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A Modern "Micro-Ice Age": Implications for Treeline Ecotonal Climate Change Ecology

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ABSTRACT

In this study we focus primarily on transient ecological responses of the treeline ecotone to a break (~1940s-1980s) admidst the general climate warming of the past 100 years. The study concerns the southern Swedish Scandes and draws on rephotography of individual trees and groups of trees, systematically distributed along permanent elevational transects. The present results comprise a period of general climate cooling and geoecological destabilization, reported from different parts of the northern hemisphere. This course of change culminated during the 1980s, when winter temperatures in northern Sweden were 3-4 °C lower than the mean of the 1930s. For example, permafrost expansion, slow-down of glacier retreat, harvest/reforestation failure and faunal contractions belong to the picture of widespread periglaciation. Characteristic arboreal features in the Scandes and adjacent regions included canopy dieback, defoliation, premature mortality of individual stems, reduced tree regeneration and local minor retreat of the alpine treeline (boreal tree species). These circumstances, following on the relatively warm first decades of the 20th century, sustain the importance of climate forcing for the life and dynamics of the treeline ecotone, which is here proven to respond swiftly (position, structure and species composition) to modest short-term climatic fluctuations. The crucial importance of individual phenotypic flexibility in that respect is clearly manifested by resumed growth of stressed biological systems back to states prevailing prior to and around the onset of the concerned temperature hiatus. Given that current climatic and treeline trends prevail, a major transformation of the subalpine/low alpine landscape may eventually take place, with *Pinus sylvestris* as the winning part.

Keywords: Treeline ecotone, boreal tree species, climate variation, periglaciation, canopy dieback, regeneration failure, clonal tree growth, phenotypic flexibility. Swedish Scandes.

INTRODUCTION

Future climate change is a topic of great societal and scientific importance (Lamb 1995; IPCC 2013; Ljungqvist 2017), although hitherto mostly based on model predictions, with a certain political bias and virtually without sufficient consideration of historic patterns, reconstructed by proxy records (cf. Ljungqvist 2009). In that perspective, climatically marginal landscape elements are renowned as especially sensitive to climatic oscillations and land use changes over different periods of time. For example, dynamic patterns of alpine (upper) treelines and glacier/snow patches integrate historical and recent climate change impacts (Karlén 1976; Brubaker 1986; Kullman 1998; Payette 2007; Holtmeier 2009; Körner 2012; Zemp et al. 2015; Hedenås et al. 2016; Skre 2019; Nygaard et al. 2022; Kullman & Öberg 2022, 2023a; Hansson et al. 2023).

In recent time, much focus has been on proposed future man-made global warming and its landscape ecological consequences, following on the predominantly cold Little Ice Age (~AD 1300-1900). This was the latest, but probably not last, in a series of “neoglacial events” (Lamb 1995; Grove 1988, 2004; Matthews & Briffa 2005; Büntgen & Hellman 2014; Ljungqvist 2017; Wanner et al. 2022). These aspects have been thoroughly studied in the Swedish Scandes, which harbour the world’s most accurately *in situ-watched* treelines, both in modern time and in the distant past of the Holocene (Kullman 1979, 1995a, 2013, 2021b; Kullman & Öberg 2009, 2020, 2023a, 2024). Notably, *treeline* implies the altitude (m a.s.l.) of the uppermost trees at least 2 m high (Kullman & Öberg 2023a). A broadly used and somewhat elusive concept is *the treeline ecotone*, which is the diffusion zone between the closed forest and the treeless alpine tundra. In this context, it is important also to consider the distinction between *treeline* and *forest line* (i.e. closed forest stands). The latter is found to be relatively more resilient to climate change than the treeline (Kullman 2021c; 2022a; Nygaard et al. 2022).

Overall, treelines along the entire Swedish Scandes have advanced by >200 altitudinal meters over the past 100 years, broadly consistent with summer temperature rise by c. 1.8 °C (Kullman 2017, 2019). However, with respect to attribution and projection, “devil is in the details”, as expressed by the large interannual variance, instrumentally recorded for summer and winter temperatures. Furthermore, as outlined in more detail below, a distinct and virtually unexplained hiatus in the secular warming trend occurred between early 1940s and late 1980s. That episode is an anomalous and inconvenient truth in the context of commonly alleged future catastrophic “greenhouse warming”. Associated ecological imprints, e.g. premature stress and dieback of cold-marginal trees, are the central focus of this article, which is a reiteration and update of previously published data (Kullman 1989a,b,c, 1990a, 1992a, 1993a, 1994, 1996a,b, 1997), here viewed in perspective.

The mentioned 50-year break (~1940-1990) in the secular warming trend is recorded by robust observations over large regions of the northern hemisphere, particularly at the fringe of the Arctic (Eriksson 1988). This course of change forced conspicuous ecological, biogeographical destabilization, physical repercussions and permanence on different levels of the northern landscape, as abundantly reported below in contemporary geoscientific literature. In Sweden, the contemporary climatic situation fostered an animate common discourse concerning the appropriateness of commercial forestry in the last primeval cold marginal, high-elevation boreal forests. It is a well-established fact that these forest ecosystems are exposed to an historically fluctuating climate and associated dramatic changes in vigour and regeneration (Kullman 1985a, 1986b; Kullman & Hofgaard 1987).

Particularly highlighted aspects, of post-1940s meteorological performance, i.e. a subtle climate cooling, are biogeographic shifts, enhanced periglaciation, slow-down of glacier retreat, permafrost expansion, treeline stress and marginal retreat, impaired natural high-elevation forest regeneration, silvicultural failure, agricultural stress; faunal retraction (Bergström 1955;

Larsen 1965; Eiche 1966; Lundqvist 1969; Mikola 1971, 1977; Seppälä 1971, 1990, 1998; Bryson 1974; Thie 1974; Holtmeier 1974; Kallio 1975; Parry 1975; Dickson et al. 1975; Hustich 1978a,b; Ford 1978, 1982; Heino 1978; Varjo 1978; Grove 1979; Vorren 1979; Schunke 1979, 1983; Pohtila 1980; Harley 1980; Auger & Payette1980; Payette & Lajeunesse.1980; Layser 1980, Seppälä & Rastas 1980; Ogden 1981; Karlén 1982; Jones et al. 1982; Sugden 1982; Elliott 1983; Karte 1983; Rapp 1983; Ives & Hansen-Bristow 1983: King 1984; Friedland et al. 1984; Jalkanen 1985; Morin & Payette 1986; Harris 1986; Wallén 1986; Davis 1986; Svensson, 1986; Hansen & Lebedeff 1987; Steijlen & Zackrisson 1987; Kullman & Hofgaard 1987; Eriksson 1988; Krüger 1988; Larsson-McCann 1988; Josefsson 1988; Massa 1988; Raatikainen & Vänninen 1988; Rapp & Nyberg 1988; Wood 1988; Grove 1988; Laaksonen, 1989; Vader & Barrett 1989; Karoly 1989; Lindgren et al. 1989; Krogerus 1989; Alexandersson & Eriksson 1989; Ericsson 1989; Meades 1989; Monitor 1989; Ritari 1990; Benedict 1990; Luckman 1990; Nyberg & Lindh 1990; Wilkinson 1990; Eriksson & Alexandersson 1990; Tikkanen & Raitio 1990; Ødum 1991; Stergiou 1991; Hofgaard et al. 1991; Read & Gould 1992; Kukla et al. 1992; Schneider 1992; Kullman 1983, 1987, 1988a, b, 1991b, c, d; 1992a,b, 1994, 2017, 2022b; Kahl et al. 1993; Allard et al. 1995; Lamb 1995; Burton 1995; Alexandersson et al. 1995; Holmlund 1998; Rapp 1996; Thórhallsdóttir 1996; Kullman & Engelmark 1997; MacDonald et al. 1998; Humlum 1999; Nesje & Dahl 2000; Barklund 2002; Holtmeier et al. 2004; Bengtsson et al. 2004; Luterbacher et al. 2004; Grove 2004; Sutton & Hodson 2005; Payette 2007; Autio & Colpaert 2005; Danby & Hik. 2007; Kullman & Öberg 2009; Box et al. 2009; Ljungqvist 2017; Lansner & Pedersen 2018; Mörner et al. 2020; Cappelen 2021).

The reports cited above are numerous and concern widely aspects of northern and cold-marginal landscapes and do support the contention of a common driver, i.e. climate change, foremost multi-decadal cooling.

The concerned kind of episodic climatic performance and associated landscape variability on decadal and annual scales are consistent with the concepts of *micro-ice ages* and *key years (climate extremes)*, as highlighted and discussed by Vibe 1982 and Hustich 1978a, b, respectively. These notions imply short-term distinct deviations from prevailing climatic and ecological states with an overaccentuated lag effect on biotic structure and composition. The climate of the concerned interval and its prior warming trend (early 20th century) are debated but not fully understood from a causal climatological point of view, although cooling by sulphur aerosols and natural internal variability are discussed (Roeckner et al. 1999; Bengtsson et al. 2004; Ljungqvist 2017; Bokuchava & Semenov 2021; Aizawa et al. 2022; Vinós 2023). The associated part of biogeographic history has received little attention by present-day ecological researchers and media, predominantly concerned with anticipated future “catastrophic” global warming.

Against this background, we here focus on documented arboreal landscape impacts over the cooling five-decade period after 1940 and particularly during the 1980s. This study is based on direct records and observations in systematically spaced networks of elevational belt transects (Fig. 1) and therein contained permanent photo-points. It is a reiteration and update of previously published data (e.g. Kullman & Öberg 2009). These records show a representative range of biotic responses, that may now be seen and analysed in a proper temporal perspective, as a kind of a ”natural experiment” (Kullman 1981, 1989a,b,c, 1990a,b, 1991a,b, 1992a, 1993a,b, 1994, 1996a,b, 1997, 2017, 2021d; Kullman & Öberg 2009, 2015). This rephoto-approach displays ground-truth responses and improves the comprehension of the way cold-marginal tree ecosystems relate to climate change and variability.

STUDY AREA

Most of the studies, referred to in this paper originate from the high-mountain area (range 600-1700 m a.s.l.) of the southern Swedish Scandes in the county of Jämtland, about 63°08´N; 12°30´E (Fig. 1). The study focuses primarily on treelines and upper boreal forests, especially in the Handölan River Valley and nearby regions. The regional climate is weakly oceanic. Mean temperatures (1991-2025) for December-February and June-August are -5.3 and 10.9 °C, respectively. These figures refer to the meteorological station Storlien/Storvallen (595 m a.s.l.).

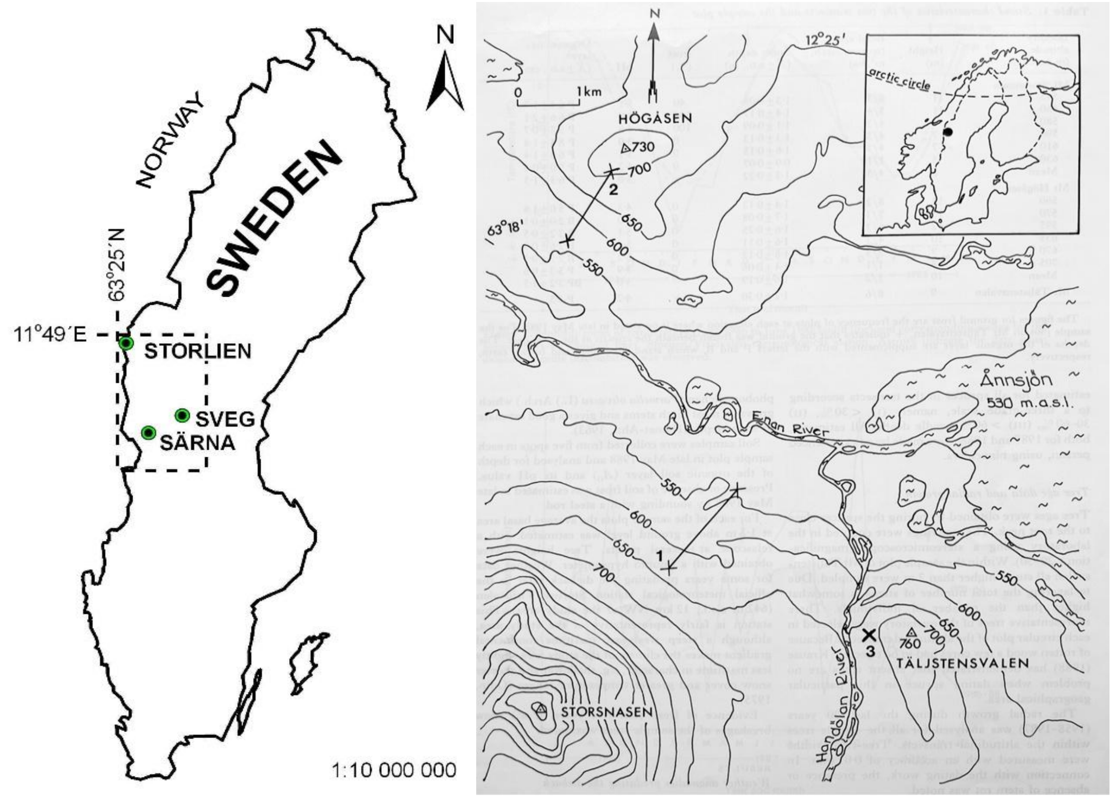


Figure 1: *Left.* Location of the main study area in Sweden (frame). *Right.* Detailed map showing permanent altitudinal transects in the county of Jämtland, from which much of reported data were gathered.

The mountain slopes below the alpine tundra are clad with an elevational subalpine birch forest belt (*Betula pubescens* ssp. *czerepanovii*), forming the upper treeline, 900-1100 m a.s.l. Interspersed at lower elevations are the treelines of Norway spruce (*Picea abies*) and Scots pine (*Pinus sylvestris*). More details of the natural landscape, physiography, vegetation flora and long-term vegetation history are given by Kullman & Öberg (2022).

MODERN CLIMATIC FLUCTUATIONS

Based on official records from Storlien/Storvallen meteorological station, summer and winter mean air temperatures are displayed annually, 1901-2025 (Fig. 2). For the summer period

(June-August), a rise of 1.8 °C has occurred. Over the same period, winter temperatures (December-February) have become 1.4 °C warmer. These figures include large interannual variance, which may be of greater importance to the physical and natural environment than the long-term mean.

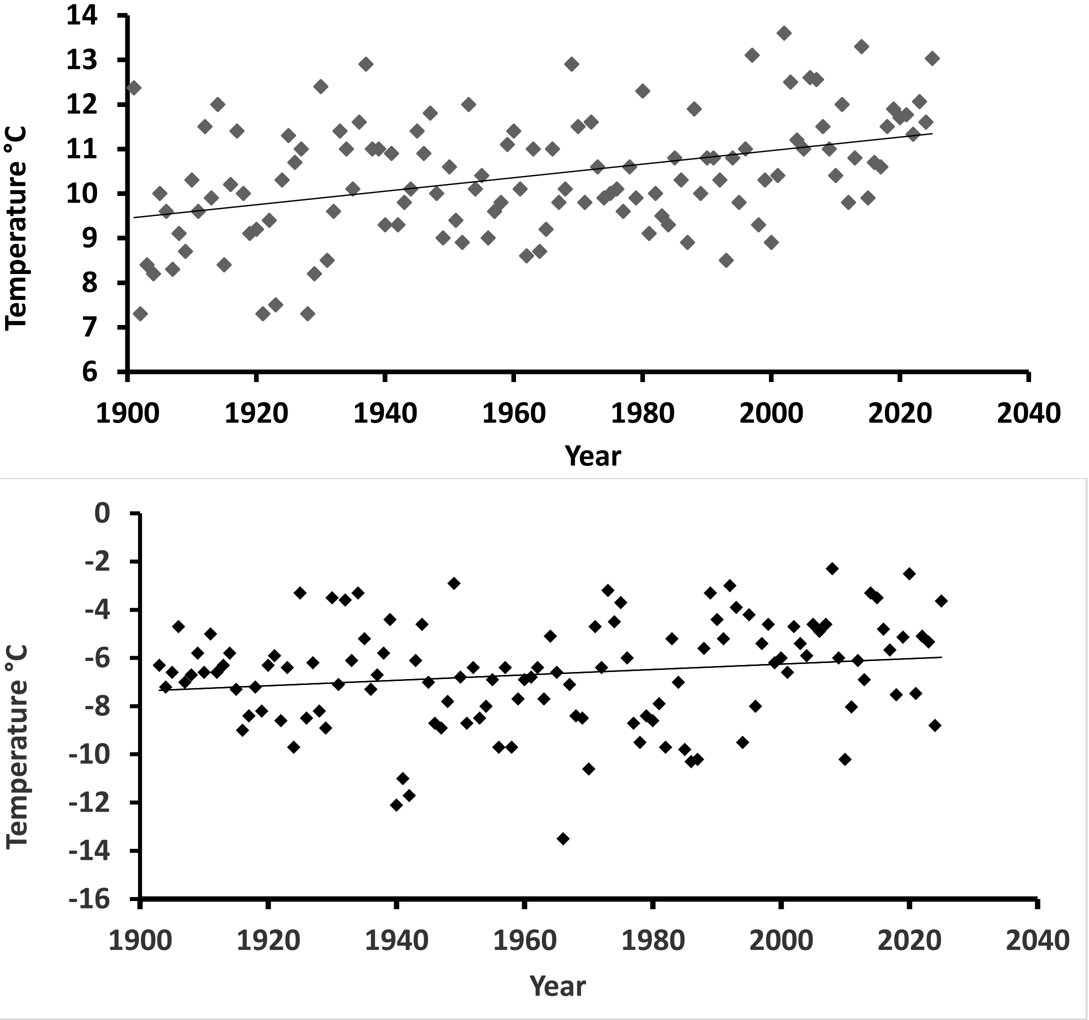


Figure 2: Annual mean air temperature records at Storlien/Storvallen meteorological station. *Upper*. June-August. *Lower*. December-February.

The above-mentioned hiatus in the secular warming trend in the North stands out between about 1950 and 1990 (summer) and 1940-1990 (winter), most clearly manifested for the winter period. Some exceptionally cold winters occurred during the latter interval, e.g. 1940-1942, 1966, 1986/87. Winter cooling in northern Sweden culminated during the period 1978-1987, when the temperature was >3 °C below the mean of the warm peak 1931-40 (Eriksson 1988). After the last-mentioned interval, annual mean temperature declined by 0.8 °C (Alexandersson et al. 1995). With respect to annual mean temperature, the same pattern of cooling was recorded at other stations in the concerned part of the Swedish Scandes (Figs. 3 & 4).

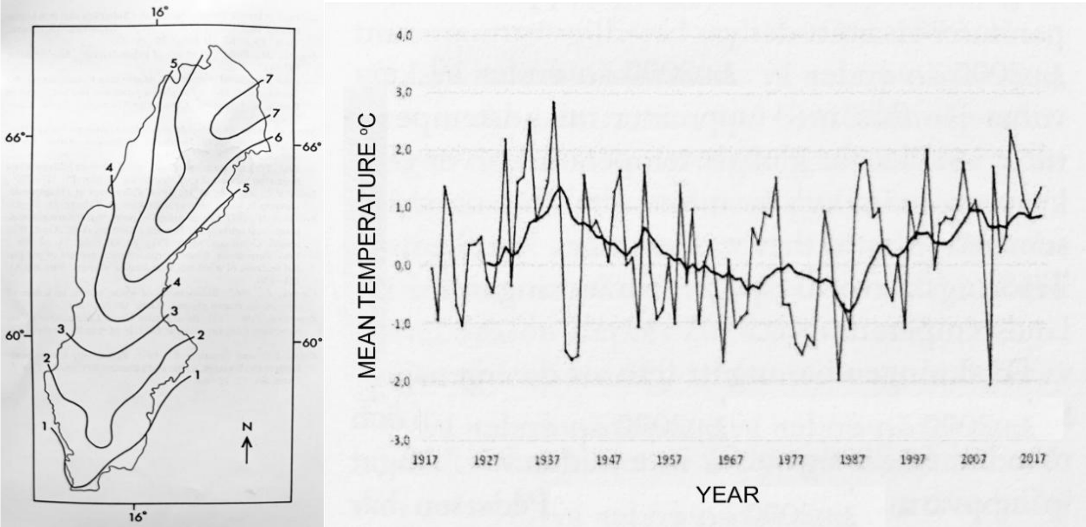


Figure 3: *Left*. Isolines depict winter cooling (December-February) in Sweden as the difference between the decadal means 1931-40 and 1978-87. Source: Eriksson (1988). *Right*. Mean annual temperatures 1917-2019, recorded at the meteorological station Ljusnedal (585 m a.s.l.). The solid line is the 11-yr running mean. Source: Börjesson (2020).

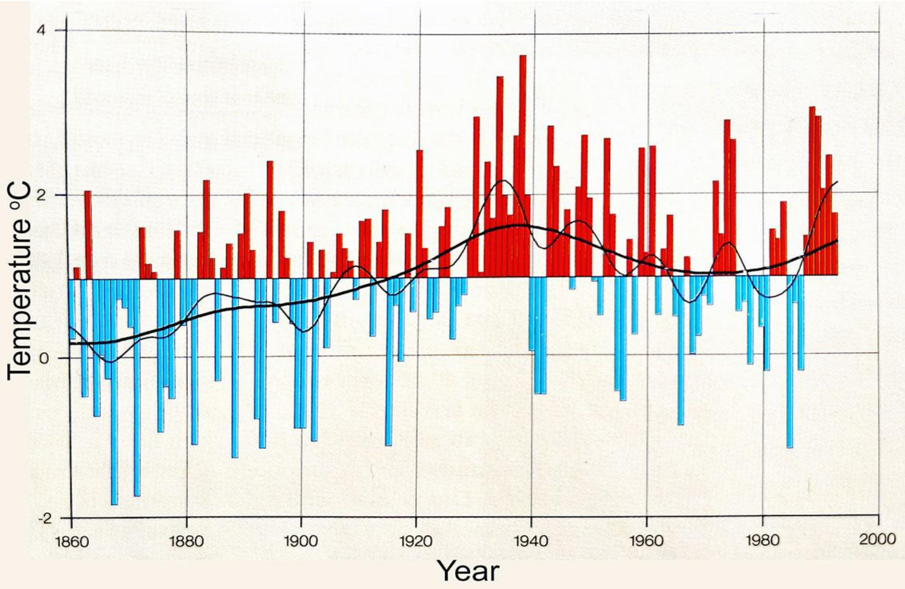


Figure 4: Mean annual temperature anomalies for northern Sweden, relative to the long-term average (1860-1993). The solid and thin line represent 30 and 10-year running means, respectively. Source: SMHI.

Viewed in retrospect, the episode here concerned may improve our comprehension of climate governance of ecological dynamism in cold-marginal environments. For that purpose, we here display representative ecological and biogeographical responses to this relatively frigid period in the recent past (Kullman 1981, 1993a, 2021d; Kullman & Öberg 2009, 2015).

PROXY CLIMATE INDICATORS

Soil temperatures are of paramount importance for tree growth and survival close to the treeline in subarctic and subalpine regions (Karlsson & Weih 2001; Körner & Paulsen 2004;

Kullman 2021a). Permafrost distribution and evolution are efficient indicators of regional climate performance (French 1999). With some exceptions, it is well substantiated that permafrost is not compatible with growth of most boreal tree species (Harris 1986). Witnesses of sites with new permafrost formation (1987) in the subalpine region and upper boreal forest in the study region are displayed in Figure 5 (Kullman 1989b, 1991a). In addition, new permafrost was found in outliers of subarctic spruce forest in northernmost Swedish Lapland, causing substantial contemporary defoliation of extant mature spruce trees (Fig. 6).

Figure 5: Peat mounds with new permafrost formed during the winter 1986/87 and persisting over the summers of 1987 and 1988. Both these features emerged south of the previously recognized limit of discontinuous permafrost in northern Sweden (Rapp 1983). Thereafter, no permafrost has been recorded at these sites. *Left.* Krabbfjällnäset, 545 m.a.s.l. Photo: 1988-10-09. *Right.* Mt. Storsnasen 680 m a.s.l. Photo: 1987-09-28. Source: Kullman (1989b).

Figure 6: *Left*. Subarctic spruce forest just outside the city of Kiruna in northern Lapland (410 m a.s.l.), displaying substantial needle loss during the winter 1986/87. About 35 % of the spruces lost 40-60 % of their foliage. *Right*. Many of the spruce trees at this site grew on peat with segregated ice throughout the summers of 1987 and 1988. This circumstance reasonably relates to their loss of vigour. Permafrost in spruce forest had previously not been recorded after the Little Ice Age in boreal Scandinavian forests. Source: Kullman (1989b, 1991a).

RESULTS

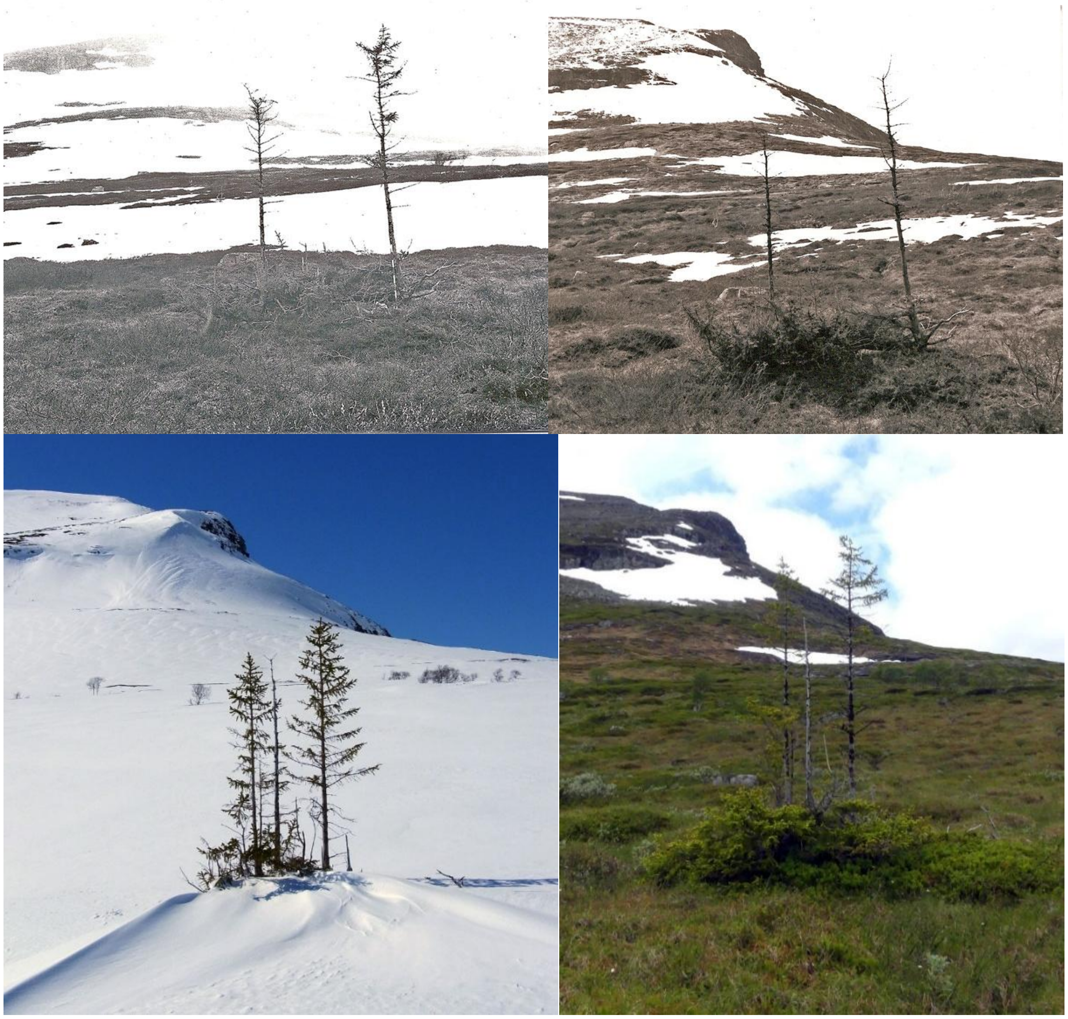
This section examines arboreal changes, mainly within the treeline ecotone of the Handölan River Valley. In most cases, these records are complemented with images representing responses to subsequent more recent and warmer conditions. The main objective is to illustrate changes in size and health over different periods of time, with variable climate trends. This approach is essential for the understanding of decisive selective forces.

Displayed changes are circumstantial and have the character of a series of randomly distributed case studies. These are based on repeat photo-views, with a primary focus on responses to a periodic reversion to cooler conditions, as generally reported by the geoscientific literature cited above. Overall, an account is made for real-world dynamism and discloses mechanisms controlling climate governance of biotic evolution in a world of steadily fluctuating climate conditions. Focus on individual trees and tree groups draw on the notion that comprehension and prediction of future responses must be grounded on long-term observations of individual plants, i.e. a kind of "phytobiography" (Däniker 1923; Tranquillini 1979; Harper 1977; Kullman 1985b).

Spruce Dynamics (Figures 7-34)

Following on progressive population and individual growth responses to the general warming until the late 1930s (Kullman 1986a), physiognomic regression in the treeline ecotone took place during the following four to five decades. This course of change coincides with the nadir of the recorded temperature hiatus, when temperatures transiently nearly approached Little Ice Age conditions (Alexandersson & Eriksson 1989). Accordingly, by the mid-1970s, spruce treeline stands were generally in a declining state of condition, with widespread crown thinning and virtually no reproduction (Kullman 1986a, 1989b). Physiological stress to arboreal growth initiated by the latter episode of cold weather, with a peak in 1986/1987, progressed well into the 1990s. These circumstances have left a still discernible impact of the crown structure of many trees in the treeline ecotone. As evidenced below, conspicuous vegetative canopy recovery has occurred in many cases, coincident with climate improvement over the subsequent 30-35 years. However, sexual reproduction has remained virtually nil.

Figure 7: *Left.* Old-established clonal spruce, growing on Mt. Stråten, 760 m a.s.l. Tree-size was contingent on the warm 1930s and was reversed by the 1970s. Photo: 1974-06-10. *Middle.* Extensive and virtually complete defoliation took place around 1987. Photo: 1995-07-13. *Riught.* Up to the present day, the spruce has, with a good marginal, regained its prior tree status. Photo: 2024-09-15.



Figur 8: ***Upper left and right*. Multi-stemmed clonal spruce, that developed from shrubby krummholz to tree-size during the relatively warm first 3-4 decades of the past century. Tree-ring growth indicates that recession of the two erect stems was initated during the mid-1960s. By 1985, both stems were dead, althogh a basal skirt of branches was alive. Photo:1974-06-05 and 1985-06-11, respectively. *Lower left*. Thereafter, the original stems are downed and replaced by two new fast-growing stems. The basal skirt of layering branches is well protected by the snow cover. Photo: 2012-04-29. *Lower right*. Since 2012, some defoliation of the new stems is evident. Photo: 2025-06-04. Radiocarbon-dated wood remnants in the soil demonstrate that this individual existed here about 6600 cal. yr. BP. Source: Öberg & Kullman (2013). Mt. Norder Tväråklumpen, 805 m a.s.l.**

Figure 9: ***Left.*** **Solitary spruce (Mt.Täljstensvalen, 700 m a.s.l.) displaying supranival needle death, following on the harsh winter 1986/87. Photo: 1988-04-14.** ***Mddle and Right*****. Eventually, the spruce has recovered to a large degree and appears more vigouros than ever before. Photo: 2016-05-25, 2025-05-27, respectively.**

Figure 10: ***Left*****. Tree-sized spruce growing in the treeline ecotone of Mt. Norder-Tväråklumpen, 790 m a.s.l. Photo: 1974-06-06 .*****Middle*****. During the late1980s, the previous main stem died. Photo: 1988-06-27.** ***Right*****. Thereafter, it was replaced by a rapdily growing basal shoot, equally tall as the succumbed one. Photo: 2023-04-22.**

Figure 11: Subalpine spruce suffering from extensive and gradual defoliation until the late 1980s. Subsquently, it has regained foliation and tree size with more than 100 %. Mt. Lill-Skarven, 920 m a.s.l. ***Left.*** **Photo: 1988-08-14.** ***Right.*** **Photo: 2011-08-10.**

Figure 12: *Left.* Multi-stemmed spruce growing in the treeline ecotone on Mt. Ottfjället, 955 m a.s.l. Gradually, it lost foliage during the cold 1980s. Photo: 1988-07-17. *Right.* Over the past few decades, the spruce has recovered greatly, in accordance with rising temperatures. Photo: 2011-06-29.

Figure 13: *Left*. Detailed view of extensive stand-level defoliation of spruce trees on Mt. Täljstensvalen, 690 m a.s.l. Photo: 1987-11-15 (cf. Figure 14). *Middle*. Crown thinning proceeded over the following years. Photo: 1989-04-14. *Right*. Since the early 1990s, the main stems have recovered, while some minor stems are downed. Photo: 2025-05-27.

Figure 14: *Left.* In the mixed spruce-birch forest on the west-facing slope of Mt. Täljstensvalen, spruces suffered extensive needle loss (> 60 % of the total foliage), during the winter 1986/87. This episode rendered the entire landscape a greyish hue. Photo: 1987-08-14. Source: Kullman (1989a). *Right.* Since the early 1990s, most spruces have recovered, which has lended the landscape a greener character. Photo: 2021-08-12.

Figure 15: *Left.* Clonal spruce in the treeline ecotone of Mt. Storsnasen (795 m a.s.l.), which lost a major part of its needles 1987, and during some following years. Photo:1989-06-23. *Right*. Up to the present day, many stems have recoverd, while some are downed and dead. Photo: 2024-07-20. Source: Kullman (2021b).

Figure 16: *Left.* Multi-stemmed spruce in the treeline ecotone on Mt. Storsnasen (805 m a.s.l.). It became extensively defoliated some years prior to the photo date, possibly by the cold 1960s. Photo: 1974-04-21. *Right.* In concert with milder winters since the late 1980s, foliage recovery has been substantial. Photo: 2025-04-13. Source: Kullman (2015).

Figure 17: ***Upper left.*** **Tree-sized spruce growing in the treeline ecotone of Mt. Högåsen (710 m a.s.l.) and in a healthy condition. Photo: 1973-06-27.** ***Upper right:*****. Defoliation was initiated in 1987 and has progressed during the following years. Photo: 1988-07-12*****. Lower left and right*****. Up to the present day, the main stems have regained some of their former stature and foliage in concert with warmer climate. In addition, the surrounding birch tree cover has declined, obviously as a consequence of soil drought following on earlier annual snow-melt. Photo: 2023-06-24, 2025-07-12, respectively.**

Figure 18: ***Left*****. Clonal treeline spruce with extensive needle loss in 1987 and 1988.** ***Right.*** **Thereafter, some stems have died, while others have increased their height and needle mass. Mt. Täljstensvalen, 740 m a.s.l. Photo: 1988- 04-14, 2025-05-27, respectively.**

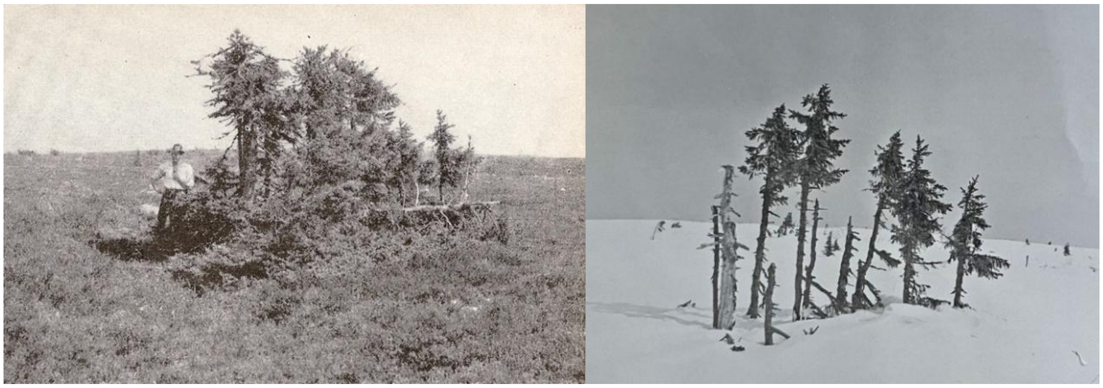


Figure 19: ***Left.*** **Recent history of an old-established spruce treeline clone (1943-2024), growing at Mt. Köarskalsfjället (825 m a.s.l.). Subfossil wood remnats in the soil testament that this individual existed here about 8000 years ago. This particular spruce was depicted by Dr. Gösta Lundqvist in July 1943. At that time its was in fairly good shape, presumably a consequece of the favourable climate in the 1930s.** ***Right.*** **Thirty years later, the general condition had deteriorated and some of the major stems have died. Photo: 1973-04-22*. Lower left and right.* Physiognomic decline has proceeded after 1973, initiated by transient "micro-ice age"conditions following on the 1930s. Photo: 2004-07-03, 2024-06-05, respectively.**

Figure 20: ***Left.*** **Multi-stemmed shrubby clonal treeline spruce at Mt. Storsnasen (740 m a.s.l.), that was severely hit by cold weather and ensuing needle discoloration and defoliation during the late 1980s. Photo: 1987-04-21.** ***Right.*** **Milder winters after the 1980s have allowed extensive canopy recovery and height increment. Photo: 2017-05-06. Conspicuously, the growth habit supports extensive snow accumulation and relatively high soil temperatures during the winter.**

Figure 21: ***Left.*** **Old-growth spruce clone growing in the treeline ecotone of Mt. Storsnasen, 685 m a.s.l. In fact, this spruce was the first to re-wrigth vegetation history. It disproves the pollen-based old myth of spruce as a late Holocene immigrant to northern and western Scandinavia.**

Radiocarbon-dated wood remnants underneath the canopy disclose that this specific individual grew here already 5585 cal yr. BP (Kullman 2001). About 50 % of the the foliage above the snow-air interface was killed by frost-desiccation during winter 1986/87. Photo: 1987-07-23. *Middle.* Needles were gradually shed during the following years, until 1995. Photo: 1995-07-23. *Right.* In concert with milder winter since the late 1980s, substantial recovery of vigour has taken place, although the prior cold years have left a faint imprint on the clonal structure. Photo: 2025-07-07. Meta-data concernig the clonal spruce structure and growth are accounted for in Figure 22. Source: Kullman (1995b).

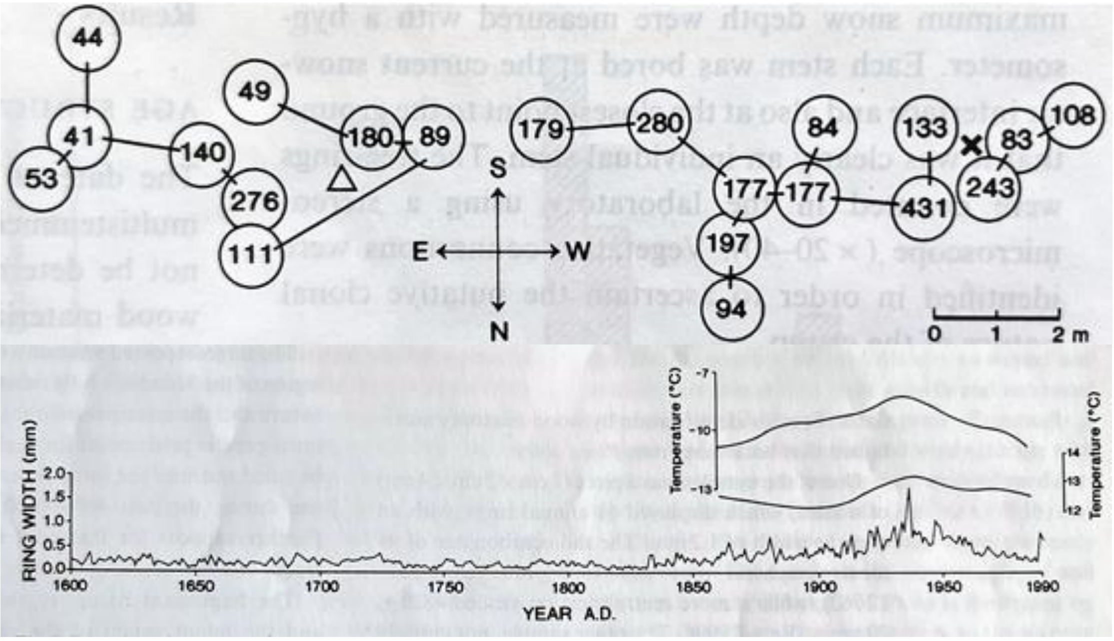


Figure 22: *Upper*. A total of 21 living stems make up the this spruce group (Fig. 21), which may represent two genets. Initiation of stems ocurred sporadically between the 1560s and 1990s. Ages of individal stems are given in relation to 1991. Vegetative connections between stems are indicated by straight lines. A general impression is one of eastward spread in accord with prevailing winds. Insert smooth graphs show the general trend for June-August (lower) and December-February (upper) mean temperatures in northern Sweden (Alexandesson & Eriksson 1989). *Lower*. A tree-ring chronology representing an average of all 21 stems, shows insignificant growth between the early 17th century and the mid 19th century. A distinct peak stands out in the mid- or late 1930s, followed by a declining trend until the late 20th century, with a minor peak after the 1980s. This pattern suggests that prior to the 1930s, the entire group had a shrubby growth form, not exceeding the prevailing local snow depth (1.0-1.2 m). Source: Kullman (1995b).

Figure 23: *Left*. Clonal treeline spruce growing on Mt. Städjan (970 m a.s.l.), that suffered substantial cold-induced decline, culminating by the late 1970s, following on the relatively warm period until the late 1930s. Photo: 1975-07-08. *Right*. Since the early 1990s, the foliation has increased and the height has become more than doubled. Photo: 2023-08-11.

Figure 24: *Left*. Old-growth clonal spruce, growing 740 m a.s.l. on Mt Storsnasen. Photo: 1973-09-02. *Middle*. Twenty years later, the spruce had lost a major part of the needle mass, causing substantial crown thinning. Photo: 1993-03-21. *Right*. The regressive process has continued up to the present day. Photo: 2025-05-25.

Figure 25: ***Left.*** **Stand of mature clonal spruces, Mt. Storsnasen 625 m a.s.l., that displayed extensive defoliation in 1987, which continued for some following years. Photo: 1987-10-16.** ***Right.*** **Up to the present day, a remarakble recovery has taken place. Some of the prior large stems are downed and replaced by young growth. Photo: 2025-06-01.**

Figure 26: ***Left.*** **Multi-stemmed treeline spruce that, according to tree-ring data, attained tree-size contingent on the thermal apogee of the 1930s. Already by the early 1970s, defoliation was well underway. Photo: 1973-06-27.** ***Middle*****. More extensive needle loss occurred 1987 and 1988. Photo: 1988-07-18.** ***Right.*** **Retrogression has progressed further and this spruce, and many ohers alike, still bears witness of the past relatively cold decades, although new lower stems are in progress. Photo: 2024-06-21. Mt. Högåsen 720 m a.s.l.**

Figure 27: ***Left*****. Clonal spruce, growing on Mt. Storsnasen, 685 m a.s.l. Subsequent to the cold winter 1987, virtually total needle loss occurred during some following years. Photo: 1989-04-09.** ***Right*****. Over the past 30 years, some of the original stems are downed and dead, being replaced by other fast-growing shoots. Photo: 2025-06-08.**

Fig. 28: *Left.* Multi-stemmed spruce that displayed major needle dieback during the winter 1986/87. Photo: 1987-07-27. *Right.* Over some recent decades, a few stems have died, while others have recoverd. Overall, vigour has improved. Photo: 2025-06-11. Mt. Storsnasen, 685 m a.s.l.

Figure 29: *Left.* Spruce clone that attained tree-size shortly after the 1930s. Photo: 1972-08-04. *Middle.* Up to the 1980s, it increased in height, followed by substantial defoliation, that culminated 1987 and 1988. Photo:1988-09-21. *Right.* That course of decline has proceeded into the past few years and only one of originally six stems is still alive. Photo: 2025-06-26.

Figure 30: *Left.* Clonal spruce in a fairly good condition. Photo: 1974-06-06. *Middle.* Substantial needle death was evident by the late 1980s. Photo: 1987- 08-16. *Right.* Canopy decay has

proceeded up to the present day. Some recovery is in progress by fast-growing layering stems. Photo: 2025-07-04. Mt. Norder Tväråklumpen, 765 m a.s.l.

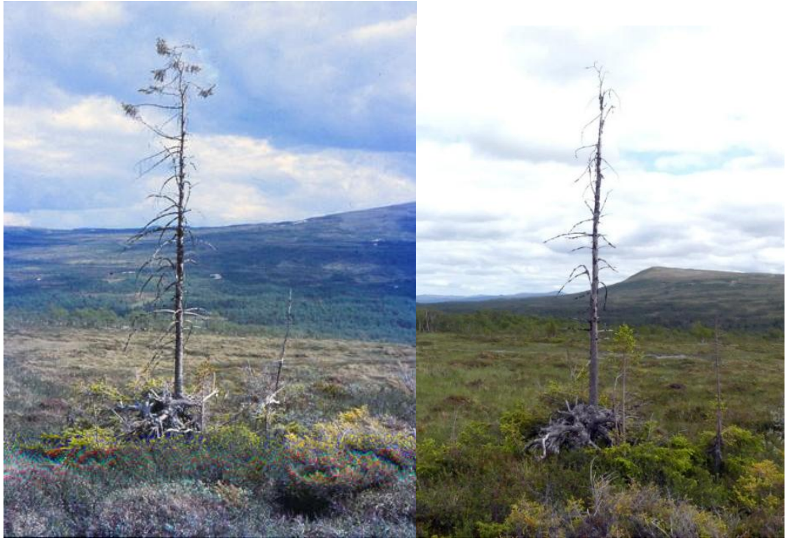


Figure 31: Spruce with one main stem with almost total defoliation during the 1980s and subsequent years. Today the dead stem is being replaced by a secondary basal shoot from layering branches to the right. Mt. Norder -Tväråklumpen, 765 m a.s. l. *Left*. Photo: 1994-05-07. *Right*. Photo: 2025-07-04.

Figure 32: *Left*. Spruces growing in the treeline ecotone, that were hit by substantial needle loss and crown thinning following on the severely cold winter 1986/87. Photo: 1988-05-23. *Right*. Subsequently, foliation has increased. Photo: 2025-08-01. Mt. Storsnasen 675 m a.s.l.

Figure 33: ***Left. Picea*-group that became heavily defoliated in 1987. Photo: 1988-01-08. *Right.* Up to the present day, some stems have recovered substantially, althogh a structural legacy of prior harsh conditions prevails. Photo: 2025-08-10. Mt. Storsnasen, 685 m a.s.l.**

Figure 34: ***Left.* Spruce clone with almost total needle loss, subsequent to the winter 1986/87. Three main stems are virutally dead. They rapidly attained tree size following on the 1920s. Photo: 1987-07-28. *Right.* Stem and branch erosion has continued up to the present day, although metre-high layering shoots are eventually replacing the demised stems. Photo: 2025-09-01.**

Pine Dynamics (Figures 35-42)

Needle desiccation was a widespread feature (browning) in high-altiude forest stands over large parts of high-elevation northern Sweden during the summer of 1987. In particular, exposed trees growing on shallow and late-thawing peat were most severely affected. Even full-sized and old-established individuals were hit and occassionally succumbed (Kullman & Högberg1989; Kullman 1991). Pines with lighter injuries survived, although with persistent structural canopy legacies of past frigid years. In sharp contrast to the spruce, pine has reproduced copiously in the treeline ecotone during the past 25 years or so (Kullman & Öberg 2022, 2023b, 2025)

Figure 35: A near-treeline stand of pine with extensive needle death (reddish foliage) during the summer of 1987. At the end of that year, the peaty soil was still frozen beneath a depth of 0.3 m. Mt. Storsnasen 570 m a.s.l. Photo: 1987-06-14. Source: Kullman & Högberg (1989).

Figure 36: Detail of the stand depicted in Figure 35, showing that the lowest branch whorls (snow-covered during most of the winter) were unaffected. The extensive defoliation of the major canopy, in combination with recorded frozen soil during the summer, indicate that frost desiccation above the snow-air interface caused this phenomenon. Photo: 1987-06-14.

Figure 37: *Left*. In the lower slope of Mt. Storsnasen, pines manifested extensive defoliation 1987, when the soil remained frozen throughout the entire summer. Annual shoots, and buds survived the first summer. Photo: 1988-07-01. *Middle.* Needle loss continued for a few years, eventually leading to individual mortality of some mature trees. Photo: !994-07-01. *Right.* At the present day, only meter-high snags of the former large pine trees remain. During the present milder phase, young trees and saplings have become established between the demised trees and in the distant fond. Photo: 2025-05-01 Source: Kullman & Högberg (1989).

Figure 38: *Left*. Pine, that gradually transformed, by means of frost-desiccation, from minor tree-size (observed 1977-07-29) to krummholz following on the cooling that culminated by the late 1980s. This process continued until the late 1990s. Photo: 1999-05-19. *Right.* Thereafter, this pine has with a good marginal regained its former tree status, demonstrating a formerly unknown capacity of phenotypical plasticity of the genus *Pinus*. Photo: 2025-05-27. Mt. Täljstensvalen, 740 m a.s.l.

Figure 39: Mature pine tree growing in the lower birch forest belt, affected by winter-desiccation on the south-facing side of the crown. Mt. Storsnasen, 700 m a.s.l. Photo: 1987-07-17.

Figure 40: Pines and spruces (reddish) suffering from extensive frost desiccation injuries during the winter 1986/87. Permafrost developed in the central bog and prevailed in mid-December 1988. Mt. Täljstensvalen, 650 m a.s.l. Photo: 1988-09-13.

Figure 41: *Left.* Edge of an outlying pine forest, severely affected by frost desiccation and some defoliation 1987. This stand was virtually extirpated during the Little Ice Age and was restocked in response to the warming of the early 20th century. Currently, pine is centrifugally expanding into adjacent mires, which appears as a common phenomenon in the treeline ecotone. Source: Kullman (1986). Photo: 1987-07-04. *Right.* Foliation and general vigour have perceivably increased after the 1980s. Photo: 2025-08-05.

Figure 42: *Left*. Treeline stand of *Pinus sylvestris*, that displayed extensive frost desiccation injury (browning) during the winter 1986/87. Photo: 1987-07-17. *Right*. Up to the present day,

remarkable general recovery has taken place. Notably, the stout tree to the left has virtually died. Photo: 2025-09-13. Mt. Storsnasen, 680 m a.s.l.

Mountain Birch Dynamics (Figures 43-47)

During the past 100 years or so, the treeline of mountain birch, spruce and pine have (with large local variation risen by more than 200 altitudinal meters along the entire Swedish Scandes (Kullman & Öberg 2009; Kullman 2021b). Since the mid-1970s, *Betula* has responded less consistently to climate change than pine and spruce. Within the advanced birch treeline ecotone signs of growth stress and disturbance were frequently assessed within monitoring elevational transects and permanent plots, following on the cooling late 1980s. Locally, treeline rise was halted or transiently slightly reversed (Kullman 1989c, 1991b, 1993a, 1997, 2005; Öberg & Kullman 2012). Some aspects of this course of change are depicted below. Opportunistic model predictions of a general birch forest expansion over a major part of the Scandes (Moen et al. 2004) seem overstated in the light of records reported here.

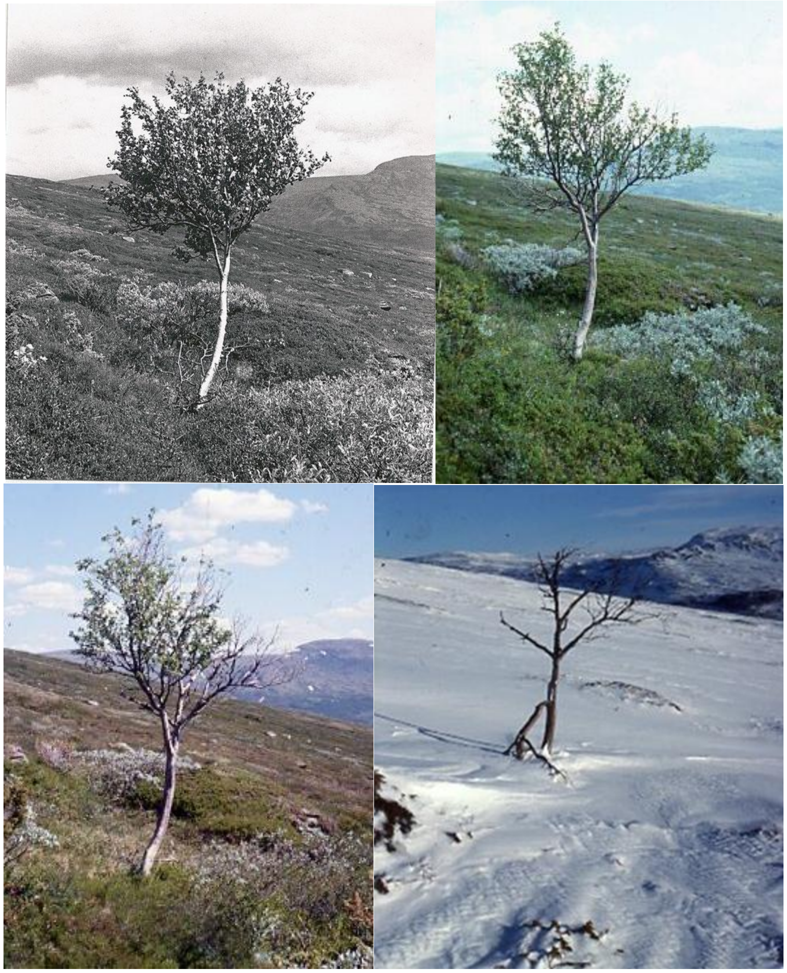


Figure 43: ***Upper left.*** **Tree-sized birch on Mt. Getryggen (930 m a.s.l.), that displayed treeline rise by c.100 altitudinal meters since 1915. Photo: 1972-08-06. Source: Kullman (1979).** ***Upper right.*** **Some thinning and signs of foliage decay are discernible at this date. Photo: 1983-07-10.** ***Lower left.*** **Defoliation proceeded substantially during the 1980s. Photo: 1986-08-10.** ***Lower right.*** **The birch was found dead by the summer of 1990. Photo: 1991-02-06. To judge from the branching structure, it may have succumbed a few years earlier, which represents temporary**

marginal lowering of the treeline. Over the past few decades, however, the treeline has advanced to 1045 m a.s.l. in this specific slope.

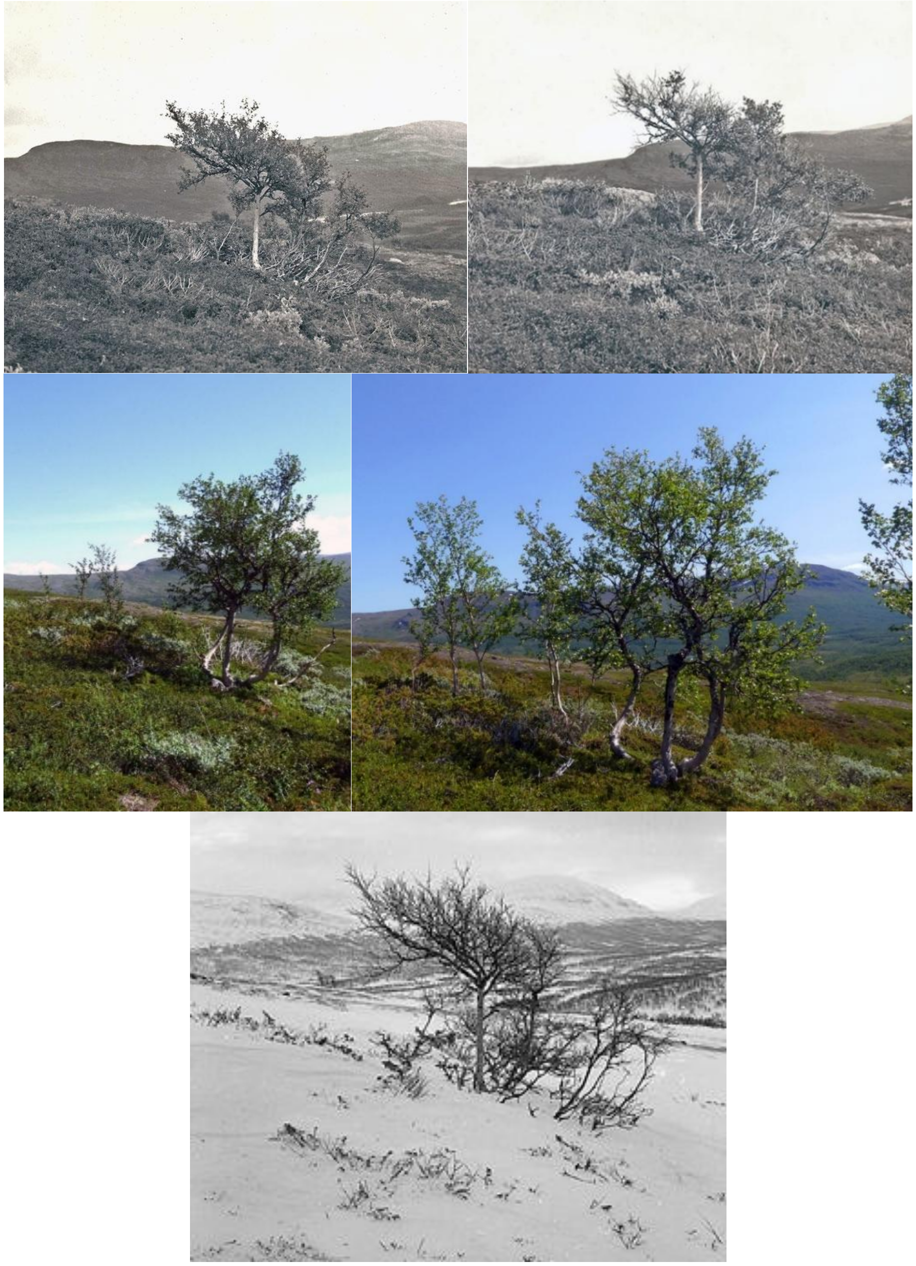


Figure 44: ***Upper left.*** **Multi-stemmed birch in the treeline ecotone (Mt. Getryggen, 905 m a.s.l). Photo: 1972-08-06. Height-growth of the main stem was initiated in the 1920s, from a cluster of interconnected low-growing shoots. This particular stem existed here by the late 18th century. Decaying wood remnants in the soil underneath the crown dated c. 5000 years before the present (Öberg & Kullman 2012).** ***Upper right.*** **Crown thinning and decay of the largest stem were well underway by the late 1980s. Photo: 1987-08-10.** ***Middle left.*** **The former main stem is broken, and the individual tree size is sustained by increased growth of pre-existing root suckers Photo: 2010-08-11.** ***Middle right.*** **The entire foliage has increased, and fast-growing secondary stems have become even more prominent. Photo: 2025-07-08.** ***Lower.*** **Typical winter-view of this birch in a snow-poor environment, which stresses its exposed situation in**

cold winters, e.g. during the 1980s. In 1987, following on a cold and snow-poor winter, the soil was frozen 30 cm below the surface by the late August, a truly rare occasion during the past 50 years or so. Photo: 1977-03-02.

Figure 45: *Left.* Tiny birch tree, growing in a thicket of *Juniperus communis* and *Salix lapponum.* Photo: 1974-07-02. *Middle.* The main stem died during 1987, and was subsequently replaced by a secondary stem from the same root stock. Photo: 1994-07- 05. *Right.* Over the past 30 years, this birch has recovered substantially and is now in better shape than by the mid-1970s. Photo: 2025-07-08. Mt. Getryggen, 915 m a.s.l.

Figure 46: *Upper left.* Solitary treeline birch in fairly good shape, growing on Mt. Ö. Barfredhågna, 920 m a.s.l. Photo:1974-07-19. *Upper right*. Crown deterioration is here evident. Photo: 1985-07-18. *Lower left*. Retrogression became even more conspicuous during the following decade. Photo: 1997-07-21. *Lower right*. Thereafter, the birch is dead. Photo: 2013-07-23.

Figure 47: ***Left*. Landscape view of Mt. Lillulväfjället, showing early-summer snow phenology and birch leafing since the early 20th century, when birch leafing and snow melt occurred much later than today. Photo: 1914-06-11 (Harry Smith). *Middle*. Only one year since annual monitoring started, 1977, had the situation a near-resemblance with that prevailing 1914. That happened in the "annus horribilis", 1987. Photo: 1987-06-10. *Right*. Therafter, the view has been virtually the same as 2024. Photo: 2024-06-12.**

SUMMARY AND DISCUSSION

This study complies with observed hemispheric cooling and highlights ecological stress and disturbance to the elevational treeline ecotone, on landscape and individual level during relatively cold period ~1940-1980. Transiently, this happening punctuated the overall warming trend of the past hundred years. This course of change supports the role of the treeline as a sensitive proxy climate (air and soil) temperature) indicator (Tranquillini 1979; Holtmeier 2009; Körner 2012; 2013; Kullman 2021a; Kullman & Öberg 2023a).

Quite commonly, the state of treeline vigour and vitality was low in the early 1970s (Kullman 1988b, 1989c) and it thereafter regressed further. In response to some exceptionally cold years (1960s and 1980s), with late thawing of soil frost, dieback of tree canopy structures built during some prior warmer decades, accelerated within treeline ecotone and progressed until the mid-1990s. A general pattern of individual foliage recession and crown thinning and some mortality emerged.

Minor and transient elevational treeline retraction was recorded following on the cold late-1980s (Kullman 1989a, 1991a, b., 1993a, 1996a, b; Kullman & Högberg 1989). In some cases, contemporary canopy injuries still coin the treeline ecotone, despite ensuing warmer conditions. Moreover, age structure patterns obtained in the treeline ecotone of all species bear clear signs of the relativelyunfavourable interval, 1940-1980, particularly during its latest part (Kullman 1983, 1989a, b, c, 1991b, 1993a.b, 1996a,b, 2017). Quite frequently, recovery has been remarkable during the past 30-35 years. On the landscape-scale, spruce displays the most lasting imprint of the past cooling interval, although cases of substantial individual recovery are documented. The latter ability is part of the explanation of documented extreme longevity of spruce clones at the treeline in a constantly changing climate (Öberg & Kullman 2011).

Extant tree species responded idiosyncratically and with a remarkable phenotypic flexibility and vegetative reproduction to climate extremes, most clearly expressed by the genera *Betula* and *Picea.* In the case of spruce, upper and cone-bearing parts of tree stems were most severely affected by cold conditions in the past. This circumstance limited subsequent production and spread of seeds and may be parts of the explanation, aside of declining edaphic conditions (drought), of limited reproduction of spruce at the treeline during recent decades (Auger & Payette 2010; Gamache & Payette 2004; Kullman 2022b). Pine on the other hand, suffered less in this respect, since production of cones is more evenly spread over the entire crown. Accordingly, pine has reproduced more abundantly and display a better state of vigour than spruce and birch during the past few decades (Kullman & Öberg 2025).

The obtained course of treeline change complies with multi-decadal periglaciation and ecological destabilization on a general hemispheric level (initial references). Displayed records strongly support the contention of climate-driven stress as the ultimate cause of treeline performance. However, the understanding of climate change dynamics and its impacts on treelines are still immature and insufficient to make realistic projections of future landscape evolution. Alarmistic projections of extensive expansion of forest at the expense of alpine tundra (e.g. Moen et al. 2004) appear unfounded, even in the case of continued warming.

These lagged and persistent transformations of the cold-marginal arboreal landscape comply with the concepts of *key years (climatic extremes)* and *micro ice ages* as vital aspects of treeline ecology (Vibe 1982, Hustich 1978a,b; Goedkoop et al. 2025). Legacies of this kind must be considered in efforts to model future landscape evolution in a context of ever-changing climatic conditions. With a contrafactual scenario, it seems reasonable to assume that treelines today would have been in an even better and more vigorous state, in the absence of the concerned temperature hiatus. Reasonably, the legacy of this interval will have structural and functional impacts on responses to future climate change and variability. Anyhow, today the treeline ecotone and upper boreal forest are in a better or equal state of vigour than prior to the here concerned temperature hiatus. Given that the net warming trend of the past 100 years prevails, a great progressive transformation of the forest-alpine tundra transition may be foreseen to continue, particularly executed by *Pinus sylvestris* (Blüthgen 1942; Holtmeier 2005; Kullman 2004, 2010; Kullman & Öberg 2023b, 2024, 2025). Based on recent performances, the present-day subalpine co-dominants, *Betula pubescens* ssp. *czerepanovii* and *Picea abies,* are not likely to expand to the same extent (cf. Scharn, Negri, Sundqvist 2022).

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