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Accelerated Pine (*Pinus sylvestris*) Rise in the Alpine Treeline Ecotone of the Swedish Scandes - Demographic Data 1973-2024

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ABSTRACT

In a context of post-Little Ice Age (AD 1300-1900), climate warming and associated general progressive high-mountain landscape transformation, demographic changes in the pine (*Pinus sylvestris*) treeline ecotone were monitored over the years 1973-2024. The main focus was on a system of 18 permanent plots, randomly located within the pine treeline ecotone of the southern Swedish Scandes. Overall, unprecedented population growth (>300 %) was recorded, with a particularly high rate after the year of 2010, contingent on markedly increased seed viability, that significantly correlated with summer air temperature rise. The obtained changes are part of reponses to summer and winter regional climate warming and associated elevational treeline advance, encompassing the past 100 years or more. At a local scale, soil temperatures during the winter have increased over the past few decades, which has reduced the incidence of needle and shoot injuries and ensuing individual mortality, caused by winter desiccation and fine root dysfunction. Over the same period of time, winter precipitation (snow cover) has decreased. The latter circumstance implies earlier snow melt and a lowered risk of mechanical stress to young seedlings and saplings, as well as injuries by parasitic fungi. Another important aspect of decreased winter precipitation is that the growth period is prolonged, which may be a benefit to an evergreen species like *Pinus sylvestris*. The future evolution of the pine treeline ecotone is uncertain, given the unpredictable character of future climate change and its interactions with extant forest communities. Nevertheless, we may be currently witnesssing an embryonic new treeline ecotone under evolution, with pine as an increasingly important subalpine constituent.

Keywords: Treeline ecotone transformation, *Pinus sylvestris*, young-growth demography, seed viability, climate change, soil temperatures, Swedish Scandes.

INTRODUCTON

Pine (*Pinus sylvestris*) is currently on a general rise in the Swedish Scandes. Given that the climate trend of the recent past prevails, it may eventually transform the structure and position of the treeline ecotone and gain predominance over mountain birch (*Betula pubescens* ssp. *czerepanovii*) (Kullman & Öberg 2022, 2023a). That is what this paper is about, embodied in Figure 1.

Figure 1: Since the turn of the century, growth and reproduction of Scots pine (*Pinus sylvetris*) has increased markedly in the southern Swedish Scandes. Pine is currently spreading and invading snow-poor subalpine heaths. Early pioneers have produced abundant offspring during the past 20-30 years. Since 1998, the pine tree in the centre, that germinated in the late 1950s, has increased in height from 2.1 to 5.5 m. Mt. Storsnasen 690 m a.s.l. *Left.* 1998-11-10. *Right.* 2025-03-29.

On a general level, it has been stressed that "the aim of ecology is to see what happens in Nature" (Sjörs 1979). Accordingly, and in the modern era of ecological and societal concern with alleged future climate warming, it is increasingly recognized that time (past, present and future) is a fundamental aspect of ecological analysis and comprehension (e.g. di Castri & Hadley 1985; Franklin 1987; Gitzen et al. 2012; Lindenmayer et al. 2012; Wolkovich et al. 2014). In particular, different dynamic aspects of the alpine treeline *s.str.*; isolated trees > 2 m tall, and the treeline ecotone, i.e. the transition between closed forest and alpine tundra, constitute indicators of climate-mediated ecological and biogeographic change. Although differently defined by individual researchers, these concepts are recognized to be controlled ultimately by heat deficiency and may vary expressionally in concert with air temperature and snow cover varability, modulated by local topography and associated ecological variables (Aas 1969; Tranquillini 1979; Grace & Norton 1990; Kullman 1998, 2021a; Lavoie & Payette 1992; Smithson et al. 2002; Holtmeier 2009; Körner & Paulsen 2004; Kharuk et al. 2009; Hagedorn et al. 2014; Wieser et al. 2014; Paulsen & Körner 2014; Bruening et al. 2018; Trant et al. 2020; Dandan et al. 2022; Grigoriev et al. 2022; Kullman & Öberg 2023a, 2024a).

Surprisingly few studies do report long-term observational demographic time-series of natural tree species populations in cold-marginal situations (but see Tasanen et al. 1998: Juntunen et al. 2002; Juntunen & Neuvonen 2007). In contrast, projective model studies, with more or less realistic assumptions of future climate evolution and variable amount of direct recent biogeographic observational support, are legio (Kellomäki et al. 1997; Moen et al. 2004; Kaplan & New 2006; Sormunen et al. 2011; Matías & Jump 2012; Bognounou et al. 2018; Barredo et al. 2020).

In the case of seed-regenerating invasive tree taxa, such as *Pinus sylvestris* (cf. Richardson & Bond 1991), continous monitoring studies of demography (natality and mortality), particularly focusing on seed viabilty and early stages of plant life, are indispensably needed for the development of solid treeline theory, and comprehension of the past, as a basis for predictive modeling of the treeline ecotone in a proposed future warmer world (Moore 2003; Mamet & Kershaw 2012; Wieser et al. 2014; Normand et al. 2014; Trant et al. 2020). In this context, consistent upslope advance of *Pinus sylvestris* treeline and densification of marginal stands during the past 100 years are evidenced from different parts of Fennoscandia (Hustich 1958; Kullman 1981, 2007, 2017; Kullman & Öberg 2009, 2023b; Aakala et al. 2014). This course of change is suggested to progress furher, given that recent climatic trends prevail unabatedly (Holtmeier 2005; Bognonou et al. 2018; Kullman & Öberg 2023a,b), although questioned by Young et al. (2011).

Nevertheless, the dominant subalpine birch belt (*Betula pubescens ssp. czerepanovii*), fringing the alpine tundra in the study area, is currently largely stable in position (Kullman 2022), although recently beeing invaded or even leapfrogged by sparse pine trees (Kullman & Öberg 2023a,b). This kind of biogeographic transformation and stability is analogous to pine (*Pinus wallichiana*) and birch (*Betula utilis*), displaying species-specific performances in the Karakoram-Himalaya (Ali et al. 2002) and *Pinus peuce* in Bulgarian mountains (Meshinev et al. 2000).

In this paper we report and analyze annual surveys of demographic change (1973-2024) of pine (*Pinus sylvestris*), recorded in permanent plots within the treeline ecotone of the southern Swedish Scandes. These aspects have been casually addressed in prior studies at a landscape level and with a long-term historical perspective (Kullman 2007, 2014, 2017, 2018, 2021a,b; Kullman & Öberg 2022, 2023a,b). Here these studies are updated and complemented with a strict attention to local-scale early-life population dynamics in the same region.

The main focus is on the relative effect on treeline ecotonal performance of summer and winter temperatures, respectively. Advocates of the former option, soil temperatures in particular, are Körner & Paulsen (2004), contrasted with more balanced views, stressing the importance of both summer and winter conditions (e.g. Lavoie & Payette 1992; Payette 2007; Kullman, 2007; Devi et al. 2008; Harsch et al. 2009; Kharuk et al. 2009; Mathisen & Hofgaard, 2011; Elliott 2012; Shiyatov & Mazepa 2015; Petrov et al. 2015; Trant et al. 2020; Hansson et al. 2021; Grigoriev et al. 2022).

STUDY AREA

This study encompasses the floor and northern part of the Handölan river valley in the southern Swedish Scandes (Fig 2). The area trends north to south c. 40 km, from Lake Ånnsjön (526 m a.s.l.), extending from boreal forest up to the treeless high-montains and plateux around the massifs Sylarna and Helags (c.1000-1800 m a.s.l.). Stands of *Picea abies* and *Pinus sylvestris* prevail on the lower slopes and floor in the northernmost 4-5 kilometers of the valley. Gradually towards the south, these stands trail off and are gradually replaced by subalpine mountain birch forest (*Betula pubescens* ssp. *czerepanovii*), reaching 950-1000 m a.s.l., and about 30 km south of the valley mouth.

Just prior to the 20th century, the floor of the valley harboured old-growth stands of pine, which had thinned year by year during the Little Ice Age, AD 1300-1900 (Grove 1994), and were eventually replaced by pure and dense birch forest (Fig. 3). This situation was described by local eye-witness reports by competent botanists and geographers (e.g. Sernander 1899) and in retrospect documented as a generic historical pattern in northern Fennoscandia by analyses of radiocarbon-dated megafossil tree remains (Kullman 1987, 2015; Kullman & Öberg 2021b). Within the valley here concerned, the treelines (defined above) of *Betula, Picea* and *Pinus* are positioned about 975, 865 and 800 m a.s.l., repectively. *Betula* and *Picea* have shifted upslope by 215, 180 altitudinal meters, respectively, during the past 100 years, concurrent with regional temperature rise, predominatly by phenotypic respones of old-established individuals Concurrently, the treeline of *Pinus* has advanced by 130 m, achived mainly by migration of seed-generated specimens (Kullman & Öberg 2022).

Plots were spaced within the lower part of the closed subalpine mountain birch forest at the transition to the uppermost closed pine stands or solitary trees. The ground-floor vegetation is composed predominnatly of sparse mat-forming dwarf-shrubs; *Calluna vulgaris, Betula nana, Empetrum hermaphroditum, Vaccinium vitis-idaea, Kalmia procumbens, Diapensia lapponica and Arctous alpina,* growing on podzolic soil with a maximum snow depth of 0.2-0.3 m. Frequently, open patches with remnants of lichen thalli (*Cladonia* spp.), grazed by reindeer, prevail between the dwarf-shrubs, which has enhanced cryogenic processes, creating minor mounds.

Prior to the past century, the valley forests were more lichen-rich than today (Sernander 1899). Intensified reindeer grazing and trampling over the past 100 years (Kullman 2017) have reduced the lichen cover to the favour of pine. Possibly, this course of change relates to increased soil temperature, enhanced nutrient cycling and removal of the “barrier” to germination, establishment and early growth growth imposed by allelopathic effects associated with a dense cover of dwarf-shrubs and reindeer lichens (Sedia & Ehrenfeld 2003; Kullman 1981, 2017; Weih & Karlsson 1999; Tømmervik et al. 2009). However, the direct impact of reindeer browsing on extant pine growth is found to be relatively small (Kullman 1981). Disturbance by fire is part of the natural history of the study area; with little currently discernible impact on the extant arboreal structure in the study area (Kullman 1983; Kullman & Öberg 2022).

This valley and its Quaternary geology, climate, past and present plant cover, treelines and land use, are accounted for by Lundqvist (1969), Borgström (1979), Kullman (2013), Kullman & Öberg (2022). The plots are located close to the pine treeline as it was positioned by the end of the Little Ice Age and until the mid-1970s. Thereafter, the treeline, in the form of scattered young pine trees, has migrated about 12 km southwards into the valley and to a 100 m higher elevation (Kullman & Öberg 2022).

The climate is intermediate oceanic and continental. Data (1991-2020) from the nearest official weather station, Storlien/Storvallen (583 m a.s.l.), c. 20 km northwest of the study area, have been compiled from the Swedish Metrological and Hydrological Institute. Mean temperatures for the periods December-Februari and June-August are -5.3 and 10.9 °C, respectively. Annual mean temperature and precipitation are 2.0 °C and 921 mm, respectively. Former local mining, summer livestock grazing and haymaking have impacted the local landscape by selective felling of pines and spruces (mostly dead trees), conceivably not to the extent that tree distributional

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limits have been affected. Although, removal of old-age trees may have reduced the seed-source basis for advace of the treeline. The entire valley is part of an ancient Sami and summer farming cultural landscape, which has left subtle traces, here as well in any other parts of the Scandes (Löffler et al. 2004; Eriksson et al. 2007; Bryn 2008; Josefsson et al. 2009).

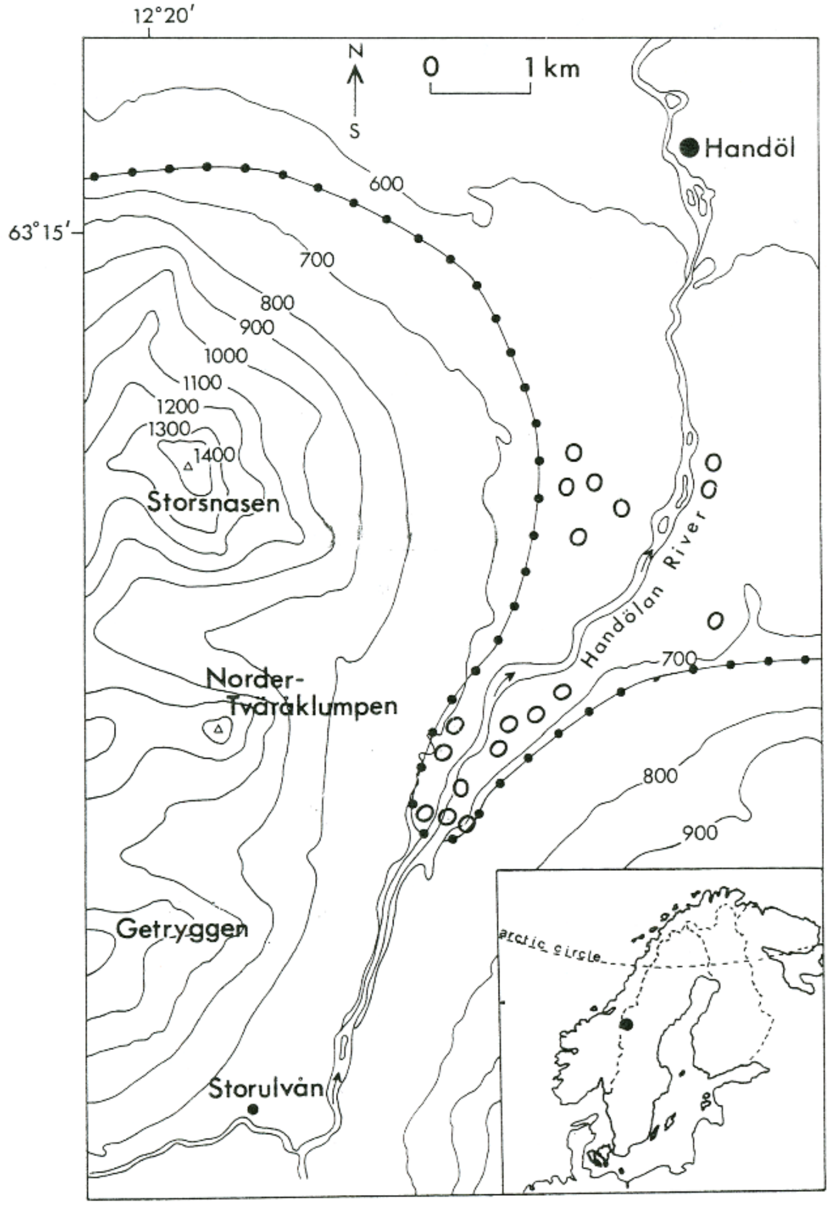

Figure 2: Map showing the location of the permanent plots (circles) and the maximum extent of the pine treeline by the early 20th century (filled black circles). Mountain birch forest prevails further some 20 km towards the south and clads the mountain sides.

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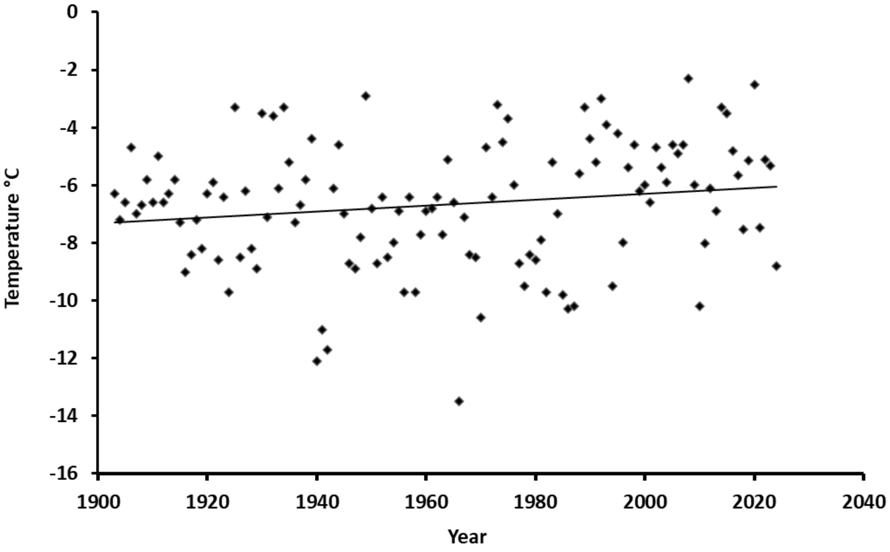
Figure 3: Remnant pine representing prior pine stands right to the south of the permanent plots (690 m a.s.l.), which died during the Little Ice Age, around the mid-16th century. At the present day, heath birch forest, with a dense under-storey of dwarf-shrubs, prevails at this site. 2024-08-25.

This study is broadly contextualized by regional air temperature evolution since the early 20th century, recorded at Storlien/Storvallen meteorological station (see above). Figure 4 displays annual mean monthly records for the summer (June-August) and winter (December-February) periods, 1901-2024. These parameters have increased by 1.8 and 1.4 °C, respectively. Notably, a cluster of relatively mild winters prevailed after the late 1980s and up to the present day, following on a cold-dip during the 1940s to the 1980s. This pattern is discernible also for the summer period although less pronounced. Since the mid-1990s, both early- and late winter precipitation have decreased substantially, yielding a reduction of the snow depth by about 20 cm (Fig. 5). Over the same 29 years, regional subalpine snow melt and growth season initiation in this valley have occurred earlier by at least two weeks (Kullman & Öberg 2023a).



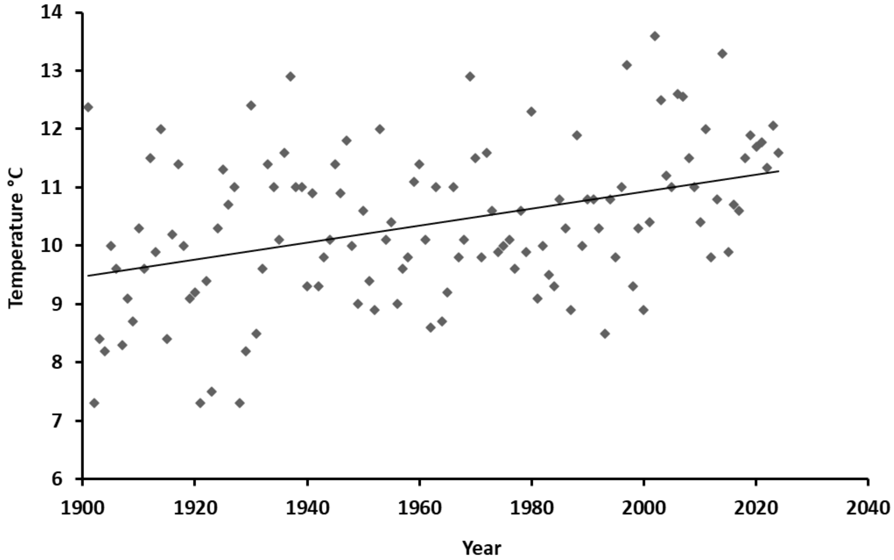


Figure 4: Mean annual air temperatures recorded at Storlien/Storvallen meteorological station 1901-2024. *Upper*. December-February. *Lower.* June-August.

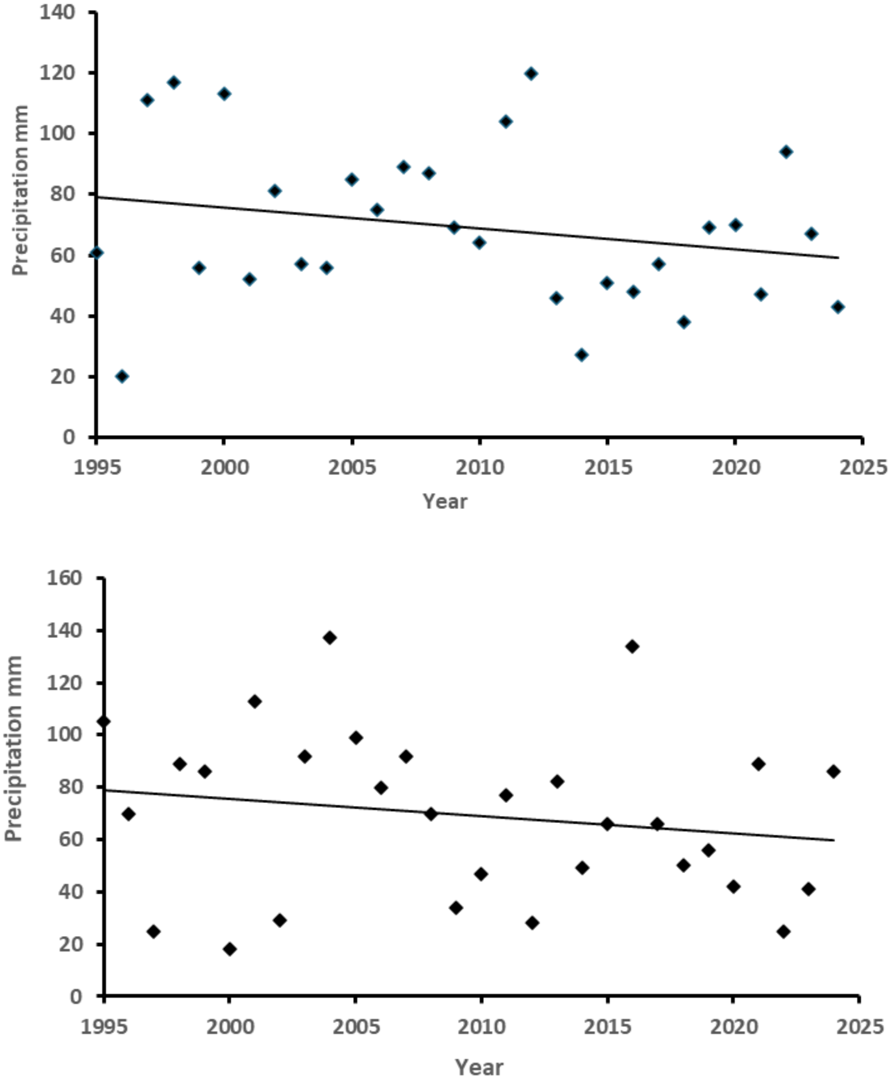


Figure 5: Annual records (1995-2024) of mean precipitation for the periods January-March, November-December, *upper* and *lower* respectively at Storlien/Storvallen meteorological station.

METHODS

This study draws on a set of 18 premanently marked plots (10 x10 m), anually surveyed 1973-2024, with respect to recruitment, individual mortality and injuries. Plots, distributed 670-715 m a.s.l., were randomly located around or adjancent to solitary old-growth tree-sized pines (200-400 years old), including their nearest offspring, within the pine treeline ecotone in the Handölan river valley, Swedish Scandes (Fig. 2). All plots are close to the treeline position prevailing during the early 20th century, following the common pine retraction durning the Little Ice Age, prior the the onset of the modern climate amelioration.

In addition to the count of the number of living pines, each annual survey (late summer) included a visual assement of the freqency of saplings with more than 20 % of the foliage dead (reddish needles) during the current-year winter, as well as a count of saplings that had died since the previous census. Other injuries were noted, e.g. fungi infection or mechanical impacts by reindeer or moose.

Annually, by the late winter, 25 cones were collected from the south-facing side of a total of 10 veteran pines, depicted in Figures 8 and 12. Germinabilty (%) was tested in the laboratory according to the procedure described by Kullman (1984).

Since 1985, root zone temperatures (30 cm below the ground surface) have been recorded by resistance thermistors (TO-03R), manufactured by T. Johnsson Inc., in one of the sample plots (Fig. 8). At this level, short-term temperature variations are significantly damped (cf. Harris 2001; Körner 2007). Thus readings once a week would provide a fairly true representation of relevant annual variations in soil temperature regime for the winter and summer periods. For the present study, the lowest records of February-March and the highest for June-August are presented. A more detailed account of the sampling approach and the setting is given by Kullman (2021a).

RESULTS

Demographic Evolution

A composite annual population account of the total number of living pines, encompassing all 18 permanent plots is shown in Figure 6. This is the net outcome of both natality and mortality. Over the years 1973-2000, the sapling cohorts were quite stable in numbers, followed by a minute rise until 2010. Subsequently, a dramatic and prolific growth in plant density took place, particularly in the most exposed plots, with a sparse ground- and birch cover. Seedling/sapling densities of >50 000 ha was locally recorded in the near circumference of the old-growth and putative mother pines and partly included in some of the permanent plots.

After the early 1970s, the entire population has increased by > 300 %. Following 2013, observed individual mortality has been insignificant (annually < 1%), particularly when viewed in relation to the size of the expanded population (Fig. 7). The average size in 2024 of the population members (all 18 plots with mother trees excluded) is 0.7±0.3 m. Prior to the mid-2010s, winter desiccation and ensuing mortality were conspicuous phenomena in the treeline ecotone (Kullman 2007, 2014; Kullman & Öberg 2023b).

To the best of knowing, young growth crowding of this magnitude is previously never recorded in the treeline ecotone of the Scandes. The general character of some of the last-mentioned plots, as they presently appear during summer and winter, is shown in Figures 8-14.

Conspicuously, most of the study plots show scattered signs (decaying logs) of having been gradually deprived of pine tree growth during past cold centuries of the Little Ice Age (Kullman 1987; Kullman & Öberg 2021b (Figs. 11 - 13).

No signs of fungi infections, reindeer or moose interactions with extant pines were recorded during the past few decades, although that kind of stress was quite common in the plots during the first three decades of monitoring, as well in other parts of the region (Kullman 2014).

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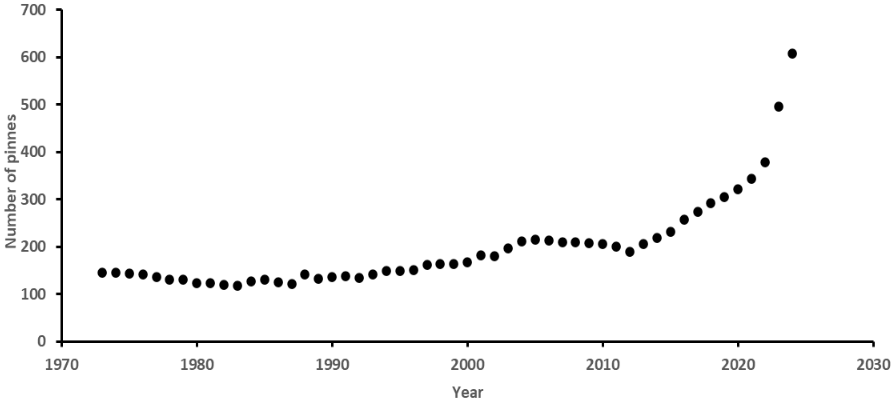

Figure 6: Total counts of living pines (seedlings and saplings), annually sampled as the pooled population of the 18 permanent plots.

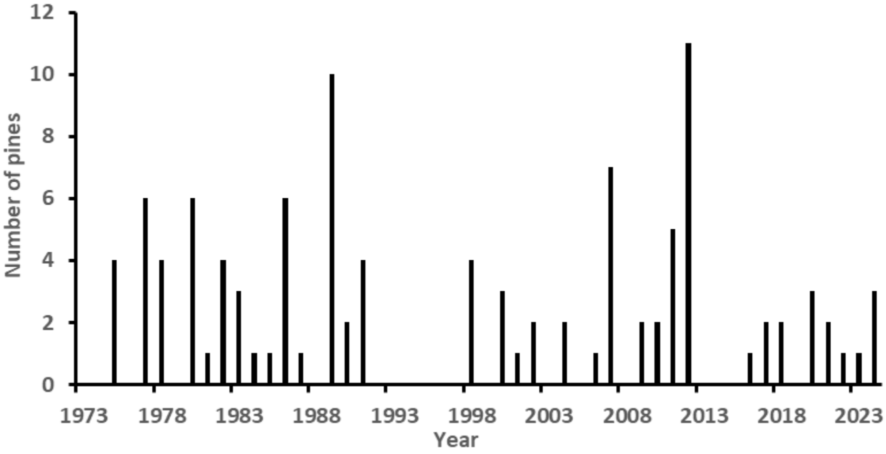

Figure 7: Annual individual mortality, composite sample of all 18 plots.

Figure 8: Summer view of one permanent plot (680 m a.s.l.) that contains an old-established tree, which germinated in the late 17th century. Soil temperature recordings were carried out

close to that old tree. The ground cover is predominantly *Calluna vulgaris*, and interspersed patches with remnant lichen thalli (*Cladonia* spp.). The latter feature is a consequence of intense reindeer grazing and trampling. 2024-06-25.

Figure 9: During the late winter, saplings are partly or totally hidden by the snow cover and are still vulnerable to late-winter weather hazard. That kind of stress has virtually not manifested during the past 30 years. *Upper*. 2023-04-11. *Lower*. 2025-03-07.

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Figure 10: Young pine saplings and seedlings are part of continuous recruitment over the past 20-30 years. 2025-03-07.

Figure 11: Pine remnant in the exposed and deforested (Little Ice Age) plateau to the west and windward of the permanent plot depicted in Figures 8-10. 2025-03-07.

Figure 12: Permanent plot, extending from a closed pine grove into local open subalpine tundra (670 m a.s.l.), where decaying tree remnants indicate that a pine tree stand prevailed during the Medieval Climate Optimum and until the end of the Little Ice Age. The stump in the foreground was radiocarbon dated AD 915, when the pine stand had a wider extension towards open subalpine heath. 2023-05-30. Source: Kullman & Öberg (2021b).

Figure 13: Permanent plot situated at transition between pine- and birch forest, where the current pine regeneration pulse is regaining ground lost during the Little Ice Age. 690 m a.s.l. 2025-03-11.

Figure 14: Permanent plot (695 m a.s.l.) centred on two ancient parent pine trees. By the early 1970s, this plot embraced 10 young pines, 0.3-2.0 m tall. Three of these are now full-grown trees, and the plot contains 25 saplings, 0.2-1.2 tall. *Left.* 1979-02-21. *Right*. 2025-03-14.

Seed Viability

In the case of pine, production of viable seeds is a vital aspect of population and treeline dynamics. Notably, a distinct step towards steadily higher viability emerges after the year 2000 (Fig. 15).

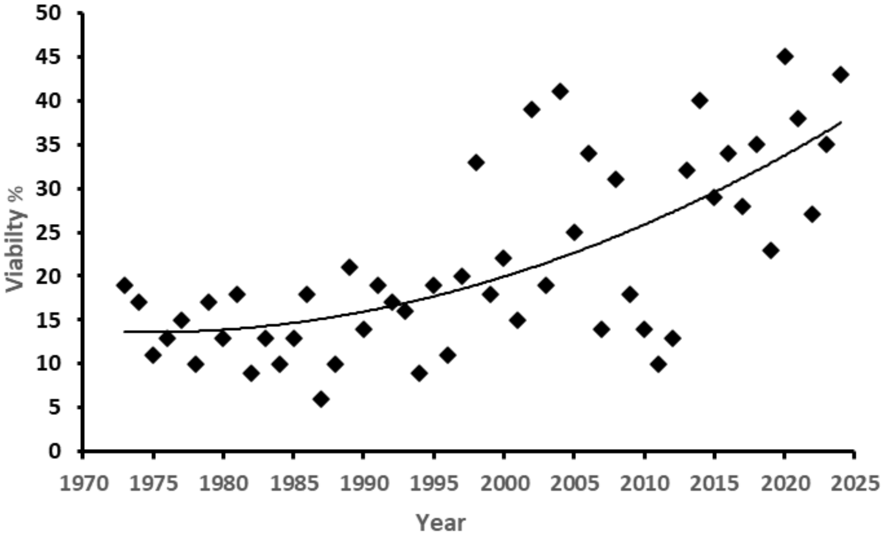


Figure 15: Seed viability recorded annually as a pool from 10 trees within two of the most exposed sample plots.

Winter Defoliation and Other Stressors

Foliage dieback manifested as reddish needles is recognized as an obstacle to pine regeneration in the treeline ecotone. The principal mechanism is commonly considered to be winter desiccation of needles and shoots, because of low (sub-zero) ground temperatures, with water replenishment constricted (Tranquillini 1979; Ritari 1990; Kullman 1990; Veijola 1998; Tuovinen et al. 2005; Kullman 2007; Holtmeier 2009). The present data set shows that this kind of stress syndrome was regularly occurring until the mid-1990s. Thereafter, it has virtually ceased (Fig.16). In contrast to earlier periods (cf. Kullman 2014), mechanical injuries caused by reindeer rubbing their antlers against young pines have been virtually absent during the past few decades. The same is true concerning fungi infestations (*Phacidium infestans* Karst.).

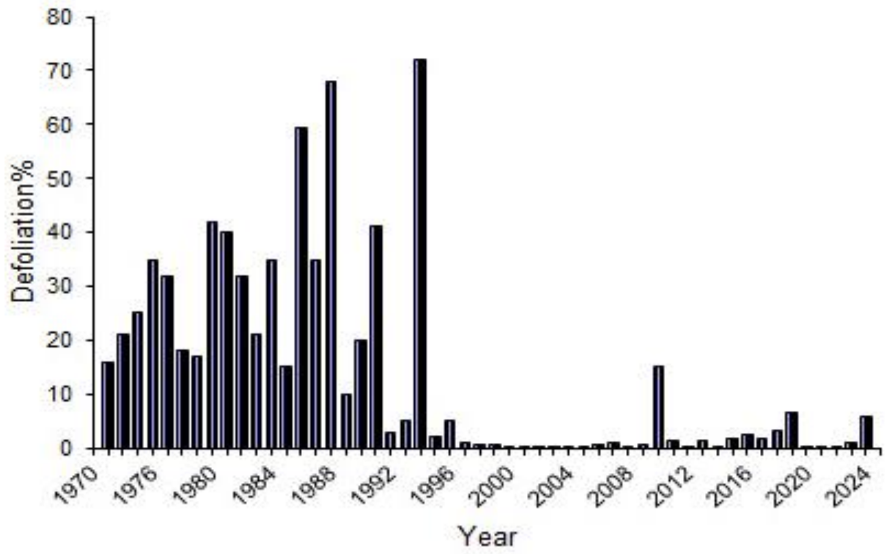
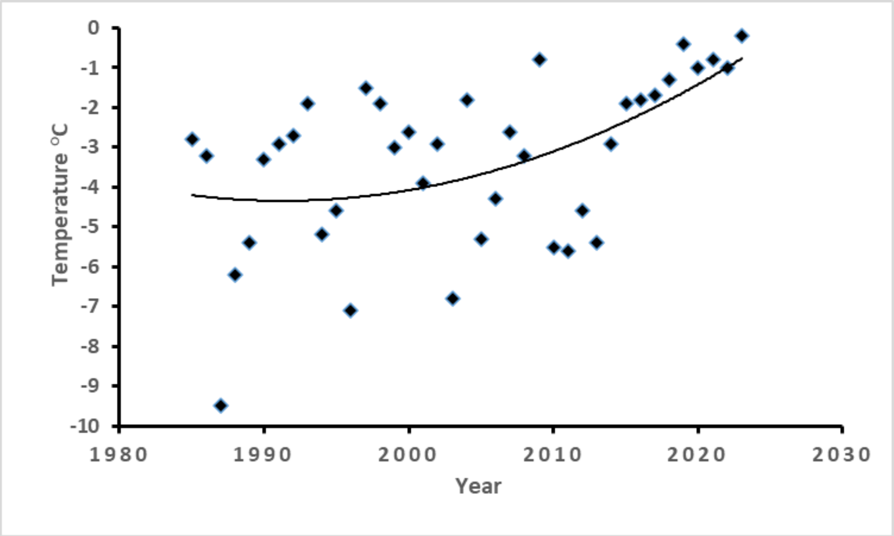


Figure 16: Annual frequency of pines (18 plots) that had suffered > 20 % defoliation (reddening) of the extant foliage.

Soil Temperature Records

Following a nadir by the late 1980s, soil temperatures (summer and winter) have consistently increased up to the present day (Fig. 17).



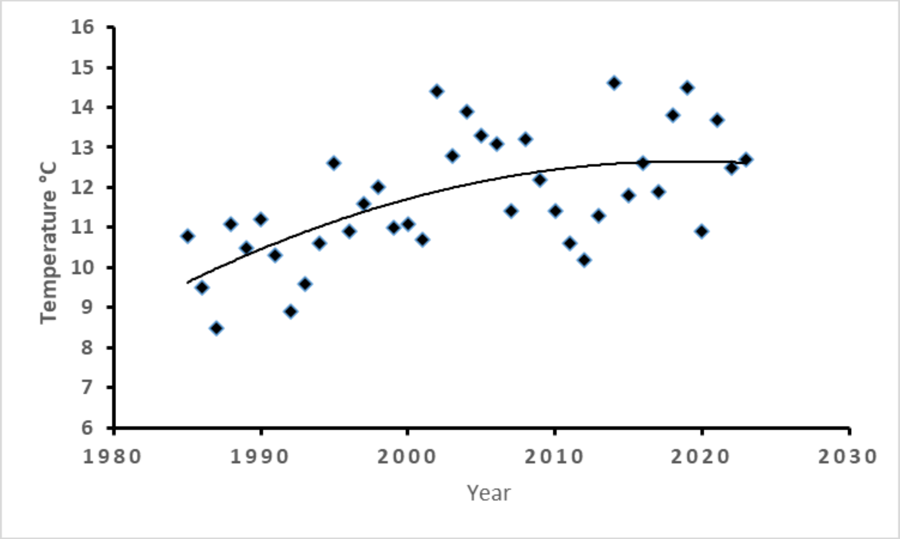


Figure 17: Annual soil temperatures, February-March (*Upper*) and July-August (*Lower*), recorded within one of the permanent plots.

DISCUSSION

In all temporal and spatial scales, *Pinus sylvestris* growing at the upper margin of the boreal forest relates to a continental climate with a sparse snow cover. That contention, as expressed by performance during the recent past and with a possible bearing on the future (Kullman 2017, 2021b; Kullman & Öberg 2022), is supported in detail by the present study.

Current pine progression in the Swedish Scandes, is ultimately contingent on the warmer climate, which discontinued the cold centuries of the Little Ice Age, AD 1300-1900 (see above). During that interval, pine treeline in the region was depressed 100 m or more in altitude, and upper pine stands became increasingly sparse, due to insignificant regeneration and mature tree mortality (Kullman 2013, 2015; Linderholm et al. 2014). Thereafter, in concert with a general climate warming and landscape-scale biotic "thermophilization", manifested e.g. by sparse encroachment of broad-leaved nemoral tree species into the subalpine birch forest (Kullman 2019, 2023; Kullman & Öberg 2022). Concurrently, treelines of boreal species have responded progressively. In the southern Swedish Scandes (the study area included) maximum elevational treeline advances by more than 200 m took place up to a position, that may be unsurpassed during the past 7000 years (Kullman & Öberg 2009; Kullman 2017). Prior to that, during the Holocene thermal optimum (Helmens et al. 2018; Paus 2021), pine was a dominant tree species at forest-alpine tundra transition, locally extending 600-700 m higher than today (Kullman 2013; Kullman & Öberg 2020, 2024b).

To the best of knowing, the obtained local pine population rise by > 300 % since the early 1970s is remarkable in the perspective of recorded treeline dynamics in the Swedish Scandes and elsewhere in Fennoscandia, with a possible bearing on future course of change and evolution of the treeline ecotone.

In contrast to the treeline, the upper limit of closed pine stands, as well as other tree species ("forest limit"), has remained virtually constant in position over the past 100 years (Kullman & Öberg 2022). This pattern complies with evidence from other parts of northern Fennoscandia, although sparse marginal stands are commonly found to have densified (Kallio et al. 1971; Kullman 1981; Hustich 1983; Franke et al. 2015; Vuorinen et al. 2017; Kullman & Öberg 2023a). Widely scattered well-grown young pine trees, growing high above the studied plots, suggest that, in terms of climatic tolerance, stands of pine should be able to exist at much higher elevations than manifested today (Kullman 2017).

Since forest limits of *Betula*, *Picea* and *Pinus* have not shifted substantially in elevation during the past 100 years (Kullman 2021c, 2022), it is likely that future climate-driven change will predominantly concern tree species diversity within the realm of present-day tree- and forest cover, or formation of outlier stands, rather than broadscale shifting of present-day zonation patterns. That notion is supported by paleoecological data, representing warmer-than-present periods in the distant past (Kullman & Öberg 2020).

Apparently, any broad-scale elevational migration of closed pine stands presupposes reduction of the dense subalpine birch forest (Kullman 1981; Holtmeier & Broll 2011; Hofgaard et al. 2013; Kullman & Öberg 2022), which often acts as a filter, preventing extensive and abundant seed dispersal and consequent stand expansion (Wistrand 1981; Kullman, 2010, 2021b). That contention gains support from the fact that the abundance of young pine growth was most conspicuous in plots fringing open and treeless sites, e.g. convex or flat low-alpine heaths or open mires (Figs. 8 - 13). A further obstacle to pine establishment in subalpine birch forest is a dense ground cover in combination with deep and late lying snowpack, exerting stress by protracted snowmelt and persistent ground frost. This hazard is most critical during the late spring, when sun radiation is particularly high and may impose severe tissue desiccation. Accordingly, a previous study indicated that a maximum snow depth of 0.2-0.3 m offered optimal conditions for pine regeneration and growth at the treeline (Kullman 1981). That contention is further supported by the present study.

The pine progression focused on in this study represents a kind of partial reclamation of pine habitat lost during the Little Ice Age (Kullman & Öberg 2021b), although the tree cover structure prevailing during the preceding Mediaeval climate anomaly has not been fully restored. Analogous state of the art is experienced in subarctic Canada (MacDonald 2010), which further stresses the idiosyncratic responses to climate change by treeline and forest line (Kullman 2021b). Only time will tell whether closed stands will keep up with the treeline.

The documented course of change is broadly in concert with regional summer and winter air and soil temperature rise (Figs. 4, 5, 17), although at odds with suggestions that milder winters cause reduced growth (Linderholm 2002). Thus, according to the present results, pine treeline performance cannot be exclusively contingent on thermal conditions during the summer period, as generalized by Körner & Paulsen (2004). Notably, winter precipitation has decreased throughout the entire observation period, particularly after 2012, coinciding with enhanced population growth (Fig. 5). This contention is in line with records in the Canadian Rocky Mountains (Trant et al. 2020). Overall, winter conditions appear as a vital part in pine performance in the treeline ecotone (Kullman & Öberg 2024a).

A shorter snow period also and a thinner snowpack reduce the risk of pathogenic fungi infections by e.g. snow blight (*Phacidium infestans*), as well as break of young stems (Holtmeier

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2009; McKinney et al. 2009). In addition, early snow melt enables evergreen pine to benefit from a longer growth period (Kullman 1981; Oksanen & Virtanen 1995; Kullman & Öberg 2022). Furthermore, experiences from practical forestry in the north have evidenced impaired survival of young pines at sites in the local topography with a particularly long-lasting snow cover (Hagner 1975; Holm & Kullman 1983). Accordingly, the present results are at odds with experimental studies, indicating reduced prosperity of pine seedlings in response to a thinner snow cover (Domisch et al. 2018).

This most recent phase of conspicuous ecotonal pine transformation, displayed by the present study, contrasts sharply with pine treeline stress and recession during the frigid years of the 1980s. During that period, mortality of saplings and mature trees were conspicuous features on the high-mountain landscape in northern Fennoscandia and the local treeline retreated locally and marginally (Mikola 1978; Kullman & Högberg 1989; Kullman 1991).

A high rate of seed viability is a prime prerequisite of pine population growth and treeline rise. In general, production of viable seeds, depends on relatively favourable summer thermal conditions during a sequence of at least three consecutive years, while the entire regeneration process is a complex multi-year affair (Holtmeier 1974, 2009; Hustich 1978; Mikola 1978; Kullman 1981). Optimal conditions in these respects have been constantly fulfilled in the study area since about the year 2000 (Fig. 4). In that perspective, the present case of population expansion is understandable in terms of seed germination success over the past 20-25 years or so (Fig. 15). Accordingly, seed viability and summer temperature (J, J, A) were positively correlated ($r^2 = 0.526$, $P < 0.01$). In the context of recent population proliferation and growth progression, a complementary factor is the drastic reduction of winter foliage dieback and individual mortality over the past 10 years (Figs. 7 & 16), which make sense with above-average winter air and soil temperatures (Figs. 4 & 17).

The present narrative concerning growth progression of treeline pines is further substantiated by enhanced height-growth of old-established krummholz pines in this specific area (Kullman & Öberg 2024a).

Any discussion of pine regeneration at the treeline needs to consider ground cover structure and dynamics (cf. Zackrisson et al. 1995). In general, treeline pines prefer to establish in plant communities, supported by a relatively thin humus layer and an early melting snow cover, particularly on south-facing hillocks or plain terrain (Wistrand 1981; Kullman 1981, 1983), as displayed by the present study.

Except for *Pinus sylvestris*, other dominant treeline species, i.e. *Picea abies* and *Betula pubescens* ssp*. czerepanovii*) have not responded accordingly, i.e. by individual extra-limital population growth and spread of new individuals or stands to higher elevations above or within their respective treeline ecotones, during the past 100 years or so (Kullman 1986 a, b, 1996 a,b, 2014, 2021c, 2022). That pattern is recorded also by observations in northernmost Sweden (Zackrisson et al.1995; Kullman & Öberg 2016), which falsify general model predictions that *Picea abies* would expand its range in response to alleged future climate warming (Prentice et al. 1991). Idiosyncratic responses of currently prevailing tree species suggest that compositionally and structurally novel treeline communities may develop in the future, given that climate trend of the past 100 years proceed unabated. That option appears as generic pattern world-wide (Edwards et al. 2005; Kullman & Öberg 2009; Macias-Fauria et al. 2012; Trant & Hermanutz 2014; Williams & Jackson 2007).

In summary, higher summer air temperatures and decreased winter precipitation have promoted seed viability and individual height growth, while warmer air and soil temperatures during the winter conditioned survival and sustained growth of young individuals. Thus, a rare coincidence of favourable summer and winter air and soil temperatures has favoured extensive pine proliferation, as a possible embryonic precursor of future ecotonal landscape transformation. Although a controversial effect, rising concentrations of atmospheric CO_2 need to be considered in the context of present-day and future pine progression (cf. Zhu et al. 2016; Wieser et al. 2014).

Present data stress the option that treeline performance is dependent on summer as well and winter weather conditions. It remains to be observed whether the concerned young growth populations will transform into stands of mature pine trees. Given that current temperature trends prevail, that course of profound biogeographic transformation appears conceivable (Kullman & Öberg 2023a, b). However, history learns that climate and high-elevation tree communities perform hazardously and unpredictably (Hustich1978; Kullman 1991; Kuuluvainen et al. 2017; Vinós 2022), which urge for unprejudiced monitoring rather than presumptive and futuristic modelling. Just a few exceptionally cold years, with persistent and severe ground frost and late snow melt, may extirpate pine treeline populations built up over decades, of the kind presented in this paper (Mikola 1978; Kullman & Högberg 1989; Kullman 1991).

CONCLUSIONS

Climate warming in the Scandes and increasing prominence of *Pinus sylvestris* over the past 100 years have initiated a fundamental regional restructuring of entire forest-alpine tundra ecotone.

Since about the year 2010, ecotonal pine populations have progressed dramatically by prolific seed regeneration, consistent with substantially increased seed viability. Possibly, intensified reindeer grazing and trampling have facilitated the recruitment process by reducing the barrier to seed germination and establishment imposed by a dense lichen cover.

The course of change here concerned is ultimately contingent to rising regional summer and winter air temperatures, as well as decreasing winter precipitation (snow).

Importantly, soil temperatures during winter and summer have increased over the past few decades, facilitating intense and successful recruitment. Warmer soils during the winters have reduced the hazard of winter desiccation and fine root dysfunction. These circumstances have lowered the incidence of individual mortality and have contributed to net population growth. In addition, winter precipitation (snow cover) has decreased. Thereby, the preconditions of fungi infections have become reduced. In addition, the growth period is prolonged in its early part, to the benefit of the evergreen pine, which can use a longer period for photosynthesis and growth.

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Overall, the studied pine progression has the character of reclamation of ground lost during the cold centuries of the Little Ice Age, AD 1300-1900.

Continued monitoring will show whether the prevailing young growth pines may attain tree size and reproductive maturity. However, that course is long, conditional and still virtually unpredictable.

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