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Research Article

HISTORICAL PERFORMANCE OF AN OUTLYING SUBARCTIC SPRUCE (*PICEA ABIES*) POPULATION IN NORTHERN SWEDISH LAPLAND

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ABSTRACT

Peripheral populations of cold-marginal tree species are often supposed to serve as dispersal nodes in relation to rapid climate warming. The history and evolution of a discrete outlying subarctic stand of Norway spruce (*Picea abies* (L.) Karst.), growing in northern Swedish Lapland, was investigated. Accordingly, it was hypothesized that climate change and variability over the past century have evoked substantial population growth and spread in the surrounding subarctic landscape. Radiocarbon-dating of megafossil spruce tree remnants preserved in the soil revealed that spruce was present at the study site by 7125 cal. yr B.P., contrasting with orthodox pollen-based interpretations of late-Holocene first spruce immigration to northern Sweden. Subsequently, the stand history is unknown until the mid- 17th century AD, when the first specimen of the extant population emerged. Continuous presence and build-up of the spruce stand was initiated by the early 18th century. All-time- high initiation of new stems occurred by the 1920s, i.e. shortly prior to the first warming peak of the 20th century. This process shows no positive correlation with summer or winter temperature rise. Overall, the existence of the spruce population, as we see it today, may relate to the general post-Little Ice Age warming of all seasons and release from permafrost and severe seasonal ground frost. In perspective of these results, no broad-scale expansion of spruce forest is likely to take place in the case of hypothetical future summer climate warming.

INTRODUCTION

Understanding past and projected future climatically forced biogeographic dynamics emerges as increasingly relevant and urgent fields of scientific inquiry. Alleged future anthropogenic climate warming (IPCC 2013) is commonly assumed (right or wrong) to induce substantial transformation of high elevation and northern vegetation structure, biodiversity and ecosystem services, with feedbacks on climate evolution (Betts 2000; Theurillat & Guisan 2001; Malcolm *et al*., 2002; Koca *et al*., 2006; Kullman 2010). Ecotonal areas, i.e. transition zones between different ecosystems, are often stressed as particularly vulnerable in that respect (ACIA 2005; Kaplan & New 2006). For example, the forest-alpine/arctic tundra ecotone may show the earliest and most profound changes in response to climate change and variability, as plant and animal species and their societies here exist close to the margin of their climatic tolerances with respect to growth, survival and regeneration (Kullman 1998; Fagre 2003; Walker *et al*., 2010; Hallinger *et al*., 2010; Mamet & Kershaw 2012). Notably, however, many associated model predictions within this field are considered to be overstated as they are not supported by observational data (Kullman & Öberg 2009; Mathisen *et al*. 2013; Hofgaard *et al*. 2013). Anyhow, focus on the cold-marginal tree and forest cover performance has a wide relevance beyond its own, since its presence or not may influence the ground flora and vegetation with repercussions on wildlife and aesthetic landscape qualities (Kullman 2002, 2007; Theurillat & Guisan 2004; Selsing 2010). Overall, changes in the composition, position and structure of the treeline ecotone, appear as the most sensitive and unequivocal ecological attributes of climatically altered growth conditions in general in the high-mountain world (Kullman 1998, 2010, 2014; Fagre *et al*. 2003; Holtmeier & Broll 2005; Elliott 2011). Studies in widely different parts of the world, Scandinavia included, provide clear evidence that treeline elevational advance during the past 100 years or so is a common phenomenon, ultimately forced by a warmer climate, modulated by local geomorphology, herbivory or land use abandonment (Kullman 1979, 1986; Esper & Schweingruber 2004; Kharuk 2005; Kapralov *et al*.

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2006; Danby & Hik 2007; Kullman & Öberg 2009; Harsch *et al*. 2009; Kirdyanov *et al*. 2012; Mamet & Kershaw 2012; Elliott & Kipfmueller 2010). This purported tight coupling between climate and treeline performance can be inferred also from paleoecological records (Shiyatov 2003; Bergman *et al*. 2005; Paus 2010; Kullman 2013, 2015ab; Kullman & Öberg 2015). The postglacial history of *Picea abies* in northern Scandinavia, has recently became fundamentally revised, as megafossil, pollen and DNA records sustain that *Picea* was an early Holocene immigrant to central and northern Scandinavia, including the high mountain regions of Swedish Lapland (Kullman 2001, 2008; Kullman & Öberg 2015; Parducci *et al*. 2012).This new view contrasts with old-established palynological "truth", claiming that spruce is a late- or mid-Holocene immigrant to high-mountain regions of northernmost Sweden (Moe 1970; Huntley & Birks 1983), which has not yet reached its climatically constrained distributional limit. Accordingly, it has been frequently speculated (see review by Kullman & Engelmark 1997), but without hard empirical data, that spruce is still gradually advancing its limit towards the west and in elevation (Fries 1913; Frödin 1916). This option contrasts with Kallio *et al*. (1971), who stressed the seemingly unchangeable nature of the subarctic spruce forest border during the late Holocene (cf. Kullman & Engelmark 1991).

In the context of north-European biogeogeography, it appears that centrifugal expansion from scattered pre-established "cryptic" outlier founding populations and their subsequent coalescence had a pivotal role for near infectious tree dispersal following the latest glacial phase. In northern Scandinavia and particularly in the case of Norway spruce (*Picea abies*), this may have many after happened millennia after the deglaciation, when orbitally forced climate evolution (cf. Berger & Loutre 1991) crossed a critical level and local spruce populations expanded their ranges and became generally more abundant in the landscape (e.g. Anderson *et al*. 2008; Kullman 2002, 2001a, b; Aitken *et al*. 2008; Kullman & Öberg, 2012, 2015). In northern Sweden, the coniferous forest border (boreal/subarctic) is made up predominantly of Scots pine (*Pinus sylvestris*), with widely scattered minor outlying stands or solitary trees of *Picea abies* in a matrix of subarctic birch forests (*Betula pubescens* ssp. *czerepanovii*) to the northwest. It has been inferred that this type of peripheral populations and their widespread distribution enabled the rapid regional spread of *Picea* forest over northern Sweden during the late Holocene (von Post 1930; Kullman 2000; Giesecke & Bennett 2004; Heikkilä 2010).

It is a relevant question with this background is whether extant peripheral and well- established tree populations of this kind may play an important role as infection nodes in the future, in cases when the plant cover and its geographical distribution are about to adjust to climate change (cf. Trant *et al* 2001; Bhagwat & Willis 2008). We comply with the notion that Holocene migrations of tree species may be understood by retrospective analyses of peripheral populations (Davis 1987; Kullman 1991). The present study focuses on the evolution of an outlying subarctic population of Norway spruce (*Picea abies*). *Picea abies* is a late-successional, nutrient-demanding, shade-tolerant species, adapted to relatively cold and humid climate. Survival and growth of seedlings and saplings require a protective snow cover in combination with ample soil moisture during spring and early summer (cf. Tallantire 1977; Hafsten 1987). In addition, *Picea abies* suffers from severe and late-thawing seasonal ground frost (Kullman 1991).

Study area

The study was carried out in the bottom of the valley Visttasvaggi, 490 m a.s.l. (67° 56´. 18° 56´ E), in northern Swedish Lapland, c. 9 km northwest of the small village Nikkaluokta (Fig.1). The concerned spruce stand occupies an area of about 100 x 50 m and occurs as a distinct "island", growing on the south-facing side a low morainic accumulation, in a matrix of extensive open sedge-mires with patches of subarctic birch forest (*Betula pubescens* ssp. *czerepanovii*) (Fig. 2), surrounding the river Visttasjohka. The spruces are mixed with a sparse cover of tree-birches and some shrubby willows (*Salix glauca* and *S. phylicifolia*).

Prominent species in the field layer are: *Empetrum hermaphroditum*, *Betula nana, Vaccinium vitis-idaea, V. myrtillus, V. uliginosum, Andromeda polifolia, Rubus chamaemorus, Rubus arcticus, Carex globularis, Ledum palustre, Pedicularis lapponica, Arctostaphylos alpinus, Deschampsia flexuosa, Saussurea alpina*. The bottom layer is predominantly composed of bryophytes, foremost *Pleurozium schreberi* and patches of reindeer lichens (*Cladina* spp.).Extensive stands of pine (*Pinus sylvestris* L.) and aspen (*Populus tremula* L.) occur in the surrounding mountain slopes, at substantially higher elevations than the spruce stand. The nearest closed spruce stand (475 m a.s.l.) located about 35 km to the southeast.

The concerned spruce population grows on peaty podsol soil with a 10-20 cm deep moor humus layer. Towards the periphery, the ground gets wetter, with increased predominance of *Sphagnum* hummocks. Externally, the concerned spruce stand provides an impression of predominant medium age, with scant seed regeneration in the past few decades. The tallest trees are about 10-12 m high, many of which are of good vigor and cone-bearing. According to the shape of the cone shells, most trees appear to belong to *Picea abies* ssp. *abies*. The general character of the stand is given by Fig. 2 and 3.The oldest spruces in the study population grow on minor peat mounds in the centre of semi- permanent shallow water-filled depressions, features usually indicative of prior local permafrost (cf. Viereck 1965; Kullman 1991). By early August 2015, no frozen ground could be found anywhere in this stand.

Systematic digging in the soils could not indicate any signs of past forest fires at the investigated site, e.g. charcoal fragments, charred subfossil trunks or living trees with fire scars. Except for hay-scything on mires, reindeer grazing and some logging of birch and pine (Tanner 1912), the plant cover is little affected by human activity. In the study population, a few young spruce trees show signs of having been cut, presumably for Christmas trees (Mr. Olle Sarri, oral communication).

MATERIALS AND METHODS

This study focused on an isolated spruce "island", well outside the continuous distribution of spruce forest in northern Swedish Lapland. Based on location data provided by Alm (1921), this specific object was relocated by air reconnaissance in early August 2015.

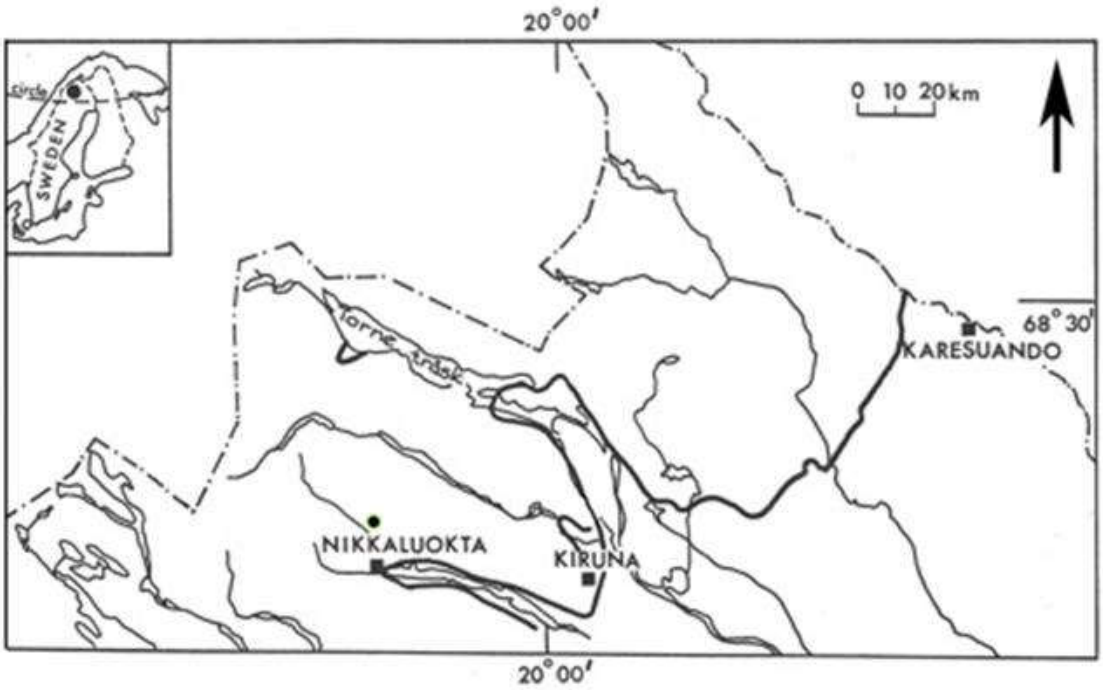


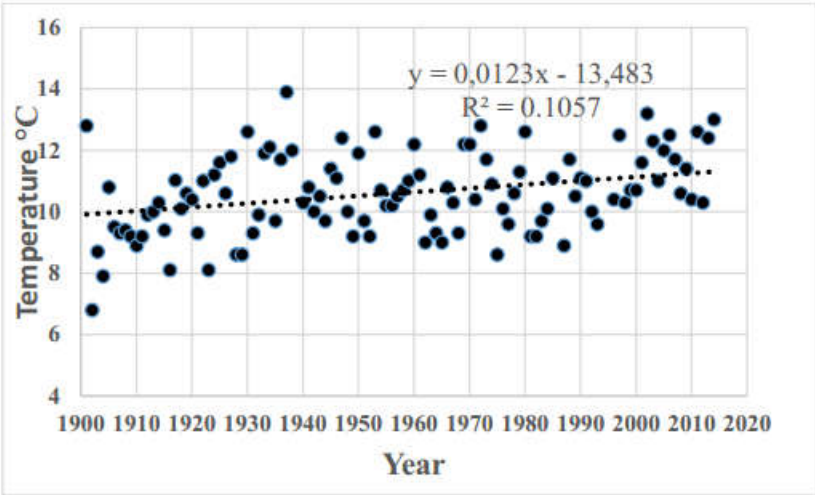
Figure1. Location map, showing the position of the investigated spruce stand (●)

Figure 2. Air-borne view of the investigated spruce stand, located in a matrix of subarctic mountain birch forest at the floor of the valley Visttasvaggi in northern Swedish Lapland Photo: L. Kullman 2015-08-04

The valley upstream the study site was thoroughly surveyed for the presence of other spruce outliers, solitary trees, megafossil spruce remnants and occasional saplings. The concerned spruce stand was first observed, although superficially described in 1909 (Tanner 1912). A more comprehensive and quantitative account was provided by Alm (1921). Langlet (1935), obviously without having seen the stand himself, discussed this population in a wider context, particular its origin and local dispersal history. Like many authors dealing with the northern spruce forest distribution, he speculated that this isolated spruce stand originated from unintentional spread by the Sami people (cf. Skoglund 1964; Schmidt-Vogt 1977).

In order to obtain a representative age structure analysis, which may define the population dynamics and its ecological correlates in the past, all living spruces, within a plot of 50 x 75 m, embracing a major part of the population, were cored at or in most cases slightly below the ground level. For multi-stemmed specimens, the stoutest stem of each individual was sampled as an approximate representative of the age of each individual spruce. Visual cross-dating based on particularly narrow rings was performed. Of course, this procedure can only provide a minimum age of each genet. This relates to the well-known fact that clonal spruce may be thousands of years older than indicated by the number of tree rings in the oldest stem (Öberg & Kullman 2011).

Figure 3. External prospect of the spruce stand from the south. *Betula nana* prevails in the foreground. Photo: L. Kullman 2015-08-04



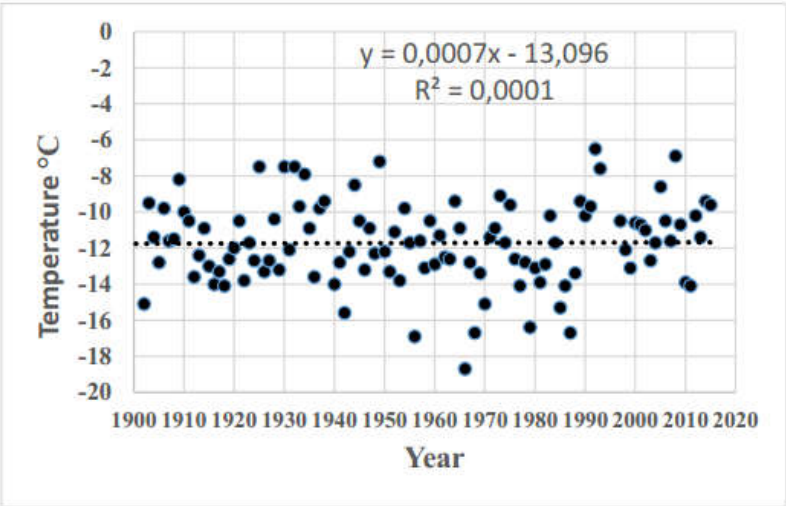


Figure 4. Annual temperature records for Kiruna meteorological station. *Upper*. Means for the period June-August. *Lower.* Means for the period December-February

Tiny seedlings and saplings (< 1 m high) were uprooted and annual rings on stem/root cross sections were counted using a stereomicroscope in the laboratory. In an attempt to find some clues to the first establishment of the population, megafossil stem remnants, were searched in the surface soil underneath the crowns of the oldest trees. These endeavours were carried out in connection with unearthing spruce stem bases for the purpose of accurate tree ring dating of individual spruces. Recovered wood remnats, were taken to the laboratory for radiocarbon dating, which was performed by Beta Analytic Inc. Miami (USA). Radiocarbon ages were calibrated to calendar years before present (cal. yr B. P. with "present" = AD 1950. Calibration was conducted by use of the INTCAL09 database (Reimer *et al*. 2009). For simplicity, the calibrated ages are quoted in the text as values of points where radiocarbon ages intercept the calibration curve. Species identification was conducted by wood anatomy analyses (Erik Danielsson/Vedlab Inc.). Seed germinabilty was tested in the laboratory according to Kullman (1984). Sedge mires outside the investigated stand were intensively searched for existing spruce megafossils. However, these attempts were entirely negative. As a background and possible explanation to the sub-recent spruce dynamics, the air temperature evolution for the summer (J.J.A.) and winter (D.J.F.) periods at Kiruna meteorological station (442 m a.s.l.) since 1901 is given in Fig. 4. Of these parameters only summer temperature displays a warming trend over the past 100 years.

RESULTS AND DISCUSSION

Already Wahlenberg (1812) distinguished the zone (*Regio subsylvatica*), practically without spruce, that contains the study site. Delayed immigration, soil chemistry, ground-layer vegetation, forest fires or climate characteristic have been discussed as the explanation for the constraint, relative to pine, of the regional spruce distribution (cf. Fries 1913; Enquist 1933; Hustich 1966; Kullman & Engelmark 1997; Sutinen *et al*. 2005, 2012). These contentions are not supported by the present study. Another common phytogeographical theory states that postglacial immigration of spruce and the subsequent spread of continuous stands into this particular region of Lapland is, for some obscure reason, much delayed. If true, this would imply continuous spread of spruce forest towards the northwest, detectable on a secular time-scale, (Birger 1912; Moe 1970). This view got a strong impetus, when spruce population growth was observed by early explorers to be in an active expansion phase by the late 19th and early 20th century (review by Kullman & Engelmark 1997). However, the theory of delayed and still ongoing geographical spread has been refuted by this and other studies based on hardcore megafossil evidence, showing presence of spruce already during the early Holocene far to the west and at high (present-day alpine) elevations in northern Swedish Lapland (Kullman 2001; Kullman & Öberg 2015). With a uniformitarian perspective, climate in this region supports severe ground frost, conditions in combination with a poor geological substrate, which have for long constrained the distribution of spruce forest in this particular region (Kullman & Engelmark 1997; Sutinen *et al*. 2005). This was made obvious in connection with an episode of severe ground frost by the late 1980s, which evoked major crown deterioration and regeneration failure in peripheral spruce stands in the concerned region (Kullman 2001a).

The history and physiognomy of the investigated population broadly mimics that of other spruce outlier stands in northern Swedish Lapland, with respect to tree, physiognomy, ground vegetation and age structure (Kullman & Engelmark 1991, 1997). This circumstance provides regional generality to the results and reason to interpret ultimately in terms of climate change and variability. Radiocarbon-dated megafossils sustain that spruce existed at the site of the concerned population somewhat earlier than 7000 years ago (Table 1, Fig. 5), which contests the supposition that spruce was spread to this site by man. In combination with other lines of evidence (Parducci *et al*. 2012; Elven *et al*. 2013), the present result adds to recent developments within Scandinavian vegetation history (Kullman 2001, 2008; Kullman & Öberg 2012, 2015), which challenge the traditional (pollen-based) view of late-Holocene spruce immigration to northern Sweden (cf. Tallantire 1977; Hafsten 1992; Huntley & Birks 1983; Giesecke & Bennett 2004).

Table 1. Radiocarbon dates of megafossil spruce remains

Sample no.	Lab. code	^{14}C yr B.P.	Cal. yr AD
1	Beta 418590	140±30	1685-1735
2	Beta 418591	100±30	1665-1780
3	Beta 418589	6130±30	7125

As evidenced also by other peripheral spruce populations in the region, spruce obviously has a history back into the early Holocene (Kullman & Engelmark 1997; Kullman 2000). Considering the scant megafossil documentation of spruce tree growth during this early period (Fig. 8), it is reasonable to hypothesize that during the past, 7000 years prevailing climatic conditions may have hampered spruce regeneration by seed (cf. Hafsten 1987; Heikkilä 2010). The populations may have been maintained by layering, as deduced from the forest tundra of northern Canada and subalpine regions in the Swedish Scandes (e.g. Arsenault & Payette 1992; Öberg & Kullman 2011). In addition and given the proximity to the southern limit of discontinuous permafrost (Rapp 1983), enhanced soil frost may have intermittently killed existing seed-producing treeline trees. Apparently, a minor analogue is offered by the 20th century, when predominantly warm conditions were interrupted with short-term cold and snow-poor intervals, e.g. by the late 1980s and occasionally later (Kullman 1989, 1991, 2014; Bjerke *et al*. 2014).

Extensive tree mortality occurred in cold-marginal tree populations during the cold centuries of the Little Ice Age (Grove 1988; Kullman 2015a) and paved the way for spruce establishment as competition from a dense pre-existing tree cover had decreased and climate started to ameliorate way by the end of the Little Ice Age, from the mid-19th century and onwards (Fig. 8). This process coincided with permafrost thawing in subarctic Sweden (Kullman 1991; Kullman & Engelmark 1997; Åkerman & Johansson 2008).The size of the stand at this early time and during subsequent millennia cannot be deduced from available data. Given the possible extreme longevity documented for individual cold- stressed spruces, i.e. > 9000 years (Öberg & Kullman 2011), it is a reasonable, although not conclusive option, that the present-day population has a more or less unbroken continuity with the recovered early-Holocene megafossil (see above) and the oldest currently living spruce tree, that dates back to the 1660s (Fig. 5).

Figure 5. *Left*. The major spruces on the picture date to the 1920s. *Right*. Preserved in peaty topsoil between the largest trees, subfossil spruce wood was recovered, dating 7225 cal. yr. B.P

Figure 6. Cored at the root collar, somewhat below the ground level, the oldest living spruce tree dates back to the 1660s. Two dichotomously spreading stems occur 1 m above the ground level, indicative of reiterated winter desiccation injuries when crossing the snow surface by the 1940s. Photo: L. Kullman 2015-08-04

Thereafter, the age structure indicates that the generation of new stems was none or scant for at least 7 decades until the emergence of a distinct peak by the 1840s. Whereupon and consistent with the final phase of the Little Ice Age (Grove 1988), stem initiation has occurred uninterruptedly, although with variable rates until the second decade of the present century present day.

The growth investigated population experienced an all-time-high during the second decade of the 20th century and displayed nadirs during the 1960s and 1980s, followed by substantially increased regeneration/initiation rates during the following 2-3 decades.Over the past century, a total of initially c. 20 trees (Alm 1912), a figure supported by the age structure analysis, has grown to about 150 tree-sized specimens at the present day,

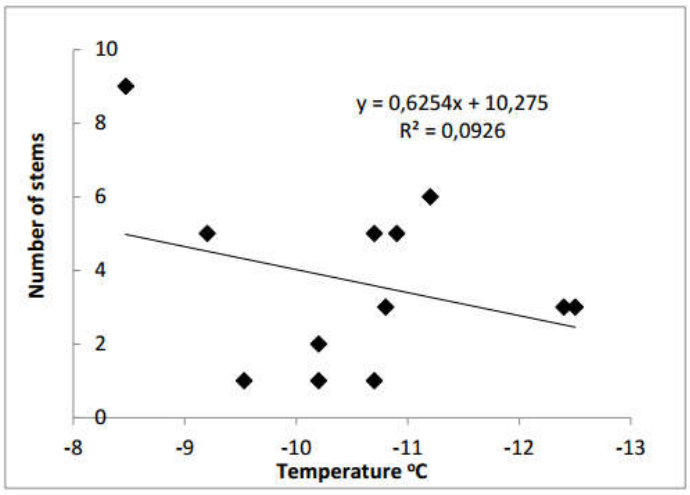


Figure 7. Relationship between numbers of spruce stems initiated during 10-year periods with variable winter (D, J, F) mean temperatures

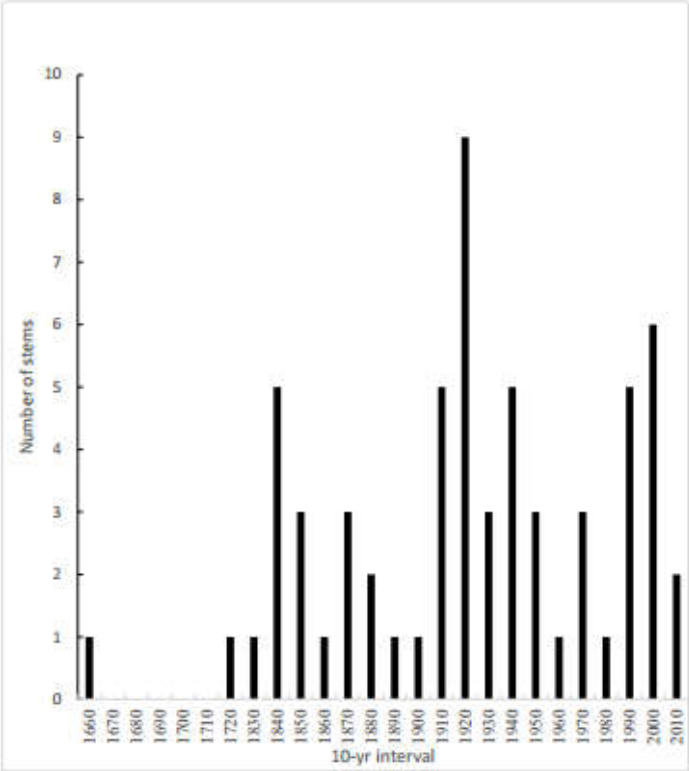


Figure 8. Age structure (10-yr intervals) of the investigated spruce population

of which fairly few are multi-stemmed layering clones. Most of the spruces are surprisingly well-grown and with symmetrical crowns, considering that they represent a presumed climatically constrained outpost. Relative to the living population, few dead trees are recorded and little dead wood occurs visible on the ground. These circumstances suggests that the continuity of the closed should be spruce forest stand, as we see it today, has a fairly short history in the perspective of the entire Holocene. Apparently, this is not a question of immigration history, but rather population growth and expansion of old-established stands (cf. Kullman 2001a).The stem initiation/regeneration rate, as expressed by the static age structure of survivors, displayed with ten-year intervals (Fig. 7), showed no significant correlation with summer or winter temperature for the same periods.

A weak tendency for regeneration success seemed to relate to particularly low winter temperature (Fig. 7.). The latter result may be an artifact, relating to difficulties to accurate date layering cold-marginal spruces by ring counting. In this context, it should be kept in mind that, also under more optimal circumstances, analyses of static age structures do not necessarily reflect seed regeneration dynamics in detail, but rather survival to the present day (Kullman 2015b). Moreover, the small size of the investigated population cautions against drawing too detailed and definite conclusions from emergent patterns (cf. Kullman 2015b). Seeds extracted from cones laying on the ground (August 2015), yielded germinabilty amounting to 48 %, although few seedlings from the past two decades were recorded. Thus, lack of germinable seed is unlikely to cause insignificant regeneration success during

recent decades, which reasonably reflects poor seedbed conditions and soil moisture deficit (Kullman 2015b). This situation is paralleled at *Picea*-treelines in other regions (Zackrisson *et al*. 1995; Hofgaard *et al*. 2013; Gaire *et al*. 2014). Viewing population development in detail during the past 100 years (Fig. 8), i.e. as far back in time as age structure and standard instrumental meteorological records are available, does not suggest that climate warming in general has a direct, decisive and promoting influence on the detailed stand evolution or the regional distribution of spruce forest in the landscape. This is particularly emergent as i.e. tree recruitment displayed relatively poor regeneration/initiation, associated with the relatively warm summers of the 1930s (Fig. 8). Similar inertia of *Picea* regeneration and lack of forest advance into the tundra, during epochs with climate warming, has been reported from other parts of the Scandes (Kullman 1986; Kullman & Öberg 2009; Rannow 2013; Mathisen *et al*. 2013; Kullman 2015b) and other treeline ecotones throughout the world (review by Kullman 2015b). This circumstance is in line with experimental studies, indicating that high temperature *per se* does not necessarily stimulate spruce seedling recruitment (Tingstad *et al*. 2015). Notably, no centrifugal expansion into the surroundings of the study site appears to have taken place during the lifetime of the population, although the build-up of the local population may have benefitted from the general post-Little Ice Age climate warming (air and soil) of most seasons (Holmgren & Tjus 1996; Callaghan *et al*. 2013.) Thus, projected warmer climate in the future, if becoming a reality, is likely to promote local stand densification of spruce, but unlikely to cause widespread biogeographic spruce expansion at the northern margin of spruce distribution.

Conclusion

- This subarctic peripheral spruce population was founded more the 7000 years ago, thereby supporting the view that spruce was an early Holocene immigrant to northern Sweden and with little association to human action.
- For some subsequent millennia, the population appears to have persisted in a more contracted form than today, possibly constrained by unsuitable climatic conditions – soil drought and permafrost.
- By the mid-18th century A.D., substantial population growth was initiated. Likely in response to release from severe soil freezing conditions in association with the general post-Little Ice Age climate warming.
- Despite substantial summer warming during the 20th century, spruce has not spread outside its present-day site and into the subarctic birch forest.
- No landscape-scale expansion of spruce forest is likely to take place in a hypothetical case of future summer climate warming.

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