

Praealpine Spruce (*Picea abies*) Forest Dynamics During the Current Post-Little Ice Age Climate Era: A Case in the Swedish Scandes

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ABSTRACT

This study focuses on structural change of a praealpine stand of Norway spruce (*Picea abies*), in a context of centennial climate warming, in the Swedish Scandes. Progressive stand building followed on the end of the Little Ice Age by the late 19th century. A distinct hiatus of this process occurred during the 1980s, as a consequence of exceptionally cold winters with a sparse snow cover, particularly 1886/87. Extensive defoliation, caused by frost desiccation and fine root mortality, followed and culminated 1994 and 1995. Subsequently, climate warming resumed and stand foliation increased steadily up to the present day, when the forest appears equally healthy as prior to the 1980s. Hereby, recent spruce stand evolution adds to current progressive climate-mediated restructuring of upper montane forests.

Key words. Praealpine forest, *Picea abies*, canopy structure, foliation dynamics, climate variability, Swedish Scandes

INTRODUCTION

The current concern about climate change in the "Anthropocene" has highlighted the importance of the time dimension in ecological research (Wolkovich et al. 2014). Time-series of cold-marginal forest dynamics provide pertinent study objects in this context.

Worldwide, post-Little Ice Age climate warming has changed the face of the living and physical world (Lamb 1982; Grove 1988). In that context, cold-marginal trees and tree stands are generally renowned as efficient sentinels of past and present climate change and variability (Tranquillini 1979; Kullman 1979, 1998; Holtmeier 2009; Körner 2007; Smith et al. 2009). This circumstance motivates their continuous survey and analyses, as a basis of proper landscape management and an independent cheque of meteorological records.

The altitudinal tree- and forest zonation in the Swedish Scandes is currently characterized by an upper broadleaved subalpine birch forest belt (*Betula pubescens* ssp. *czerepanovii*). This belt grades upslope to the alpine tundra and downslope into more or less closed coniferous stands of Norway spruce (*Picea abies*), mixed with birch and scattered pine (*Pinus sylvestris*). According to prevailing phytogeographical terminology, these forests with a high admixture of birch, belong to the "northern boreal forest zone" or "mountain taiga" (Ahti et al. 1968; Kullman 2005), more specifically termed as the praealpine belt (Wistrand 1962). The ecology and long-term successional trajectories of these high-elevation forest have been analyzed and discussed

by some authors (Sirén 1955; Hofgaard et al. 1991; Odland et al. 1992). Hofgaard et al. (1991) evidenced that old-growth and moribund spruce stands, often predicted for autogenic gradual senescence and virtual extirpation, have revitalized between the late 1930s and late 1980s, apparently in response to post-Little Ice Age climate warming (Hofgaard et al. 1991; Kullman & Öberg 2009). However, at more explicit treeline sites, modest crown thinning as well as stand decline were well underway by the early 1970s in the southern Scandes, possibly in response to transient climate cooling following the warm 1930s (Kullman 1988).

The late-1980s mark intensification of regressive stand-level processes, also below the treeline ecotone. Primarily, this was a consequence of a decade with substantial early-winter cooling, in combination with a sparse snow cover and even the spread of sporadic and occasional permafrost, causing frost desiccation and fine root mortality (Jalkanen 1985; Eriksson 1987, 1988; Lindgren et al. 1989; Ritari 1990; Kullman 1989b). All over northern Fennoscandia, cold-marginal tree stands suffered heavy defoliation, canopy thinning and even minor treeline retraction during these years (Raitio & Tikkanen 1988; Kullman & Högberg 1989; Kullman 1989a, 1991 a,b, 1996 a,b; Josefsson 1990; Tuovinen et al. 2005).

By the early 1990s and onwards, climate resumed its prior, centennial warming trend, which halted prior modest regressive ecological processes, which had prevailed for some decades after the 1930s. This most recent climate shift manifested firstly as resumed treeline advance and associated population growth in concert with increased alpine plant species richness (Kullman 2007 a, b; Odland et al. 2010; Michelsen et al. 2011; Felde et al. 2012). Moreover, scattered spread and elevational upshifts of thermophilic tree species was recorded in the subalpine and alpine belts (Kullman 2008, 2010, 2020), which heralds improved climate conditions. Accordingly, recent resurveys of older vegetation records in the coniferous treeline ecotone point to an ongoing structural reorganization and adjustment to a novel climatic situation over the past few decades (Kullman 2019, 2021b).

In this context, little data exist concerning the most recent evolution of the upper closed, praealpine conifer forest stands in the Scandes, right below the treeline ecotone. These forests frequently suffered heavy canopy dieback during the cold phase of the 1980s (references above), when temperatures transiently reverted to near-Little Ice Age conditions, i.e. the coldest period of the entire Holocene (Grove 1988; Leonelli et al. 2010; Ljungqvist 2017).

The main objective of the present study is to display and analyze structural change of a typical praealpine spruce forest stand (*Picea abies*) since the late 1980s and up to the present day. This specifically focused time interval is characterized by climate warming, subsequent to a relatively cold decade with extensive canopy decline locally over much of northern Fennoscandia.

Hopefully, the results may serve as analogues in the context of trials to project future high-elevation landscape ecological evolution in future altered climates.

STUDY AREA

The concerned study site is close to the mouth of Handölan valley in the Swedish Scandes, 63°15'N; 12°26'E, 625 m a.s.l. (Fig. 1). The concerned spruce stand is the last outlier of closed forest towards the south and higher elevations in the Handölan Valley (County of Jämtland).

The tree cover is a mixture of spruce and mountain birch, 60 and 50 %, respectively (Fig. 2). A few old-growth pines are interspersed in the stand together with scattered trees of *Sorbus aucuparia* and *Populus tremula*. The average height of dominant polycormic spruces is 10-11 m, while the birches are 2-3 m shorter. The spruces occur mainly in clusters, as layering clonal individuals, although monocormic and relatively young individuals occur at a lower frequency. The nearest treelines for birch, spruce and pine are at 925, 860 and 800 m a.s.l., respectively, high above the stand focused by this study.

The forest stand is characterized by distinct spruce tree clusters with open treeless glades, maintained for long by abundant snow accumulation (Fig. 2). In these setting, scattered mountain birches and bush-forming junipers (*Juniperus communis*) prevail.

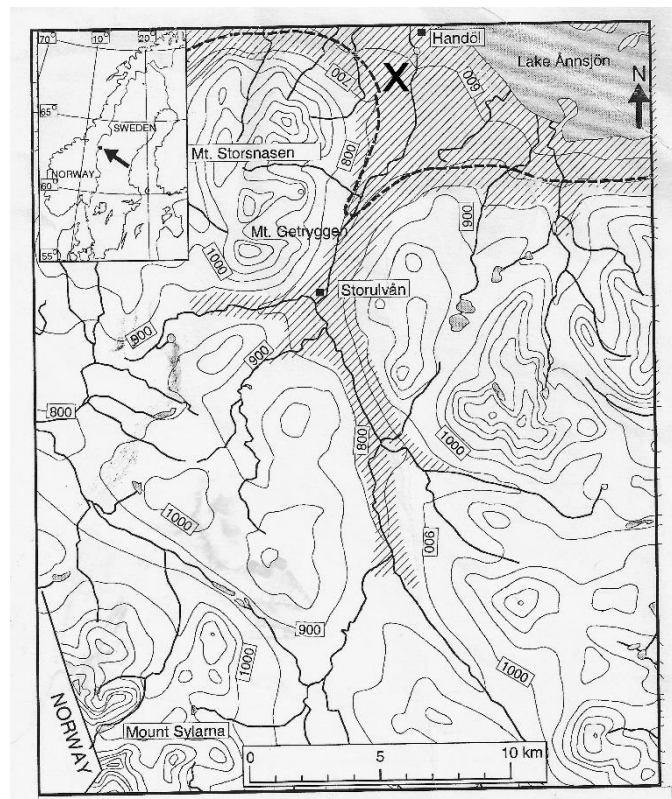


Figure 1. Location map, showing the study area (X) at the mouth of the Handölan Valley in the southern Swedish Scandes. The hatched area denotes the cover of mountain birch forest, fringing treeless alpine tundra. The dashed line indicates the distribution limit of closed conifer stands



Figure 2. Late autumn aerial view of the core of the studied stand, displaying almost equal proportions of spruce and mountain birch. Overall, spruces are currently in a healthy condition, with fully foliated treetops. This appearance contrast with the situation by 1987-1995, when the majority of extant spruces displayed more or less defoliated canopies. 2021-11-01

The field-layer vegetation has the character of dwarf-shrub heath with *Vaccinium vitis-idaea* (dominant), *Vaccinium myrtillus*, *Empetrum hermaphroditum*, *Phyllodoce caerulea*, *Lycopodium alpinum*, *Avenella flexuosa*, *Linnaea borealis* and *Cornus suecica*. Predominant in the bottom layer are *Hylocomium splendens*, *Pleurozium schreberi*, *Dicranum* spp., *Barbilophozia lycopodioides* and *Ptilium crista-castrensis*. A more detailed description of the plant cover is provided by Kullman (1996).

There are virtually no signs of major anthropogenic disturbance to this forest stand, although fire and small-scale selective logging (pine in particular) is part of its history in the past millennium. The stand history was extensively studied by radiocarbon-dated wood remnants, preserved on the ground underneath the moss cover, in combination with static age structure analysis (Kullman 1996).

Following at least six centuries of cold-climate conditions and high-elevation forest decline, spruce dominance developed gradually after the 1850s, in line with post-Little Ice Age warming. Prior to that, pine and birch seem to have dominated the scene for at least 1000 years. The extant spruce-birch stand evolved following major disturbance by fire, and possibly a devastating windstorm in 1837 (Kullman 1996). The latter cataclysmic episode affected high-elevation forests over large regions of northern Scandinavia (e.g. Hagemann 1905).

A prior spruce age structure analysis shows that initiation of new stems within the clones, distinctly peaked in the warm 1930s, followed by gradual decline of stem acquisitions up to the present day (Kullman 1996). The restocking process was ultimately facilitated by rapid growth of new stems, belonging to old-established clones. This course of change has manifested the

structure displayed at the present day and which constitutes the main object of the present study.

Standard-level temperature data (1991-2020), relevant to this study, refer to Storlien/Visjövalen meteorological station, 642 m a.s.l, 13 km NW. The temperatures for January, July and the year are -5.5, 12.3 and 2.0 °C, respectively. Annual precipitation amounts to c. 1000 mm/year.

METHODS

Based on extensive reconnaissance surveys, a representative sample plot (85 x 80 m) was selected for long-term study, with particular focus on the vigor of extant spruces, specifically crown condition. This endeavor was initiated in late 1985. Annually in September or October, assessments were visually conducted as percentage needle loss, to the nearest 5%, relative to a fully foliated tree. The total sample comprised 184 overstorey trees, chosen at random and tagged for repeated monitoring. Multi-stemmed individuals were treated and judged collectively as one entity. Conventionally, the estimates refer to the upper half of the crown (cf. Westman & Lesinski 1986). The character of canopy dynamics was evidenced by repeat photography of a subsample of representative trees. Some of which are presented here.

Soil temperatures were measured in an open space 3 m outside the canopy of a nearby spruce, where relatively large amounts of snow use to accumulate. These measurements were carried out once a week, 1986 to the present day, by a resistance thermistor (TO-03R), manufactured by T. Johnsson Inc. The sensor was installed in the upper mineral soil at a depth of 20 cm and annually calibrated. Because of the thermal inertia of the soil, the measured temperatures quite truly represent thermal soil conditions and their annual variations (Deming 1995; Harris 2001; Körner 2007).

Seed viability was tested annually on a composite sample of cones originating from all surveyed spruces. Ten cones were sampled, representing all aspects of the crown. The germination tests were carried out on moist filter paper in Petri dishes (5x100 seeds). For further details, see Kullman (1984).

RESULTS

The present study takes place in a regional context of oscillating secular summer- and winter climate warming, with a temporary and distinct dip in the 1980s (Fig 3). During that period, local soil summer and winter temperatures were particularly low (Fig. 4 & 5), at the same as a relatively sparse snow cover prevailed (Fig. 6). Subsequently, soil temperatures and snow cover have increased substantially up to the present day. In late-1987, prevailing spruces displayed a high degree of needle browning, with indications of pending canopy decline. During the following years, culminating in 1994 and 1995, needles were extensively shed, with consequent landscape-scale crown thinning. This process was followed by consistent recovery up to the present day. Currently, foliation of the entire stand is even larger than in 1987 (Fig. 7). Overall, stand-level foliation (gain and loss) has changed in congruence with soil temperature and snow cover evolution since 1985.

The character of individual crown foliation dynamics in the study site is depicted in Figure 8-10. An analogous course of change is perceivable also for praealpine stands in a larger landscape-scale perspective (Fig. 11).

Over the entire surveying period, the germinability of spruce seed has increased steadily (Fig. 11), and a certain degree infill of stand gaps has occurred (Fig. 12). However, the spruce forest has not expanded into the surrounding mire/subalpine birch forest mosaic during the past 100 years.

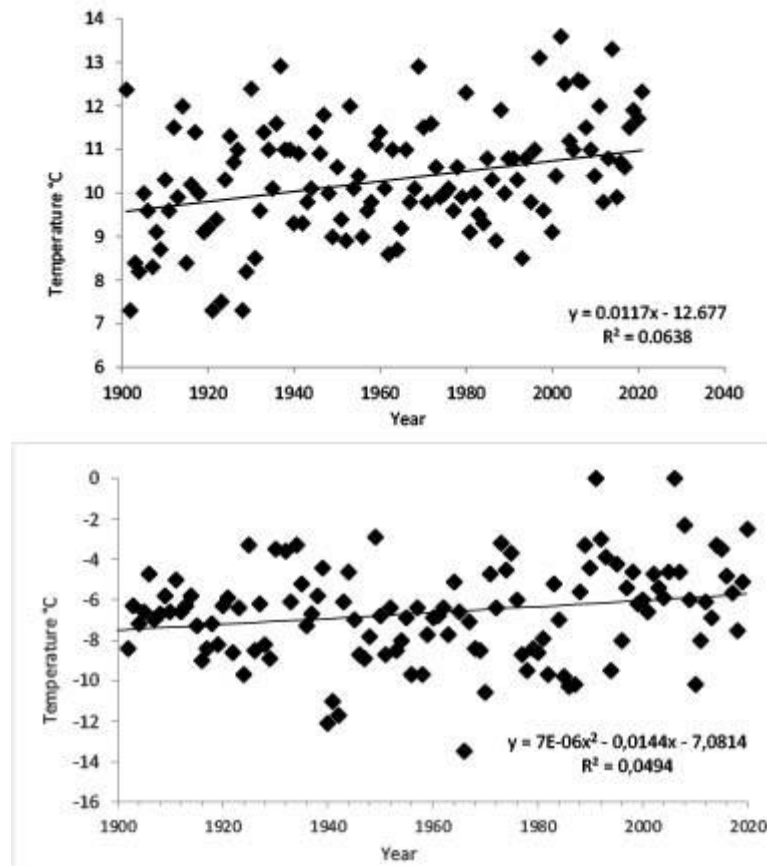


Figure 3. Mean annual regional air temperatures recorded at Storlien/Visjövalen meteorological station (1901-2021). Upper. June-August. Lower. December-February

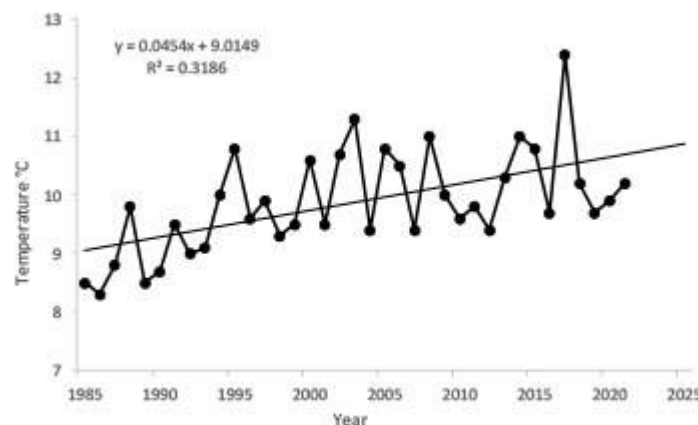
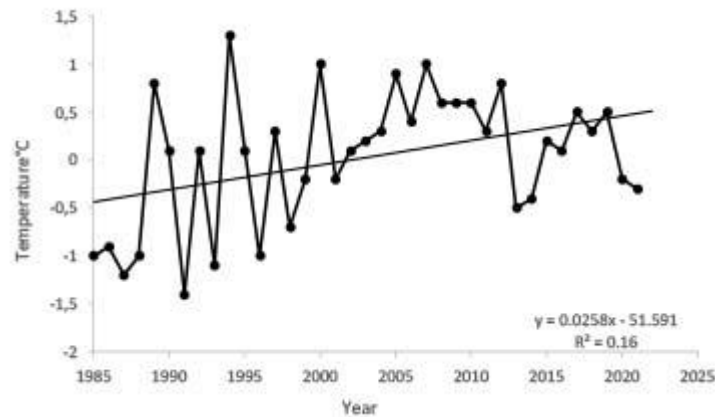
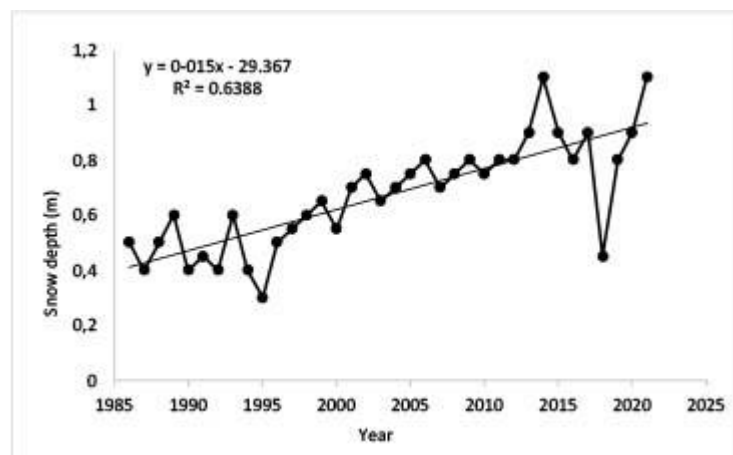
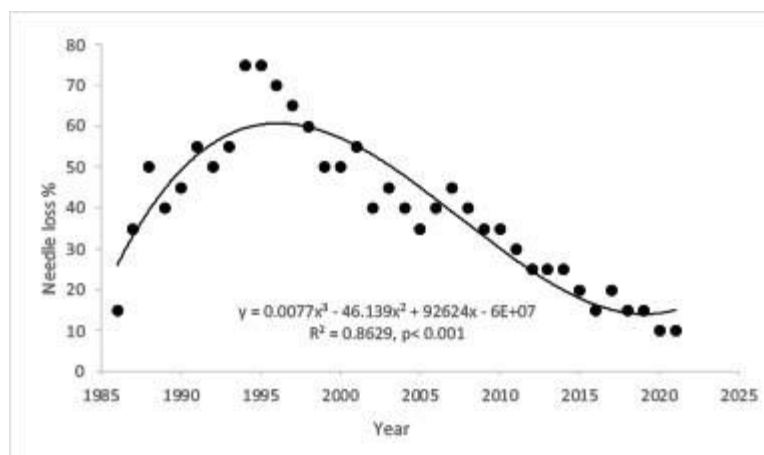


Figure 4. Mean annual soil temperatures (June-August), 1985-2021**Figure 5. Mean annual soil temperatures (December-February), 1985-2021****Figure 6. Maximum snow depth, 1986-2021, in the stand gap close to the soil temperature measuring spot. Annual records and trend****Figure 7. Annual estimates of cumulative needle loss, 1986-2021**

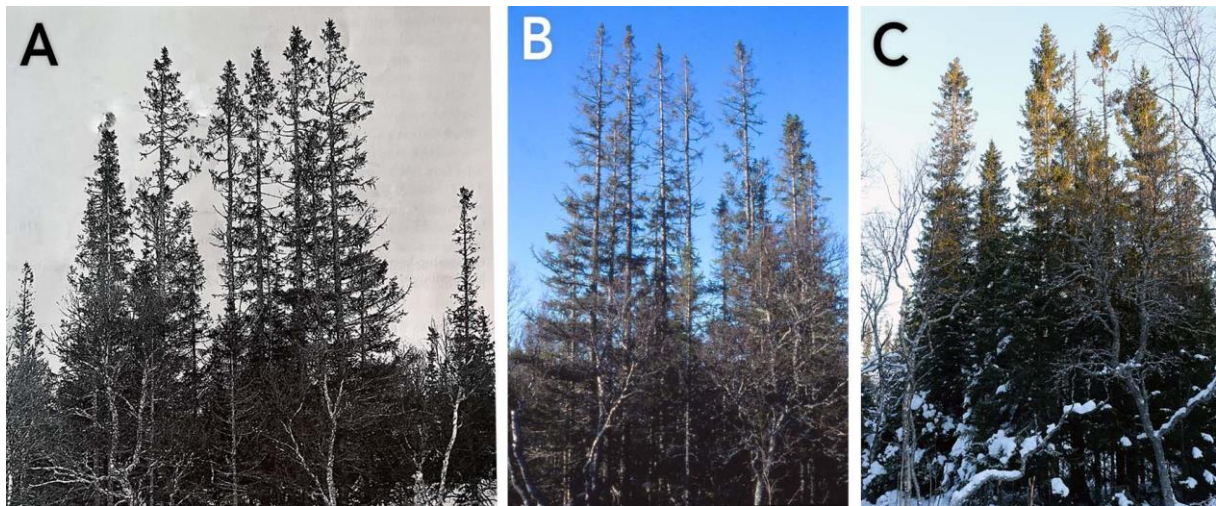


Figure 8. The same clonal group of spruces, captured at three occasions, 1987-2022. Typically, needle loss was perceptible in 1987, but had culminated by 1994-1995. Thereafter, recovery is striking, although one stem is downed. A. 1987-10-15. B. 1994-06-24. C. 2022-01-01

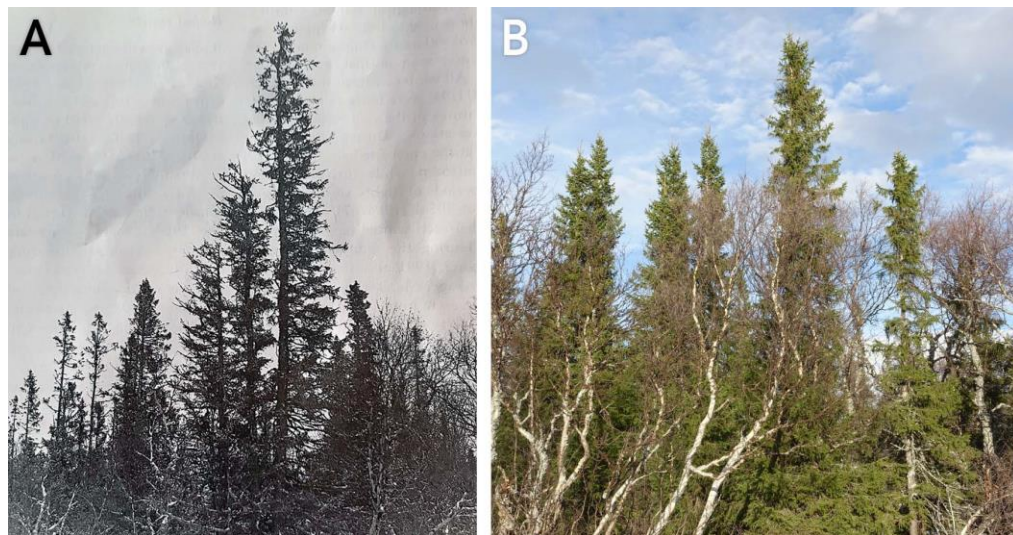


Figure 9. Clonal spruce group with substantial needle loss in the autumn of 1987. Recovery up to the present day is blatant. A.1987-10-15. B. 2021-10-25

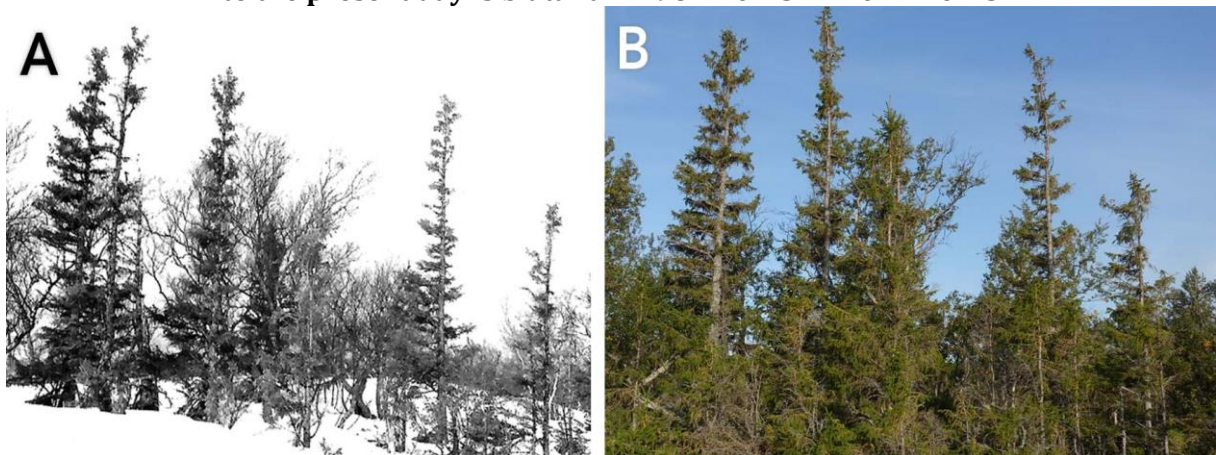


Figure 10. Typically, clonal spruces evolved severe defoliation between 1987 and 1994. Subsequently and up to the present day, stunning recovery has taken place. The second stem from the left (1994) is downed. A. 1994-04-15. B. 2021-09-04

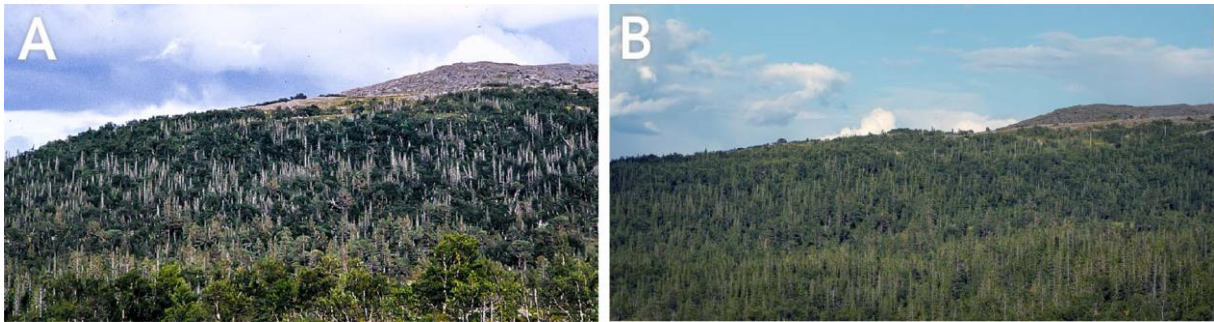


Figure 11. The course of changes evidenced at the local stand-scale, represents a generic regional pattern. Accordingly, this landscape view depicts an entire mountain slope in the study region, showing canopy progression between a vigor nadir in 1987 and subsequent regain of foliation. A. 1987- 08-14. B. 2021-08-12

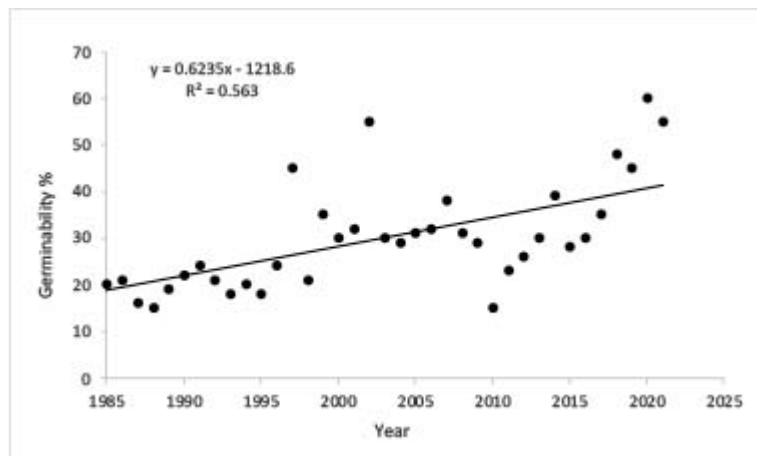


Figure 11. Annual records of percentage spruce seed germinability, 1985-2021



Figure 12. During the past 30 years, with increasing seed viability, a tendency of gap-infilling by young seed-regenerated spruces is evident. Most birches are old moribund, indicative of a trend towards a more closed spruce stand structure. 2021-09-25

DISCUSSION

The present study supports the contention (Kullman 1998) that praealpine spruce forests are finely attuned (progressively and regressively) to climate change and variability at centennial and decadal scales. Overall, the current state of condition, after a century of climate warming, with short-term interruptions, is substantially improved. The landscape has gained a more lush and healthy appearance than a century ago. That process is likely to be continued, given the uncertain assumption that climate warming continues in the future.

By the late 1980s, the present stand and others alike in northern Sweden had declined in vigor, as a proximate consequence of a decade early winter cooling, associated with a sparse snow cover (Kullman 1996). Since 1994-1995, the regressive stand-level process has reverted, and canopy conditions are back to their relatively healthy appearance prevailing prior to 1986. That state related to 20th century climate warming since the late-1930s (Kullman 1986 a,b), as evidenced also from analogous forests further north in Sweden (Hofgaard et al. 1991).

The displayed canopy progression by the mid-1990s, coincides with rising regional summer and winter air and soil temperatures. The crucial importance of soil temperatures for sustained growth in cold-stressed environments has been stressed previously (Körner & Paulsen 2004; Leonelli et al. 2010; Kullman 2021a). The present results and their causalities should be interpreted in that context.

Spruce has regenerated mainly by vegetative layering and individual height growth after the Little Ice Age, during the past 100-150 years, with intermittent reversals (Kullman 1986a), thereby stressing the climatic marginality of the concerned stand. Seed regeneration appears as a recent phenomenon, related to substantially increased seed viability, which exceeded 50 % in recent years, to be compared with about 20 % by 1985. In general seed regeneration was scant in high-elevation forests prior to the latter date, particularly during the warm 1930s to 1950s (Kullman 1986a, b). Hofgaard (1993), reported germinability figures of <1 % from biogeographically similar forests in northern Sweden (1984-1992).

The present results highlight a novel functional aspect of the mountain taiga, stressing still ongoing and possibly future transformation of high-altitude ecosystems in the post-Little Ice Age era (Willis & MacDonald 2011; Macias-Fauria et al, 2011; Kullman 2019; Schickhoff et al. 2022). In the present case, this implies closure of the spruce stands, a process which eventually may be enhanced by the accumulation of coarse woody debris, as older stems die and accumulate on the ground. The importance of the latter aspect has been stressed by several authors (Engelmark 1993; Hofgaard 1993a,b). Moreover, results from a nearby treeline ecotone have evidenced recent canopy recovery, analogous the present study and contemporary increase of seed viability (Kullman 2021b). Lack of seed regeneration may relate to sparsity of coarse woody debris, provided by relatively young and tiny trees in sparse stands. In this study, the spruce has demonstrated a remarkable ability recover by phenotypic plasticity from severe physical stress, consistent with its extreme (multi-millennial) individual longevity (Öberg & Kullman 2011).

In line with some prior case studies (Rössler et al. 2008; Hofgaard et al. 2013, the current results do not support contentions of future forest area expansion into the alpine tundra, as envisioned by certain authors (Moen et al. 2004; ACIA 2005; Kaplan & New 2006). This view of landscape-

scale forest area resilience is supported also by case studies from subarctic Sweden (Kullman 1991; Kullman & Öberg 2017).

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