A Recent and Distinct Pine (*Pinus sylvestris* L.) Reproduction Upsurge at the Treeline in the Swedish Scandes

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Abstract: *Demographic monitoring of Pinus sylvestris in the treeline ecotone of the southern Swedish Scandes, has been conducted in permanent plots since 1973. Prior reports of the population evolution were published by the present author 1993, 2007, 2014a. Here, results from the most recent survey period, 2013 to 2018, are presented and analyzed. This particular interval stands out with an unprecedented reproductive upswing, relative to the situation prevailing for some decades prior to 1995. Accordingly, the incidence of winter desiccation injury to needles/shoots and associated individual mortality has decreased. In addition seed viability increased significantly after about year 2000. Apparently, treeline performance of Pinus sylvestris is tightly related to air and ground temperatures, during both summer and winter. The obtained results are relevant the in the context of a hypothetical novel biogeographic zonation pattern, lending relevance to a notion that Pinus sylvestris may gradually increase its prominence as a treeline species in a potentially warmer future.*

Keywords: *Treeline ecotone, demographic monitoring, Pinus sylvestris, reproductive upsurge, winter desiccation, seed viability, climate change, Swedish Scandes.*

1. INTRODUCTION

Alpine treelines integrate temperature on decadal to millennial scales and respond sensitively, by position and structure, to climate change and variability. Thus, they define reliable proxy indicators in these respects, particularly where local site conditions are optimal (e.g orography, snow cover, soil, herbivory) and do not constrain upslope shift (Smithson et al. 2002; Fagre et al. 2003; Kullman & Öberg 2009, 2018; Holtmeier 2009; Holtmeier & Broll 2011; Körner 2012). This contention is supported worldwide by studies, displaying various magnitudes of treeline up shifts during the past 100 years or shorter periods, ultimately in concert with climate warming (Aas 1969; Kullman 1979, 1981, 1998, 2010, 2015b, 2016, 2017, 2018a, b; Esper & Schweingruber 2004; Danby & Hik 2007; Shiyatov et al. 2007; Harsch et al. 2009; Kharuk et al. 2009; Elliott 2011; Harsch & Bader 2012; Kirdyanov et al.2012; Aakala et al. 2014).

In many cases, there are almost insurmountable problems to disentangle effects of abandoned land use from pure climate change responses (cf. Hofgaard 1997, 1999; Karlsson et al. 2007; Palombo et al.2013; Bryn & Potthoff 2018), since entirely pristine treeline systems are rare in all parts of the world. Overall, however, treeline change stands out as the easiest interpreted indicator of climate-mediated changed plant growth conditions in the high mountain world (cf. Behringer 2010).

The concept "treeline" is here used in a narrow sense, as the maximum elevation (m a.s.l.) of the uppermost individual, at least 2 m tall (Fig. 1). It differs from the "forest line", which is the upper margin of closed forest. The latter displays a relatively subdued response to climate change, and is less suited to provide an early alert signal of ongoing or pending ecological change in the high mountain world (Enquist 1933; Kvamme 1993; Körner 2007; Rannow 2013, Kullman 2014a, b; Kullman & Öberg 2018).

Treeline shifts may proceed by two different modes: *phenotypic* and *genotypic*, respectively (cf. Kullman 2005). The first-mentioned process implies fluctuations between stunted growth, "krummholz", sensu Holtmeier (1981), and upright tree form, as consequences of an oscillating climate with opposite directions. According to Holtmeier (2009), this should not be considered as *real*

treeline change. The last-mentioned author claims that this option necessitates genotypic change, i.e. establishment or extirpation of individual tree specimens, leading to treeline rise or retreat, respectively. In the case of *Pinus sylvestris*, regeneration takes place almost exclusively by genotypic change.

Fig 1. *Treeline of Pinus sylvestris on the south-facing slope of Mt. Djupgravstöten, 990 m ö.h. This treeline advanced by 120 m in elevation during the past 100 years, by means of genotypic change. 2013-07-27.*

In the Swedish Scandes, both modes of treeline shift have been recorded over the past 100 years. At the end of the day, they have yielded virtually the same maximum extent of advance, irrespective of regeneration strategies (Kullman & Öberg 2009; Kullman 2018a, b).

Phenotypic response, predominantly characterizing *Betula pubescens* ssp. *czerepanovi*i and *Picea abies*, has implied a relatively rapid response to past-century climate change, *n.b.* warming. In contrast, genotypic change, depends on sequences of critical stages and therefore this type of treeline change has tended to be relatively more sluggish (Kullman & Öberg 2009). However, over the past few decades, *Pinus sylvestris* has paced up with the other major tree species, by real, i.e. genotypic advance. Thereby, it has approached its historic high levels during the Medieval Warm Period and the warm early Holocene, about 1000 and 7000 years ago, respectively (Kullman 2015a, 2017). The regional 20th century treeline history of *Pinus sylvestris* is reconstructed and portrayed by Kullman (2017). A comprehensive review of *Pinus sylvestris* and its anticipated performance at the range limit in a warmer context, is provided by Matías & Jump (2012).

Projections of 20th century treeline processes and the generation of realistic prospective climate-treeline models, necessitate, as a first step, improved understanding, founded on long-term continuous demographic monitoring with focus on the early life-stages (cf. Juntunen et al. 2002;Bűchler et al. 2004; Graumlich et al. 2005; Holtmeier&Broll 2005). Ideally, such models need to be based on consistent field observations at the level of individuals, over sequences of years, concerning seed quality, growth, natality and mortality of saplings (cf. Ågren & Zackrisson 1990; Graumlich et al. 2005; Holtmeier & Broll 2005). A long-term open-ended project on these premises, concerning *Pinus sylvestris*, has been conducted since 1973 in the southern Swedish Scandes and is reported below. The main objective concerns treeline formation and maintenance.

 Reports of the demographic progression of the concerned system have be given intermittently (Kullman 1993, 2007, 2014a). The present study accounts for the most recent census, i.e. demographic change 2013 to 2018. Current update after such a short interval is motivated by general observations in the region. It appears that pine regeneration in the treeline ecotone has taken a large and fast step forward over just a few past years (cf. Kullman 2017). This course of change has some bearing on speculations that continued warming may reshape an arboreal situation in the high mountains analogous to the one prevailing at the thermal optimum of the early Holocene, as discussed by Hustich (1948). In some areas in the southernmost Swedish Scandes, pine has recently "leap-frogged" over the subalpine birch forest belt, which hereabouts is severely stressed by soil drought as a consequence of increasingly early vanishing snow patches (Kullman 2014b, 2016).

2. STUDY AREA

The study is carried out in the southern Swedish Scandes and more precisely in the Handölan Valley (64°14´ N; 12°25´ E (Fig. 2). The valley floor, with most of the sample plots, is at 650-710 m a.s.l. Flanking mountains rise to 1100-1500 m a.s.l. The nearest meteorological station Storlien-Visjövalen is at 642 m a.s.l. and 20 km to the northwest. For the months January, July and the year, the mean temperatures are -7.6 °C, 10.7 °C, and 1.1 °C, respectively. The annual precipitation is about 850 mm, of which 45 % falls as snow. Data refer to the "normal period" 1961-90 and are provided by the Swedish Meteorological and Hydrological Institute.

The maximum snow depth at the study sites rarely exceeds 0.2-0.3 m and disappears earlier than in the more closed mountain birch forest higher upslope, where it use to be much deeper.
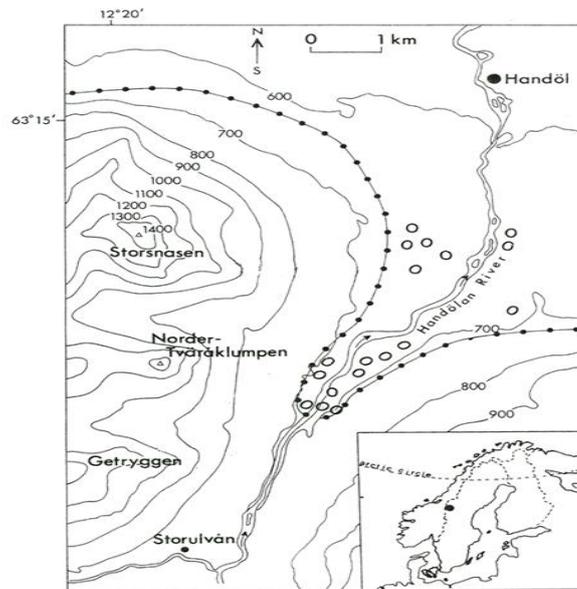

Fig 2. *Location map, showing the study area in the Handölan Valley and the individual sample plots (circles). The dotted line is the pine treeline by the early 20th century, according to Kullman (1981)*

3. METHODOLOGICAL APPROACH

A set of 18 permanent plots (10x10 m) were distributed in the Handölan Valley in 1973 (Fig.1) and have been surveyed annually up to the present day, i.e. a study encompassing 45 years, which makes it quite unique in a world-wide treeline perspective. The study area is within the Northern Boreal Zone (Ahti et al. 1968).

The plots are at the southern extremity of pine distribution in the concerned valley, 0.1-5 km south of the nearest closed stands of pine and spruce. They linger a few tens of altitudinal meters below the treeline of pine and 200-250 m below the local treeline of mountain birch (*Betula pubescens* ssp. *czerepanovii*). That is in the lower reaches of the subalpine birch forest belt. The ground floor plant cover at the study sites is characterized by dwarf shrubs, *Empetrum hermaphroditum, Vaccinium vitis-idaea, Calluna vulgaris,Vaccinium myrtillus,* bryophytes (e.g. *Hylocomium splendens*) and reindeer lichens (*Cladonia* spp.). In addition, extensive mires break up the lower parts of the subalpine belt. At the present day, *Pinus* is sparsely colonizing these habitats (Kullman & Öberg 2018).

The project was focused on the near surroundings of scattered well-established pine trees, onwards termed "*veterans*", all more than 80-100 years of age, some as old as 250-350 years and moribund. They prevail in a sparse matrix of the lower mountain birch forest belt. Most of these pines were the last survivors of a more continuous and extended pine distribution during the Medieval Warm Period (Kullman 2015a), which regressed during the Little Ice Age from the 14th to the late 19th century (Kullman 2015b, 2016).

At the onset of this project, 1973, the veterans were surrounded by scattered saplings (0.5-1.0 m) and a few minor young trees. The majority appeared within a radius of about 10 m off their putative

"parent trees". It was estimated by whorl-counting that most of them had become established between the late 1930s and mid-1950s (Kullman 1993, 2007).

For the purpose of long-term demographic monitoring, a permanent plot (10x10 m) was established around the veterans, each plot containing a large part of the local sapling cohort, presumably its progeny. Annually, by the mid-July or early August, all existing pines were carefully mapped and tallied with respect to size and vitality. New recruits were intensively searched for. However, due to their diminutive size, some specimens of this category may have been overlooked at the very first years of their existence.

A major cause of pine mortality close to the treeline, particularly concerning the sapling stage, is renowned to be winter desiccation. This is a symptomatology, which manifests as discoloration (reddish-brown) and death of needles and shoots during periods with strong solar radiation during the late winter and spring (Fig. 3). Consequently, tissue death takes place if the soil is frozen without ability to replenish evaporated water (cf. Frey 1983; Tranquillini 1979; Veijola 1998; Holtmeier 2009). Prior studies have evidenced this as a major cause of pine vitality depression and ultimate mortality at the treeline. To a lesser extent, it may combine with reindeer damage (browsing and trampling) and fungi infections (Kullman 1991, 1997, 2014a).

Fig 3. *Typical symptomatology of a pine injured by winter desiccation, i.e. the major cause of pine mortality and an effective treeline constraint. Needles which have been snow-covered during most of the winter are green and produce annual shoots. After 1995, this kind of impact has decreased significantly. Mt. Städjan, 1030 m a.s.l. 2011-06-24*

Foliar vigor was assessed at each annual survey as the percentage of needle mortality relative to the total needle mass of each pine. Data are presented as the frequency of saplings with more than 20% of the foliage dead since the previous census.

Seed viability was assessed in the late winter each year. Twenty-five cones were collected from the south-facing side of the oldest pine in each of the plots. Viability was tested in the laboratory according to (Kullman 1984).

Ground temperatures, suggested to be crucial for treeline position (Körner 2007), are monitored since 1985 at two spots (averaged), located in one of the sample plots. Measurements by resistance thermistors were carried out in the root zone, 0.3 m below the ground surface. At this depth, short-term oscillations should be damped (cf. Harris 2001; Körner & Paulsen 2004; Körner 2007). This was confirmed by daily measurements during some summer and winter weeks. Thus, readings one or two times per month should truly represent ecological relevant annual variations in soil temperature. Accordingly, the highest and lowest records for July-August and February-March are presented. A more detailed account of these measurements is given by Kullman (2007).

4. CLIMATE CHANGE

The climate evolution in the study area (1901-2018) is represented by data from the Storlien-Visjövalen meteorological station (Fig. 4). During summer (June-August) and winter (December-February), temperatures rose by 1.6 and 1.4 °C, respectively. However, inter-annual variations were large over the entire period and change was not statistically significant In the case of summer temperature, rise was most prominent during the first forty years of the record. Winter temperatures were quite low until the 1930s, when a first peak occurred. Subsequently, a cooler period prevailed up to the late 1980s. Over the following three decades, most winters have been relatively mild. Conspicuously, over the entire study period, the winter temperature variations have been much larger than those of the summer temperature.

Annual precipitation has increased by 5-10 % since the earliest part of the previous century. Over the past 2-3 decades, it rose by 10-20 % during the summer period. Winter precipitation has not changed to any degree worth mentioning (Alexandersson 2006). However, snow melt in the treeline ecotone has tended to take place increasingly early during the past few decades. After a nadir by the mid-1980s, maximum summer and minimum winter ground temperatures increased consistently by about 3.4°C and 1.0 °C, respectively, until 2018 (Fig. 5).
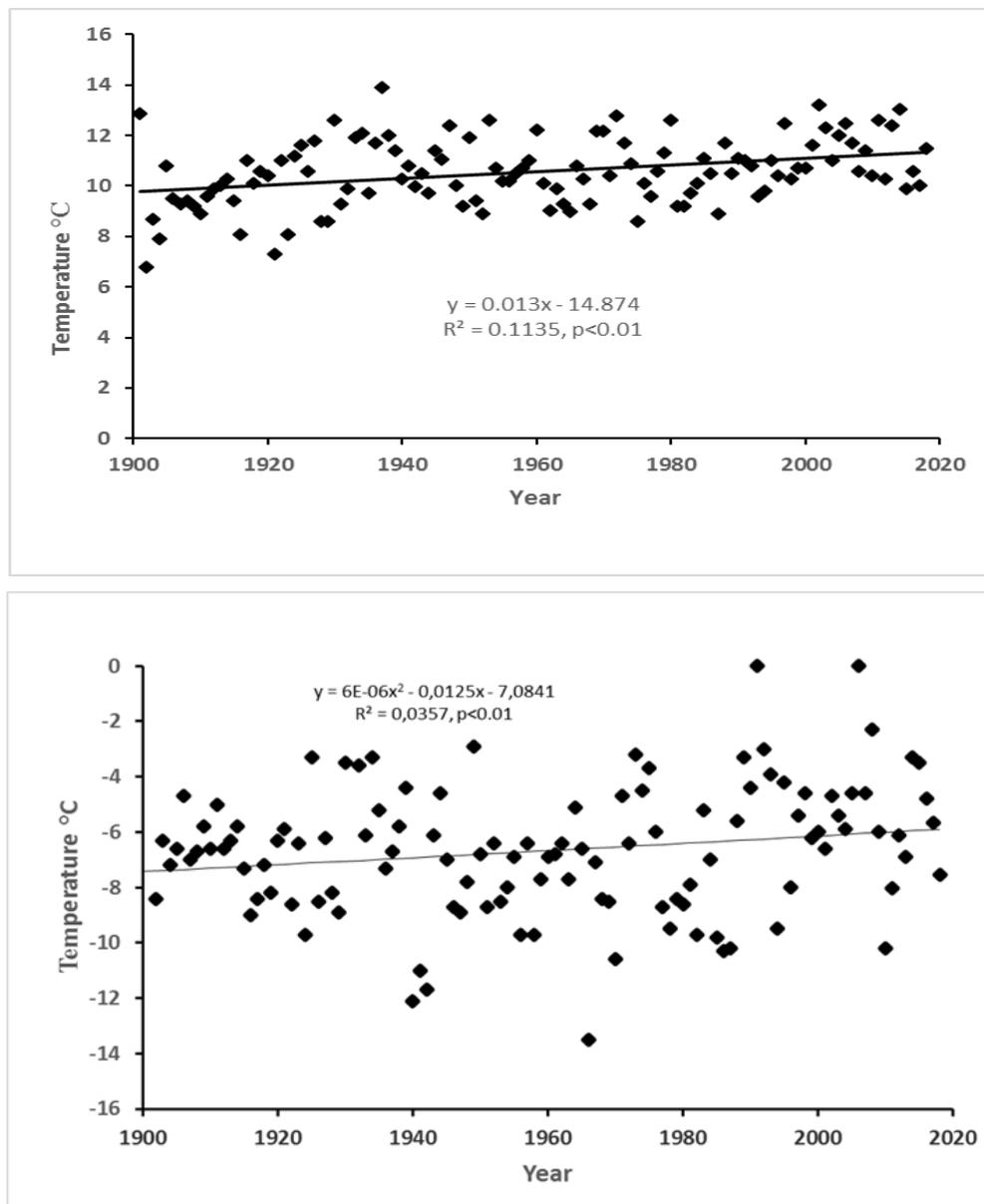

Fig 4. *Annual records of summer (June-August) (upper) and winter (December-February) (lower) mean temperatures from the Storlien/Visjövalen meteorological station.*
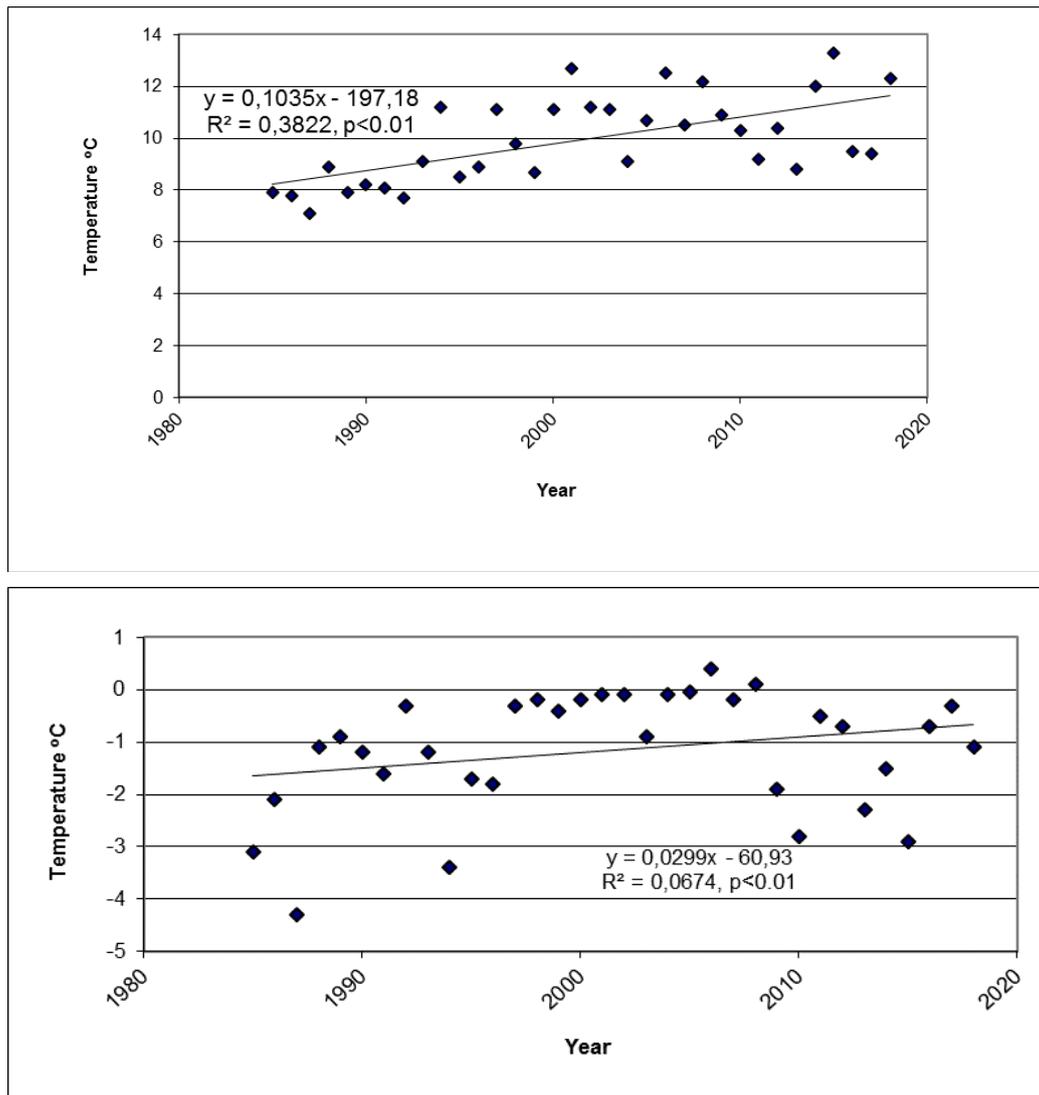
Fig 5. *Annual records of summer maximum and winter minimum ground temperatures. Upper and lower, respectively*

Proxy climate evidence consistent with the meteorologically recorded temperature rise since the early 21st century is provided by perceivable retreat of local glaciers (Fig. 6). Concurrently, permafrost has entirely vanished from the study region. Moreover, certain plant phenological phenomena, e.g. birch leafing, have occurred at earlier dates than before (Kullman 2016, 2017).

Fig 6. *Left.* *The glacier "Sylglaciären" in the province of Jämtland, about 20-25 km south of the study plots. Photo: 2001-08-01.* ***Right.*** *Up to the present day, the glacier has perceivably retreated and has been split in two separate ice masses.*

5. RESULTS

The net demographic evolution since the early 1970s is one of initially modest increase, until about 2012. Thereafter, an unprecedented upsurge by c. 150 % has taken place (Fig. 7). Mortality has been very close to zero after 2012. This most recent phase of dramatically increased reproduction broadly coincides with a cluster of relatively high summer and winter air temperatures (Fig. 4). As evident from Figure 7, the demographic course of change since 1973 comprises four fairly distinct phases of population increase and decline, respectively. Table 1 accounts for mean seasonal air temperatures for each of these periods of years. This compilation further highlights rising temperature, with a culmination coinciding with the most recent phase of population increase, i.e. 2013-2018.
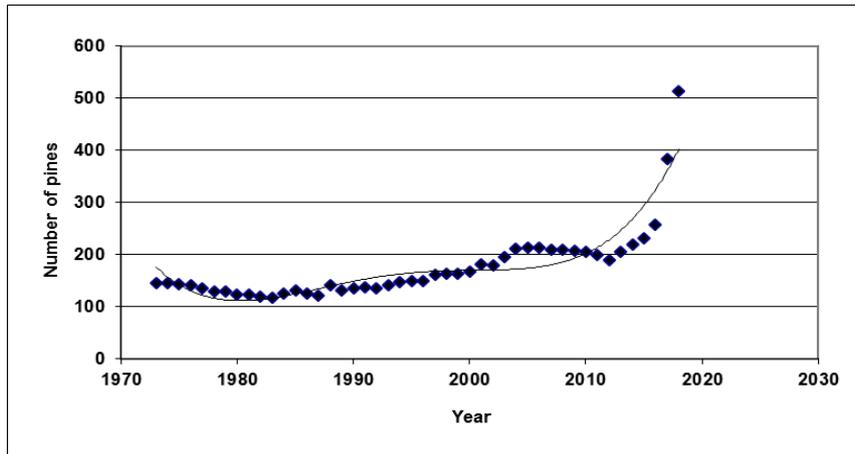

Fig 7. *Demographic evolution of the pooled population (18 plots) 1973-2018*

Over the entire period since 1985, ground temperature rise during the summer has been more pronounced than during the winter period (Fig. 5), also exceeding the summer air temperature change (Fig. 4).

Table1. *Summer and winter air temperature (°C ± SD) for periods with different population trends*

Period	Summer (JJA)	Winter (DJF)	Trend
1973-1987	10.1±0.8	-7.5±2.4	Decline
1988-2005	10.8±1.3	-5.3± 1.1	Increase
2006-2012	11.1±1.1	-6.0± 3.4	Decline
2013-2018	11.5±0.8	-4.4±1.8	Increase

A striking feature of recent change, with a strong impact on population evolution, is the substantial increase of pine seed viability over virtually the same period of time (Fig. 8). Analogously, the dramatic decrease of winter desiccation injury after the mid-1990s (Fig. 9) is followed by the recorded phase of major population growth.
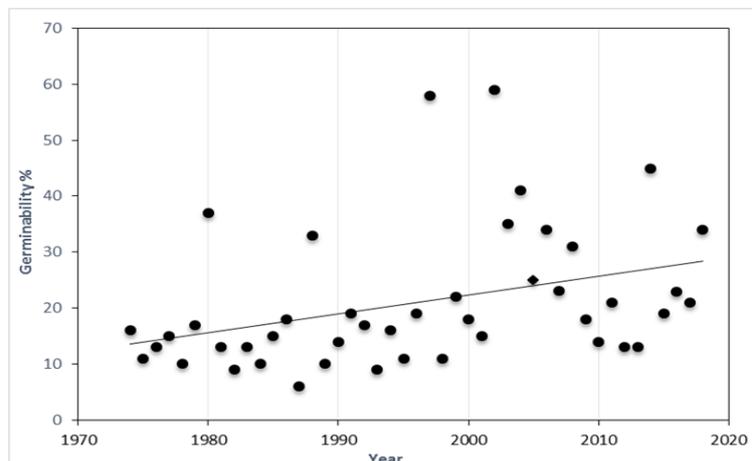

Fig 8. *Annual viability of pine seeds from one sample plot, according to laboratory tests*
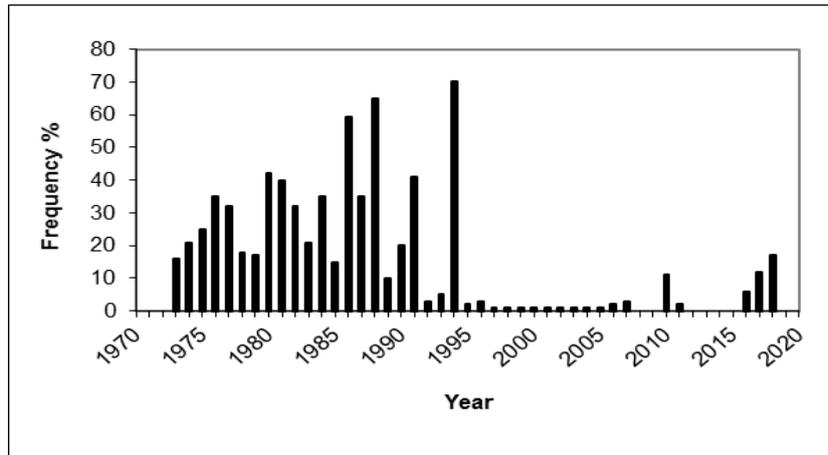
Fig 9. *Annual frequency of pines which suffered more than 20% needle loss (winter desiccation, reindeer action and fungi infections)*

Within the plots and over the entire landscape in the treeline ecotone, the ground is currently strewn with young saplings, 0.1-0.3 m high and usually younger than 10 years. This phenomenon is most distinct in open spaces and around presumptive mother pines, particularly those which established in open spaces during the warm 1930s and onwards (Figs. 10-13).

Fig 10. *Sample plot centered on a parent pine, which germinated by the thermal peak in the late-1930s. The ground is strewn with saplings predominantly established after 2013. Handölan Valley, 735 m a.s.l. 2016-09-21,*

Fig 11. *Sample plot with a dense cohort of pine sapling, all established after 2010. Handölan Valley, 680 m a.s.l. 2018-05-08*

Fig 12. *Exposed pine in the center of a permanent plot, which established by the late-1930s and recently surrounded by a dense cohort of young saplings. Mt. Storsnasen (Jämtland), 675 m a.s.l. 2018-11-30*

Fig 13. *Permanent plot with numerous young pine saplings in the foreground, presumably the progeny of the tree-sized pines in the background. Storsnasen (Jämtland), 670 m a.sl.2018-02-20*

During the past 10 years, some of the oldest veteran pines have become wind-felled (Fig. 14), although prolific regeneration in a near circumference makes provision for continued local persistence.

Fig 14. *Large and moribund veteran pine, about 300 years old, felled by a winter storm 2014. Handölan Valley, 695 m a.s.l. 2018-06-16*

6. DISCUSSION

The current results support and add detail to previous studies of recent pine treeline performance in the Swedish Scandes, which manifests as genotypic treeline rise by max 225 m altitude during the past 100 years (Kullman 1981, 2017, 2018a, b). This course of change contrasts with pessimistic views, prevailing among forest scientists by the early 20th century, maintaining that Scandinavian treelines were declining and that the barren alpine area was advancing at the expense of closed coniferous forest (review by Kullman 2015a, 2016).

The conspicuous reproduction upsurge after 2012 (Fig. 7), is contingent on a period since about 1995 with rising air and ground temperatures during both summer and winter (Figs. 4 & 5, Table 1). During the period of time, 2000 to 2018, seed viability reached relatively high levels (Fig. 8), which is the most basic precondition for population growth. In addition, the recent up shift phase coincides with a low incidence of winter desiccation injury and associated insignificant individual mortality (Fig. 9), which is understandable in the context of the fairly high root zone temperatures, recorded during the winter period. Obviously, relatively stable conditions, i.e. absence of major natural disturbances, prevailed over some recent years, which appears as prerequisite for pine treeline progression (Camarero & Gutiérrez 2004).Thus, it appears that the recent progressive population phase is basically conditioned by increased reproductive effort, which has not been hampered and balanced by a high winter mortality rate, which previously, as a rule, curtailed population growth and progression (Kullman 1993). Taken together, available evidence indicates that, in the present case, treeline performance is tightly adjusted to climate variability and its impacts on different seasonal stages of the early life cycle. Both summer and winter conditions appears to be influential in this respect. High summer temperatures are conditional on reproductive output and growth, while high winter temperatures reduces winter mortality (Kullman 2007; Harsch et al. 2009; Elliott 2011).

Whether the new pines, representing the current reproduction pulse will give rise to trees and forest stands is open to continued observations over some coming decades. Prior records have demonstrated that just a few snow poor and cold winters may more or less completely eradicate entire pine sapling populations in the treeline ecotone, primarily by winter desiccation (Kullman 1991, 1997, 2007). Nevertheless, and given that the current phase of climate improvement continues, the present emergence of the concerned cohort of young pines may give rise to a new landscape scale zonation pattern. Accordingly, pine may gradually replace much of the subalpine birch forest belt and take the role as the leading treeline species (cf. Kullman &Kjällgren 2006; Kullman 2017; Bognounou et al. 2018). This is also in line with modelling trials (Sormunen et al. 2011) and conditional on the premise that pine eventually invades a receding subalpine birch forest and forms a distinct subalpine belt adjacent to the alpine tundra, like the situation prevailing during the warm and dry early Holoecene (Kullman 2013). As mentioned above, a change of this kind appears to be already ongoing in the southernmost Swedish Scandes, where the birch forest belt since long is weakly developed (Kullman 2014b, 2016, 2017) (Fig. 15). Considering the fact the genus *Pinus* is an effective invader outside its natural distribution range (Richardson & Reymánek 2004), this is not an unreasonable option. However, since we know nothing for sure about the direction and details of future climate evolution, further speculation based on the present results are avoided.

Fig 15. *The newly emerging sparse pine belt, above the subalpine birch forest as it appears in the southernmost Swedish Scandes. Characteristically, pine exclusively grows on the exposed crests where the snow cover is minimal. Mt. Ö. Barfredhågna, 870-880 m a.s.l. 2013-07-24*

7. CONCLUSIONS

- Demographic monitoring (1973-2018) in permanent plots within the treeline ecotone of *Pinus sylvestris,* revealed a distinct reproduction upsurge between 2013 and 2018, which contrasted to mere modest change during previous decades.

- During the period 2013 to 2018, the total population size within the plots increased by 150 %. Mortality was extremely low, indicating that population growth related primarily to recruitment progression.

- The most recent demographic upswing coincided with relatively warm summers and mild winters, which indicates an ultimate causal relationship.

- The incidence of winter desiccation injury became strikingly smaller after 1995, which explains the low subsequent mortality rate. Prior to 1995, recruitment was more balanced by mortality.

- Seed viability reached particularly high levels after about 2000.

- Taken together, the obtained results sustain that the treeline performance of *Pinus sylvestris* is tightly related to air and ground temperature variability, both summer and winter.

- The results provide some substance to a notion that *Pinus sylvestris* is currently increasing its importance in the treeline ecotone of the Swedish Scandes. It may be speculated that this tendency will increase in a potentially warmer future.

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