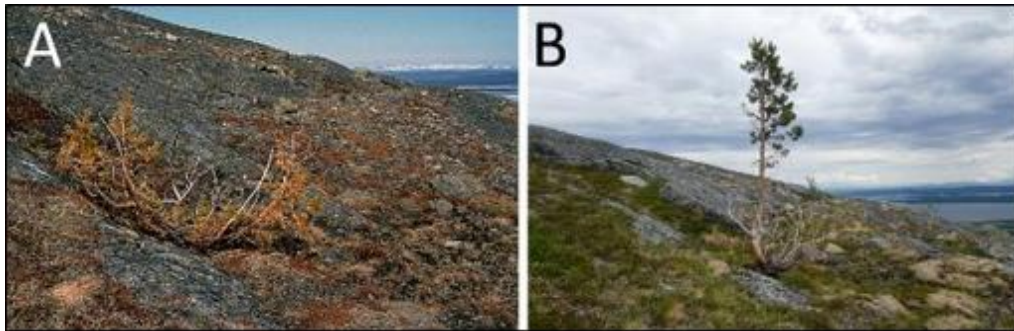


Photos: A. 2017-09-12. B. 2023-04-04. C. 2023-07-29.

Figure 25 A. Pine sapling recently established in a grass-dominated (*Avenella flexuosa*) snow-bed site with ongoing birch forest encroachment from the left, in the wake of earlier annual snowmelt. B. The same site as it appears in the winter, with a huge snow-accumulation. C. This particular site supported growth of tree-sized pines prior to the mid-Holocene Neoglaciatio. Evidence is provided by a megafossil pine trunk (up-raised), radiocarbon dated 5350 cal. a BP. Mt. Norder-Tväråklumpen (Province of Jämtland), 705 m a.s.l

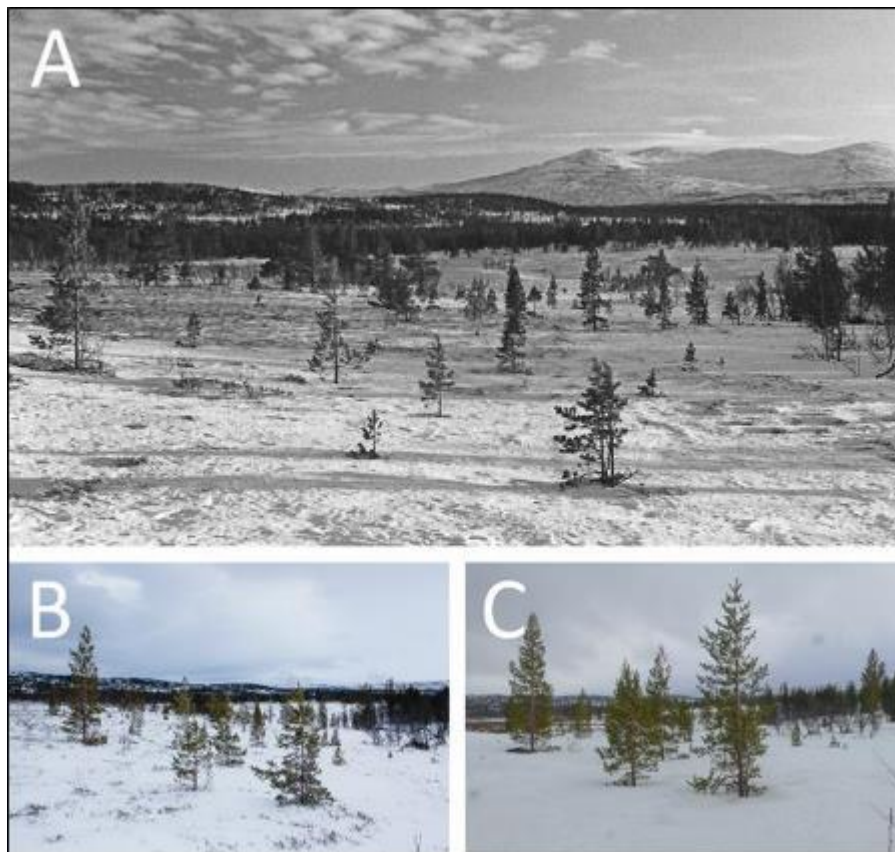
3.2.2. Rephotography

Rephotography of individual pines and landscape views provides factual evidence of individual growth and population progression over the past few decades. Below, some cases are displayed (Figs. 26-30). The photos speak for themselves and provide a general pattern of growth progression, individual recovery and prolific regeneration over the past 50 years and shorter. That pattern is broadly reflected also in the age structure analyses of an extant treeline stand (Figs. 31-33) and others in the study area (Kullman 1986a, 2005c).



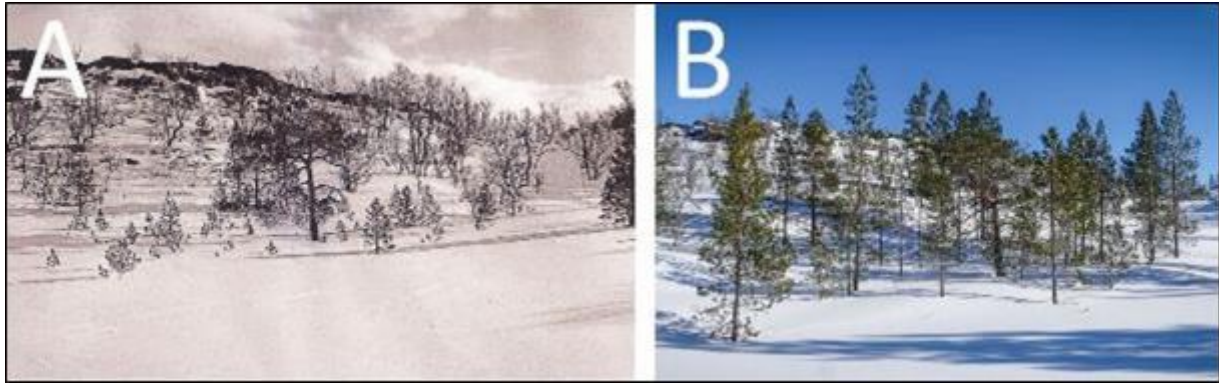
Photos: A. 1999-05-19. B. 2023-06-27.

Figure 26 A. Exposed treeline pine sapling in a miserable condition, following some recent years of severe stress by winter desiccation. B. A remarkable recovery has taken place up to the present day, reasonable a consequence of milder winters. Mt. Täljstensvalen (Province of Jämtland), 740 m a.s.l.



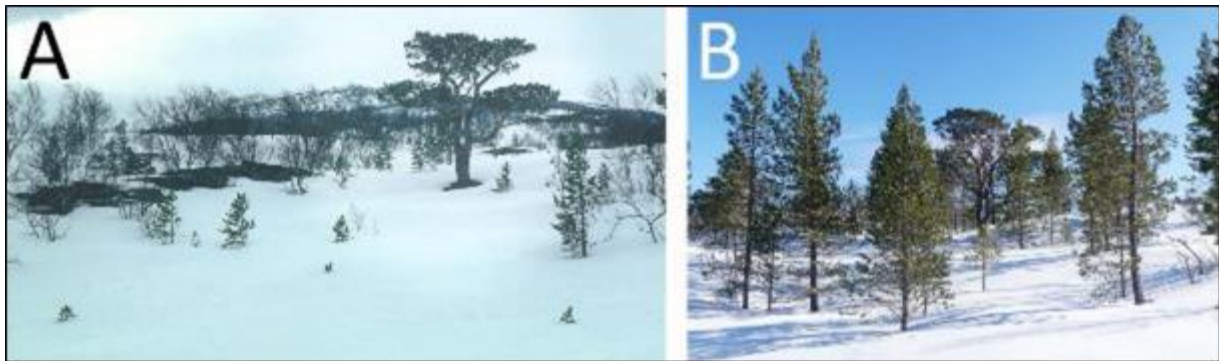
Photos: A. 2004-03-09. B. 2013-01-29. C. 2023-04-13

Figure 27 Successive landscape transformation by establishment and growth of pines on a previously more open subalpine mire (660 m a.s.l.). Mt. Storsnasen (Province of Jämtland)



Photos: A. 1986-04-04. B. 2023-03-05.

Figure 28 A. Solitary old-growth pine, surrounded by youngish offspring. B. Over the past 37 years, a distinct tree stand has emerged. Mt. Storsnasen (Province of Jämtland), 645 m a.s.l.



Photos: A. 1985-04-21. B. 2023-03-05

Figure 29 View of the lower pine treeline ecotone, 645 m a.s.l., with an older parent pine and an associated sparse sapling cohort. Up to the present day, the former saplings have turned into full-size and vigorously growing trees



Photo: 2023-06-27

Figure 30 Rapidly growing pine sapling, established within the remains of a large pine that died during the Little Ice Age, when this site was above the local treeline. Between 2015 and 2023, this pine grew in height from 0.3 to 1.1 m. Mt. Täljstensvalen, 725 m a.s.l.



Photos: A. 1914-04-12 (Harry Smith). B. 2023-04-07

Figure 31 A. The southernmost pine outlier stand in a river-side escarpment by the Handölan river valley, 690-700 m a.s.l. B. The same stand as it appears today. Photo:.. Some of the veterans are still standing and discernible, while others are downed in recent years. Overall, the population has increased centrifugally in numbers and vitality during the past 100 years, as evidenced by the age structure analysis. The emergent regeneration pattern broadly concurs with other marginal pine stands in the region (Kullman 1986, 2005c; Kullman & Öberg 2021), indicative of climate change as a synchronizing agent. The internal tree spacing structure and static age structure of the stand appear from Figures 32 and 33, respectively



Photos: 2023-04-07

Figure 32 A. Internal stand structure, showing young trees established during the past 100 years and some recently downed veteran pines. B. One of the oldest living trees germinated in the 1720s. The branching structure indicates that it initially developed in a more open stand than at the present

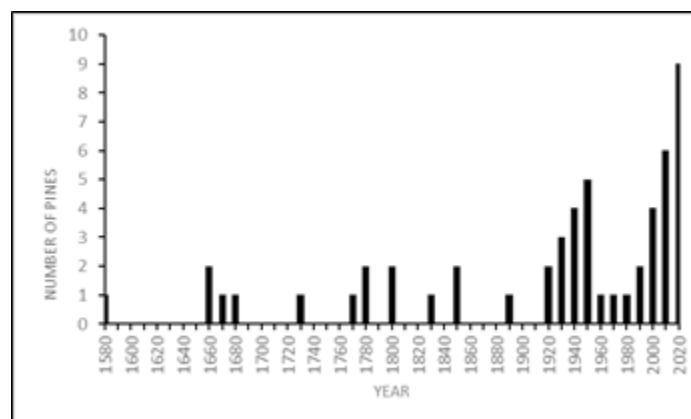


Figure 33 Static age structure of the pine stand depicted in Figures 31 & 32. The oldest tree dates to the 1580s, probably a progenitor of the extant stand, followed by a regeneration hiatus until the 1660s. A few pines became established during the 18th and 19th centuries, while the main population growth occurred during the 20th century (1920s and onwards), broadly coincident with the current warming phase

4. Discussion

A distinguished Swedish ecologist stated that “the aim of ecology is to see what happens in nature” (Sjörs 1979). In an era of climate and ecological unrest, computer modeling and remote sensing, ground-truth time series observations still have role to play in assessing and understanding vegetation dynamics. Successful and conclusive studies in that respect need to rely on “life-time” commitments (Franklin 1987)), particularly when organisms with a long life expectancy (e.g. trees) are concerned. That notion is reflected by the preponderance of the name *Kullman* in the list of references.

This paper presents factual *in situ* evidence, gathered by different researchers during more than 100 years of ongoing pine (*Pinus sylvestris* L.) treeline adjustments on different spatial scales to a new and warmer climate in the Swedish Scandes.

The main context of the present narrative is maximum treeline rise (> 200 altitudinal meters) by prevailing treeline species; mountain birch (*Betula pubescens ssp. czerepanovii*), Norway spruce (*Picea abies*) and Scots pine (*Pinus sylvestris*), in obvious response to secular warming (Kullman & Öberg 2009; Kullman 2016b, 2017a, 2021c.). The particular focus here is on the pine treeline ecotone and relates to the fact that this species displays the most consistent trend of recent treeline rise (Kullman & Öberg 2009, Kullman 2017a). Moreover, pine was the main constituent of the upper treeline ecotone during the early Holocene temperature optimum, reaching positions 500-700 m above current treelines, equally high as the uppermost contemporary birches (Kullman 2013, 2017b,c, Kullman & Öberg 2020). As described in this paper, an analogous situation appears to be pending in the southernmost Swedish Scandes, where pines have recently leap-frogged over the receding birch treeline, possibly forming a new upper treeline and treeline ecotone. An analogous shift within the treeline ecotone, in species dominance and a novel ecosystem, is witnessed in western North-America in response to climate warming over the past 100 years (Millar et al. 2015; Smithers et al. 2018).

Further north in the study region of the southern Swedish Scandes, where the climate is more maritime and snow-rich, the subalpine birch forest belt still largely holds its position, while scattered reproducing pine trees and small stands are penetrating into open habitats, e.g. mires, river-side escarpments and subalpine snow patch sites, far above and beyond the treelines by the early and mid- 20th century.

A main obstacle to further pine stand expansion appears to be competition for light with the extant dense subalpine birch forest (Blüthgen 1960; Holtmeier & Broll 2011; Hofgaard et al. 2012; Kullman 2015, 2016a, 2019b, 2021b). For the time being, the birch forest is here locally getting denser, in particular where tree growth was previously constrained by abundance of late-melting snow. Hereabouts, birch is seeding in, giving rise to fastgrowing shrubs and trees. At the same time, scattered pine seedlings have, at a low frequency and abundance started to use the same niche (Kullman 2021h). This process appears as a reversion to the situation prevailing by the relatively warm and snow-poor early Holocene. In a potentially warmer future, with less snow accumulation and earlier melt-out, pine may eventually outpace the dominant mountain birch and form a new and different subalpine belt (Kullman 2017a, 2019b; Kullman & Öberg 2021) as modeled by some authors (Kellomäki et al, 1997; Sormunen et al. 2011). That would be the largest regional-scale biogeographic transformation since the onset of the Neoglacial 6000-4000 years ago, which, at the cost of prevailing pine forests, paved the way for subalpine birch forest expansion and the regional establishment of the praealpine spruce forest below (Segerström & von Stedingk 2003; Bergman et al. 2005; Larsson et al. 2012). As depicted in this study, the most significant indication in that direction is found in the pine treeline ecotone, where extensive pine dieback and regeneration failure took place during the Little Ice Age (Kullman 1987, 2015, 2019b). Today, these sites display an unprecedented abundance of healthy and fast-growing saplings, concomitant with a significant rise in pine seed viability and a low incidence of winter mortality. Typically, this progressive phenomenon is most blatant in the vicinity of old parent trees (Holtmeier 2009; Hofgaard et al. 2013; Kullman 2015) where densities of 30 000-50 000 saplings/ha are recorded to have established during the past few years (Kullman & Öberg 2021). According to Kellomäki et al. (1997), a figure of 3000-4000 is suggested for satisfactory regeneration at the treeline. Any elevational advancement of pine stands is likely to be sluggish, since spread has to proceed upslope, in contrast to the early Holocene, when swiftly deglaciated summit areas provided ground and source for founder populations, which could enable quite rapid spread of trees downslope by wind and water (Kullman 2002b; Kullman & Öberg 2015).

Until quite recently, the incidence of winter injuries and individual mortality took a large toll of most sapling cohorts (Kullman 1983, 2007; Holtmeier 2009). This kind of winter stress has virtually ceased to manifest during the past few decades, thereby highlighting the importance of winter conditions as drivers of treeline dynamics (Kharuk et al. 2005; Kullman 2007, 2014a, 2021b; Hofgaard et al. 2012; Hagedorn et al. 2014; Kullman & Öberg 2021, 2022a; Grigoriev et al. 2022).

In parallel to climate warming over the past 100 years more intense reindeer lichen grazing, in combination with enhanced summer drought (Kullman 2017a), may have contributed to pine expansion, by reducing the "lichen barrier" to pine establishment and early growth (cf. Sedia & Ehrenfelt 2003; Tømmervik et al. 2009), At the same time, birch tree cover has demised at exposed and snow-poor sites.

Overall, the present results line up with northern Hemisphere models, indicating substantial forest-tundra progression in the future, provided that current climate trends prevail (Edwards et al. 2005; Holtmeir 2009; Macias-Fauria et al. 2017; Svenning & Sandel 2013; Lauprecht et al. 2018; Liu et al. 2021). However, this option seems unpredictable, since most climate models (IPCC 2021) do not convincingly account for past temperatures on longer and shorter time-scales in the past (cf. Vinos 2023). In addition, history has taught us that one or a few single cold and snow-poor winters may extirpate arboreal structure, accumulated over prior favourable years (Kullman 1989b).

5. Conclusion

In response to climate warming over the past 100 years, the alpine Scots pine (*Pinus sylvestris*) treeline ecotone in the Swedish Scandes is progressing with respect to elevation and density. To a large extent, this process has the character of reclamation of distributional space lost during the latest cold-climate epoch, the so-called Little Ice Age (c. AD 1300-1850). Subsequently, the pine treeline has raised by a maximum of slightly more than 200 altitudinal meters in close accord with recorded climate warming. In particular during the past 10-15 years of consistent high temperatures, sapling cohorts with an unprecedented density have emerged in the treeline ecotone. This course of change is accomplished by increased seed viability and virtual lack of winter sapling mortality. Pine is currently penetrating deep into the prevailing subalpine birch (*Betula pubescens* ssp. *czerepanovii*) forest belt, and locally even "leap-frogging" over it. Given that the current course of climate evolution continues unabated, pine may take over the role as the predominant tree species close to the alpine tundra. This pending situation would represent the most distinct biogeographic transformation of some past millennia. In a regional societal perspective, such a putative course of change is largely beneficial; increased forest productivity and plant species diversity. The prevailing landscape evolution should be monitored *in situ* during coming years and decades. A pertinent baseline is offered by the research referred to in this paper.

Compliance with ethical standards

Disclosure of conflict of interest

No conflict of interest to be disclosed.

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