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Recent and Past Trees and Climates at the Arctic/Alpine Margin in Swedish Lapland: An Abisko Case Study Review

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Abstract

For about a century, Abisko Scientific Research Station in northern Swedish Lapland has served as a logistic base for high-quality geoecological research in subalpine/subarctic environments. In recent years, and driven by the prospect of alleged man-made global warming, much of the scientific focus has been on dynamics of the treeline ecotone. In this context, field observations, analyses and interpretations emanating from research carried out in the Abisko region are discussed in perspective of recent observations and analyses. Local mountain birch (*Betula pubescens* ssp. *czerepanovii*) treeline rise by maximum 230 m during the past 100 years conforms quantitatively to data obtained further south in the Scandes. This broad-scale inter-regional coincidence indicates that a common operative agent has been responsible. The most likely candidate is recorded secular climate warming by 2.5 °C. This contention is further supported by age structure analysis in the birch treeline advance zone, indicating that the vegetative initiation of new trees peaked during the warm 1930s, when reindeer number were high and reached a nadir during the relatively cold 1960s and 1970s, coincident with smaller reindeer herds. These data suggest, contrary to previous hypotheses, stating that, relative to climate change, intensity of reindeer browsing has been of minor importance for birch treeline dynamics. The upper limit of closed stands of mountain birch and pine has shifted relatively insignificantly in elevational position during the predominantly warm past 100 years. Over the same period or longer, common aspen (*Populus tremula*) has frequently occurred as low-growing krummholz (stunted growth forms) over the entire mountain birch region. During the warm 1930s, and just like birch, rapid height increment was initiated and has continued up to the present day. Thereby, many individuals have attained tree-sized in recent decades. Accordingly, aspen (*Populus tremula*) has, presumably in response to climate warming, become a more conspicuous element in the mountain birch forest. The current analyses refute prior claims that aspen regeneration is accomplished by seed regeneration rather than phenotypic adjustment of old-growth creeping individuals. *Picea abies* and *Larix* sp. are recorded as new species in the Abisko area. In accordance with prior analyses in other parts of the Scandes, megafossil data show that the treelines of Scots pine (*Pinus sylvestris*), mountain birch (*Betula pubescens* ssp. *czerepanowii*) and grey alder (*Alnus incana*) peaked in the early Holocene. Based on the elevational difference between early Holocene and present treeline positions (adjusted for 100 m land uplift) it may be inferred that the summer temperatures exceeded those of the last few decades by about 3.0 °C.

Keywords:

Treeline; Climate change; Swedish Scandes; Mountain birch; Scots pine; Aspen; Grey alder; Holocene; Age structure; Reindeer browsing; Megafossils

Introduction

Hypothetical future climate change, with anticipated profound and extensive consequences for man and biota is one of the most addressed topics within present-day geoecology and vegetation science. In particular, marginal plant and animal communities in alpine and arctic regions are frequently concerned as objects with a high potential to manifest early biotic and landscape ecological responses to changing climatic conditions, possibly in conjunction with other drivers, e.g. ceasing human impacts [1-4]. In this context, the border zone between boreal forest and alpine/arctic tundra, i.e. the treeline ecotone, with all its component species and ecological interactions and services, is generally believed to respond profoundly to systematic climate warming [5-7].

Consequently, the steering mechanism of cold-marginal tree cover performance is essential scientific concern, which can best be understood by extensive long-term observational programmes. Presence of a tree cover impacts the microclimate and largely governs the evolution of the understory plant species performance and constrains the usefulness of this landscape for wild life and humans [8-12]. Therefore, the positional and compositional dynamics of the treeline ecotone emerges as a study field of high priority [13]. This contention is stressed by prior observational and historical studies in the Scandes and elsewhere, which have sustained that broad-scale treeline and associated plant cover dynamics are ultimately constrained by climate change and variability at different temporal and spatial scales [3,7,14-19].

Accurate temperature reconstructions based on former treeline positions are critically dependent on well-defined and precise positions, which are frequently used as reference lines when discussing past and present treeline and vegetation change in the context of climate change and variability. Unfortunately, several studies from the Abisko region in northernmost Swedish Lapland with these objectives do not fully comply with these prerequisites. For example, some prior works are founded on imprecise treeline definitions and poor up-to-date field-based reconnaissance of present-day treeline positions of defined tree species [20-27]. These circumstances have tended to yield underestimates of the current natural (climatic) elevational tree range limits by hundreds of meter. The highest subfossil pine tree record reported by Karlén is 575 m a.s.l., which was erroneously estimated to be 175 m higher than the present- day position of the local treeline, which according to recent measurement is assessed to be 520 m a.s.l. This controversy, which is of vital importance when assessing climate change between then and now, is ventilated by Kullman versus Karlén and Barnekow and is further addressed in this study in the light of accurate present-day and historical treeline data drawing on more extensive megafossil and recent treeline records [23,28-31]. Also paleoclimatic inferences, based on pollen and macrofossil data suffer from the same shortcomings as they rely on imperfect understanding of the current elevational separation between past and present-day climatic treelines in the Abisko area [22,23,32]. Drawing on these data, they postulate that treeline and climate history differ between the northern and southern Scandes [22,33]. Unfortunately, Seppä et al. used the same data for far-reaching speculations about the early-Holocene landscape structure, purporting a view that pine was a very

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rare element in the early-Holocene tree flora at high elevations in the concerned landscape [34].

In the Swedish Scandes, Abisko Scientific Research Station in northern Lapland (68° 21´N; 18°49´E) has for more than a century provided a wealth of multi-disciplinary and high-quality environmental monitoring and basic research with focus on past and present function and dynamics of the subalpine/subarctic landscape in this particular region [35-39]. In recent years, treeline change and ecology have gained much scientific attention, primarily as proxy for climate change and variability as well as vegetation dynamics [22,23,27,35,38,40]. As already mentioned, some of these studies rely on imprecise treeline definitions, mostly representing the elusive and irregular upper limit of closed tree stands, which are much influenced by local soils and biogeomorphology. This circumstance twarts comparison with studies executed in other areas and founded on a more explicite and well-defined terminology. In fact, focus on the treeline proper or the tree species line would be a more appropriate and commensurable object when discussing trends concerning potential treeline upshifts or downshifts in concert with climate change.

Since much of current and ongoing research in the Abisko area has a projective focus, with treeline as a baseline reference and climate change as the potential primary driver, a detailed and improved understanding of the treeline and its past and recent position, structure and dynamics appears particularly motivated. Relative to megafossil analysis, the traditional approach of vegetation history, i.e. pollen stratigraphical studies, is considered to be a blunt and inconclusive tool in this [12,30,41-44].

However, certain recent studies show a good agreement between pollen and megafossil/macrofossil data, depending on an unprejudiced mind of the analyst [45-47]. Megafossils are well-preserved pieces of trees (trunks, branches, bark, cones or roots), recovered from peat deposits, lake sediments or forefields of receding glaciers/snow patches. These items are not easily displaced by wind and reasonably they represent the growing sites. Recent melting of perennial ice and snow has opened a new window of treeline and alpine vegetation history as megafossils are currently exposed at high elevations, where tree growth has neither before been anticipated nor documented. This circumstance conforms to a near-worldwide pattern [28,48,49].

As a complement and answer book to more traditional methods, megafossil analyses, although somewhat discontinuous and fortuitous, provides data on local presence of specific taxa at specific points of time and with a superior taxonomic and spatial accuracy. This methodology is not surpassed by any other palaeoecological approach aiming at historical treeline and climate reconstruction. Therefore, it is remarkable that certain pollen analysts advocate that their approach to vegetation history has some right of priority relative to more robust and objective megafossil analysis. In addition, megafossils are considered to respond more sensitively to climate change than pollen [50-52]. Needless to say, comparative analyses over time of biogeographic boundaries presuppose precise knowhow about present-day well-defined distributional limits and their documented dynamic responsiveness to recent climate variability, as realized by some informed scolars [20,53,54]. For the purpose of a more conclusive situation we need a properly defined and accurate treeline concept (current and historical) and a larger sample of tree megafossils as baselines for historical reconstructions of plant cover and climate. That is one of the rationales of this paper.

The present paper aims (1) to improve the comprehension of the Holocene history of the treeline ecotone at different temporal scales in the Abisko region and (2) to provide a quantitatively accurate view of present-day tree zonation patterns and their recent dynamics at a representative site near Abisko.

A particular area of historical controversy concerns the magnitude and timing of the Holocene treeline and temperature maximum, and its geographic differentiation, which is frequently inferred to have occurred during the mid-Holocene in the northernmost Scandes and in the early Holocene further south [22,24,28,29,34,44,55,56]. In addition, a recent age structure study has suggested that reindeer grazing rather than climate change is the primary driver of birch treeline dynamics in the study area. As these inferences may be questioned, a complementary and particularly careful age structure analysis was performed in the belt where the treeline has advanced during the past century [27,28,57].

Methods

Present-day tree cover composition and structure were assessed and documented during the years 2008-2013 by systematic observations along altitudinal transects in the tree line landscape. A particular focus was on sites where the former director of Abisko Scientific Research Station, Dr. Gustaf Sandberg had determined the treeline position in the early 1950s, with virtually the same definition as the one used in the present context. Some of these data were provided to Leif Kullman in 1971 in connection with a student course in mountain ecology. The accuracy of Sandberg´s treeline measurements was assessed and largely confirmed in 1972 by boring and counting the tree rings 2 m above the ground level on particularly old-looking birch trees around the elevations given by Sandberg [28].

Treeline in the present context is constrained for each species as the maximum elevation for specimens with a minimum height of 2 m [14,33,58]. Such a strict and narrow definition is motivated when one strives to quantify treeline dynamics over time, as a measure of climate change and associated plant cover response. Focusing on the life of the uppermost solitary trees, is considered to provide a more clear-cut expression of the regional climate than any arbitrary and subjective forest-line construction [3,17,59-61]. The latter, often tend to reflect the configuration of the land surface and may be altitudinally depressed by human landuse in the past [62,63]. In contrast, human impact often ceased below the treeline proper. Thus, the treeline may serve as a better and more interpretable early indicator of potential future upward shift of the treeline ecotone [3,64,65].

The age structure of birch in the treeline advance belt was carried out in 2010 within a 50x100 m (Figure 1), slightly south of the rivulet Rihtunjira, 675-690 m a.s.l. (68°22´ N; 18°44´ E), which is 15-30 m higher than the treeline position documented by the early 20th century (Table 1). For each birch individual, 2 m or taller, the highest stem was bored close to or slightly below the ground level. Since many extant tree birches were multi-stemmed, with remnant stools of dead and living stems (Figure 2), this procedure does not, in all cases, truly represent the initial establishment of a specific individual.

Thus, it can at best provide an apprehension when substantial height increment commenced [66]. It should be realized that in general, birches of this type may be hundreds or thousands of years older than indicated by root neck borings of individual stems [67]. In order to minimize this potential bias, plant debris and soil, surrounding the stem bases were removed, which enabled boring quite close to the "seed point".

Figure 1: Interior view of the sample plot (675-690 m a.s.l.) where the birch age structure was investigated. The field layer is here predominantly composed of *Geranium sylvaticum.* Photo: 2015-08-07.

Table 1: Treeline positions (m a.s.l.) in the Abisko area at different points of time during the past 100 years. Data[1] provided by Dr. Gustaf Sandberg.

Species	1913	1950	1972	2010	2013
Birch	660	675[1]	760	850	890
Pine	475	475[1]	475	520	520
Aspen	400		460	460	510
Alder			450	540	540

Figure 2: *Left*-Establishment of individual multi-stemmed mountain birches of this type in the treeline "advance zone" is not easily and accurately dated by boring. *Right*-Even single-stemmed birches may displaying basal wood remnant structures, representing former stems, indicative of a much older age than revealed by the number of tree rings in living stems obtained at the soil surface.

During the past few years, megafossil tree remains were systematically searched above the current treelines, predominantly in alpine mires, on dry ground and at the lower margins of receding and long- lasting snow and ice fields [28,48,68]. Prior to the studies reported here, a few radiocarbon dates of subfossil reeline pines have been carried out in the specific part of Abisko-region, here concerned [21]. However, the positions are poorly defined and derive from low elevations relative to the highest known historical treeline in this specific area. Therefore these records are not included in the present analysis. Radiocarbon ages of wood remnants are given as calibrated years before present (cal. yr BP), with "present"= 1950 AD. Calibration was conducted using CALIB 5.0.2 in combination with INTCAL 04). For simplicity single dates in the text are expressed as mid points of the 2δ dating range [67-69]. Current altitudinal and latitudinal positions were determined with a GPS navigator (Garmin 60 CS), repeatedly calibrated against distinct land features on modern topographical maps. The nomenclature for vascular plants refers to Mossberg and Stenberg [70].

Study Area

The present study concerns a restricted mountain area in the close vicinity of Abisko village (68°20´N;18°50´E, 388 m a.s.l.), at the southern side of Lake Torneträsk (341 m a.s.l.) in northern Swedish Lapland. It embraces the east-facing slopes of Mt. Nuolja (1169 m a.s.l.) and Mt. Slåttatjåkka (1191 m a.s.l.). A special focus is on a plot embracing the catchment around the rivulet Rhitunjira. The plot (3×2 km) trends upslope and downslope of Lake Pompe, alias Lake Njulla (Figures 3 and 4), situated in the depression between these two mountains, 999 m a.s.l., 68° 22´N; 18°62´E. This lake is located 100 m higher than the present-day treeline of *Betula pubescens* ssp. *czerepanowii* and 480 m above the modern *Pinus* treeline. It is surrounded by dwarf shrub heaths, snowbed communities and mires. The soil is patchily podzolized, at least up to Lake Pompe, which may be indicative of a former tree cover [71]. Unfortunately and confusingly, Barnekow and Sandgren maintain that the lake is located 300-400 m higher than the modern treeline of birch and 550 m higher than that of pine [24]. Both figures are too high, which negatively impacts the accuracy of their palaeoclimatic inferences. A detailed account of the setting is provided by [10]. It is our conviction that data collected from a limited area, like the present one, may provide a better comprehension of vegetation and climate evolution, rather than from a wider geographical region [61]. As far as known, the present study is one of few, dealing with past and recent treeline history of different tree species in one and the same catchment area.

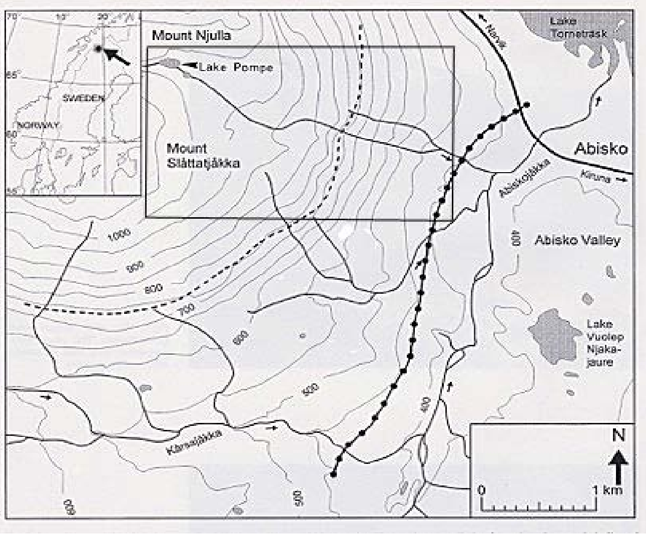

Figure 3: Location map showing the position of the study area (rectangle). The hatched line is the limit of more or less closed subalpine birch forest and the dotted line marks the limit of solitary pine trees.

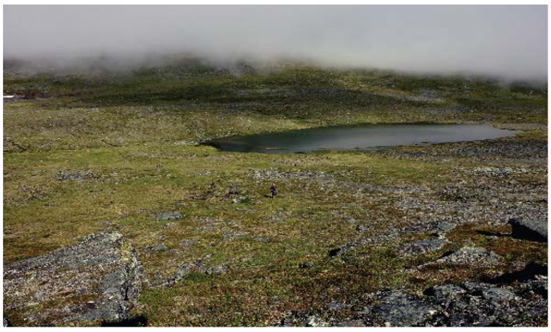

Figure 4: Overview of Lake Pompe (999 m a.s.l.) and the surrounding low alpine landscape towards south-east. Megafossils, recovered inclose to the inlet stream to the left, indicate that this lake, about 100 m above the present-day birch treeline, was surrounded by tree birches, pines and some alder during the early Holocene [29]. Photo: 2015-08-07.

The bedrock in the upper birch forest, above 550-600 m a.s.l. and in the treeline ecotone, is predominantly composed of calcareous schists, which support the growth of relatively high birches and a rich and lush meadow flora with tall herbs, (e.g. *Trollius europaeus, Geranium sylvaticum, Cicerbita alpina, Angelica archangelica*) as particularly conspicuous species[72]. Low- growing and sparse heath birch forest with predominant polycormic birches, dwarf-shrubs (*Empetrum hermaphroditum, Vaccinium vitis-idaea*), grasses, low-herbs and ferns (*Deschampsia flexuosa, Trientalis europaea, Solidago vigaurea, Gymnocarpium dryopteris*) prevail at lower elevations (below 550 m a.s.l.), with a poorer geological substrate, drier soils and a thinner snow cover. Today, solitary trees and small clumps of pine are confined to this forest matrix. Conspicuous species in the low alpine belt above the treeline are *Empetrum hermaphroditum, Cassiope tetragona, Cassiope hypnoides, Phyllodoce caerulea, Loiseleuria procumbens* and *Diphasiastrum alpinum*.

Climate characteristics (1961-1990) of the study area are provided by the official meteorological Station Abisko (388 m a.s.l.). The mean annual temperature of the year and the periods December- February and June-August is - 0.8, -10.6 and 9.7 °C, respectively. Annual precipitation amounts to 310 mm. Data provided by the Swedish Meteorological and Hydrological Institute. During the period 1913-2006, the mean annual temperature rose by 2.5 °C, while winter and summer temperatures increased by 2.9 and 1.6 °C, respectively [39].

In recent years it has become increasingly inferred that high-mountain Fennoscandia and the area here specifically concerned is far from pristine in structural and compositional character in perspective of the entire Holocene, which complicates the evaluation of ongoing and future landscape processes in terms of climate change and variability [12,14,72-75]. In general terms, this aspect is highlighted by Mattsson, who maintains that there exist practically no entirely virgin mountain birch forests in Scandinavia [76-78].

The lower reaches of the mountain birch forest belt in the study area have for long been utilized by man. Extensive logging operations in the valley bottom and lower slopes, took place in connection with the building of the railway (1895-1903) between Sweden and Norway. These operations have affected the forest structure within a distance of 1 km upslope [37,79,80]. Currently, the stands are reforested by dense and rapidly growing birch forest, a process coincident with, but primarily not conditional upon climate warming and which complicates the use of the Abisko area for landscape ecological change related to recent climate change [74]. At higher elevations, more diffuse impact on the tree cover, not easily distinguished today from a natural state, may have been accomplished by centuries-long land use practices by the indigenous Sami population, foremost local logging for fire and construction wood, in combination with grazing by semi-domesticated reindeer [74,81]. The lasting impact of reindeer grazing around the treeline is somewhat ambiguous, as some researchers, based on extensive field-observations, found no clear evidence of impacts on the birch cover and regeneration in the study area [36,82-85]. Other authors, drawing on detailed field studies, state that only few sites around Lake Torneträsk and adjacent regions in Sweden and Norway have a birch forest with a structure that entirely relies on spontaneous regeneration and being unaffected by Sami activities [9,76]. On the balance of existing long- and short term historical evidence, it appears that positional treeline (current definition) change in this region is predominantly a common and natural climate-driven process with little connection to local drivers such as fire, logging, insect attack, reindeer or livestock grazing [28,35,53,83]. In this context, it needs to be stressed that the characterization of the Scandinavian mountain range as a cultural landscape is an overstatement and a violation on the language [75]. This distinction does not mean that the general structure of the subalpine vegetation landscape is unaffected by direct and indirect human actions.

Results and Interpretation

Modern structure and dynamics of the birch treeline ecotone

Currently, the mountain slopes facing east and southeast of Mt. Nuolja and Mt. Slåttatjåkka are clad with extensive belts of mountain birch (*Betula pubescens* ssp. *czerepanovii*) forest, extending between the valley bottom with Lake Torneträsk (342 m a.s.l.) and the spatially variable limit of closed birch forest around 680-720 m a.s.l. This level is a few tens of metres higher than the birch treeline by the early-20th century, 660 m a.s.l., as deduced by boring particularly old-looking birch stems, 2 m above the ground-level in 1972 (Figure 5), supported by older observational data. Small local forest outliers, in the form of clumps or "fingers" exist above the limit of closed forest, with stems initiated predominantly during the 1930s. A similar result was obtained by [79,86-88]. Treeline positions (birch, pine, aspen, grey alder) measured by different researchers at different points of time during the past 100 years are displayed in Table 1.

Today, the highest positioned birch treeline in the study area is at 890 m a.s.l., in the form of a few rapidly growing small and slender trees (Figure 6). This implies, by definition, a treeline rise by 230 m over the past 100 years, a value almost identical with a record (225 m) at another site in the Abisko region and in the southern Swedish Scandes [19,28].

This coincidence supports the contention that broad-scale secular climate warming, rather than local circumstances, has been the driving force. Concurrently, and likely for the same ultimate reason, the upper subalpine birch forest appears to have increased in density and cover, as previously inferred by some local studies [35,40,43,83,89]. This feature is highlighted by moribund old-growth birches with particularly wide crowns, indicative of growth in previously more sparse and open stands. Currently they prevail in dense and uniform stands of young birch trees (Figures 5,7). Judging from the tiny appearance of the treeline markers and observations made in 1998 and a treeline record at 775 m a.s.l. (Kullman, unpublished), it appears that about 100 m of the total secular treeline change (230 m) took place over some past few decades, partly as accelerated height growth

Figure 5: Old-growth moribund mountain birch, indicating the minimum position of the treeline by the early 20th century, 660 m a.s.l. Photo: 2015-08-07.

Figure 6: The highest present-day birch treeline, 890 m a.s.l. on the east-facing slope of Mt. Slåttatjåkka. This specimen was 1.6 m high in 2010 and has attained tree size, i.e, >2 m tall, during the subsequent 3 years. Photo: 2013-09-14.

Figure 7: During the early 20th century, this landscape segment was more open, with scattered trees, some of which remain in a matrix of more recently initiated trees.

of scattered old-established krummholz individuals and partly as seed based upslope upslope colonization, just like the situation in the southern Scandes [19,67,90]. In fact, Sandberg documented the presence of krummholz individuals at 760 m a.s.l., i.e. about 100 m above the contemporary treeline [87].

Conspicuously, many of the recently seed-established specimens, forming the new treeline, display morphological leaf characteristics indicating hybrid origin, with *Betula nana* and *Betula pubescens* as parental species [91]. Since hybrids, with a relatively high genetic variation are more cold-tolerant than the last-mentioned species, it seems likely that basically climate-driven treeline rise has been facilitated by this mode of hybridization [92,93].

The age structure analysis of birches making up the lower part of the treeline "advance zone" on Mt. Slåttatjåkka, for the past century (Figures 1 and 8) highlights that the majority of the tree-sized stems were initiated during the period 1930 to 2009, with a distinct peak by the 1930s and a low 1960 to 1979. An almost identical age structure was found by a regional study in the southern Swedish Scandes, which further strengthens that climate warming has been the principal driver [14].

Relative to the treeline, the limit of closed birch forest has advanced substantially less, which contrasts with assumptions of pending extensive upshifts, based on projective modeling of climate change and assumed birch responses [94,95]. This result conforms to experiences from other parts of the Fennoscandia [66,96,97].

These present results contrast with those obtained through stem boring and ring count by Van Bogaert et al [27], who inferred minimum establishment of new birches at the treeline during the warm 1930s and maximum during the relatively cold 1960s and 1970s [27]. On this basis they claimed that climate warming had only a minor influence on elevational treeline dynamics. One reason for this discrepancy may be failure to accurately date the germination point of polycormic birches with complex stools of dead and living stems. If sufficient efforts are taken to core stems below the ground surface, much higher ages may be revealed than just by coring at the soil surface or slightly above [98]. Moreover, youngish-looking and vegetatively reproducing treeline birches in other regions have proven to be several thousand years old, as revealed by ^{14}C-dating of stem remains buried in the soil right underneath the living birches [67].

Young birch and willow saplings, 5-10 cm tall, are quite frequently found in mesic sites within a zone extending high above their current treelines (Figure 9), indicating the potential for recolonization of sites, where megafossils demonstrate that these species grew by the early- to mid-Holocene. In fact, the performance of such individuals are sometimes taken as the simplest and most straightforward indicator of potentially pending change in treeline positional stability, although short-term weather anomalies are sufficient to eradicate these populations [65,99,100]. None of these observed saplings showed signs of being browsed by reindeer. This circumstance further conflicts with the view advocated by, claiming that reindeer rather than climate warming are more important for birch establishment, growth and treeline rise than climate change [27].

Modern structure and dynamics of the pine treeline ecotone

By the late 20th century, scattered specimens and small groves of old-growth pine trees reached 475 m a.s.l. (Figure 10). This

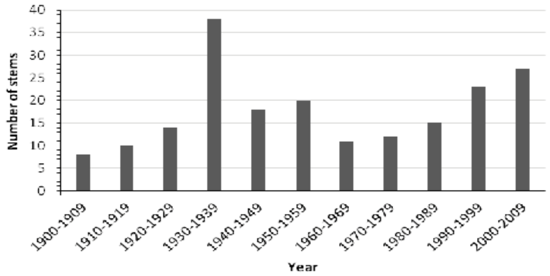

Figure 8: Age structure of all birches 2 m and taller (2010) in a sample plot (n=196), which was well above the treeline by the early 20th century.

Figure 9: Young birch (*Betula pubescens* ssp. *czerepanovii*)growing 1075 m a.s.l. on the east-facing slope of Mt. Slåttatjåkka, in the forefield of a rapidly disintegrating snow/ice patch, 185 m higher than the local present-day birch treeline. Photo: 2015-08-07.

"geriatric" pine treeline elevation was recorded at approximately the same elevation, or somewhat lower, by early explorers, and remained there by the early 1970s (Kullman, unpublished) and until the present day [79,88]. These veteran trees are often more or less moribund and between 200 and 350 years old. Scattered downed logs of stout pines occur in a 65 m broad zone above. Some of these display charred surfaces, indicative of forest fires in the past. This situation is consistent with observations in the Abisko region during the early part of the 20th century and recent reconstructions, suggesting that pine was on the brink of extermination from these high elevations, as the dying specimens were not balanced by recruitment during the relatively cold centuries of the Little Ice Age [53,79,101].

Traces of logging activities are quite frequently found in the upper pine forest belt. In addition, some old pines display signs of non-destructive bark peeling in the distant past, possibly performed by the Sami people as a more or less regular food resource [102]. Regeneration in the form of young pine saplings is currently strikingly sparse in the pine stands, although scattered large saplings and young trees occur regularly. The majority of these derive from an intensive phase of regeneration by the mid-20th century or somewhat earlier, as locally recorded by Arnborg and Sandberg and deduced in retrospect by present-day static age structure analyses (Stöcklin and Körner, 1999), conforming to a general trend over northern Fennoscandia [57,64,83,103-107]. During the past few and decades, the treeline has advanced by 45 m, up to 520 m a.s.l. (Figure 10). The majority of these quite few specimens is multi-stemmed, mainly as a consequence of moose browsing, which has substantially retarded the growth of individual pines and reduced the size of these cohorts up to the present. Just like the case of mountain birch, the upper limit of closed pine forest exclaves has not advanced significantly during the past 100 years [57-64].

Spruce and larch, new species in the Abisko area

Norway spruce, which in most of the Swedish Scandes uses to form a distinct belt of mature trees between the pine forest and the birch forest belt, was until quite recently entirely lacking in the study area [39]. However, in 2013, two young spruce (*Picea abies*) and in addition one larch (*Larix* sp.) sapling were recovered at separate sites in the upper part of the belt with mixed birch and pine trees, 415, 435 and 400 m a.s.l. respectively (Figure 11). The nearest seed producing spruce tree (4 m tall) grows at the margin of and extensive palsa mire 360 m a.s.l., near Torneträsk railway station, about 30 km east of Abisko. *Larix* is not known as currently spontaneously growing in Scandinavia, but exists with the nearest site in Björkliden village, 445 m a.s.l., 7 km northwest as ornamental trees of Abisko. Current spread of *Larix* from such putative sources into subalpine and low alpine settings is reported also from the southern Swedish Scandes [13].

Although not inferred from existing pollen records, it [22,108] is evident that both *Picea abies* and *Larix sibirica* have grown high above the current treeline elevations in northern Lapland during the early Holocene, as judged from finds of macrofossil records at the margin of the receding Storglaciären in the Tarfala-Valley, c. 35 km south-east of Abisko [48]. Both *Picea* and *Larix* grew in nearby and similar high-elevation sites further south in Lapland and elsewhere in the Scandes (Sweden and Norway) during the early Holocene, as evident from megafossil and pollen records, respectively [41,47,48,68,109,110]. It may be speculated that *Larix* was accompanied with a ground layer flora with continental climate affinities, as indicated by the rare and enigmatic presence of relict species with an eastern present-day main distribution [111].

Modern structure and dynamics of the aspen treeline ecotone

Predominantly by phenotypic transformation from krummholz to erect tree modes, aspen (*Populus tremula*) has recently become a more conspicuous component of the mountain birch forest in northern Fennoscandia, as can be easily seen during the early autumn when the intense yellow foliage frequently contrasts with the still green birch matrix. In most cases, aspen stands in subalpine settings are judged by experienced and diligent field-botanists to be old-established clones, perpetuated as low- growing individuals by extensive asexual root suckering [9,112-115]. However, some recent studies from the Abisko region have claimed, without convincingly supporting data, that a certain part of the stands have arisen by seed regeneration in quite recent time, in response to climate warming [116]. It is particularly remarkable that Rundqvist et al. maintain that aspen is a new and currently naturalizing species, that has recently immigrated to the area [89]. This claim contrasts with observations by Lagerberg, stating that aspen grew as suckering krummholz on all mountains around Lake Torneträsk, reaching 600 m a.s.l. on Mt. Njulla. Further doubt relates to the well-known fact that aspen trees are either female or male, which restricts the incidence of sexual regeneration and individual spread close to the treeline [78,88]. This entire issue, concerning the recent performance of aspen needs further study and confirmation.

Sparsity of seed production and assessed absence of true aspen seedlings during the past century in treeline situations appears as a common feature in northern and high-elevation Fennoscandia, the study area included [9]. However, seedlings are reported by [92,117].

The fact that several older geobotanical studies report isolated krummholz aspen clones of assumedly old age in the upper birch

Figure 10: Left-Old-growth pine, 475 m a.s.l., representing the pine treeline by the early 20th century, Photo: 2009-08-24. Right-Young pine, 2.1 m high growing 520 m a.s.l. and marking the present-day treeline on Mt. Slåttatjåkka. Photo: 2009-08-25.

Figure 11: *Left* and *Mid*. Vital *Picea*-saplings growing in outpost stands of pine on Mt. Slåttatjåkka 415 and 435 m a.s.l., respectively. *Right*. Young sapling of *Larix* sp.400 m a.s.l. on Mt. Slåttatjåkka in a stand of old-growth pines. Photo: 2013-09-13.

forest and far from putative seed producing trees, casts some doubt on the generalizing inferences that the abundance and elevational distribution of aspen has recently increased predominantly by establishment of new individuals from seed [116,117].

Currently, the treeline of aspen is at 510 m a.s.l. in the study transect. The treeline is represented by a tree with 102 tree rings 2 m above ground level (Figure 12). This is 110 m higher than estimated for the early 20th century [79]. At that point of time the species limit, was assessed as 0.5 m high specimens growing close to Abisko (c. 400 m a.s.l.), where a few tree sized clonal specimens, with more 70 tree rings 2 m above ground level, grew by the early 1970s. At that time, the species limit was at 760 m a.s.l. (Kullman unpublished). Still today, scattered low-growing (<1 m tall) and presumably old-aged clones occur 760 m a.s.l. (Figure 13). Apparently, aspen treeline rise and increased prominence in the subalpine birch forest appear to be predominantly accomplished by *in situ* transformation of old-age clones in response to secular climate warming.

Quite frequently in the study area, the highest treeline, irrespective of species, is formed by *Salix borealis*, which usually ascends a few tens of meters higher than the mountain birch, particularly is steep slopes with a relatively high snow avalanche hazard.

Modern treelines of grey alder and bird-cherry

Alnus incana and *Prunus padus* appear infrequently in tree form along Rihtunjira, with current treelines at 545 and 590 m a.s.l., respectively. To judge from their youngish habitus they did not grow as tree-sized individuals at these high elevations by the early 20th century.

Aspects of Holocene treeline history, as evidenced by megafossil records

Based exclusively on radiocarbon-dated megafossil tree remains retrieved from positions well above the current treeline (Table 2), it appears that during the period 9500-8500 cal yr BP pine grew in scattered patches 500-600 m above its present-day treeline position [28,68]. In the southern Norwegian Scandes, the pine limit peaked at virtually the same time [12,44]. Over the same interval, the stands were intermixed with tree birches and some common alder grew 110-140 m higher than their modern treeline elevations, which appears as a regional minimum. Prior studies in northern Lapland have revealed that during this period mixed stands of pine and birch reached 600-700 m higher than today, when they grew in currently empty snow hollows and glacier cirques [28,48]. Accordingly, rapid recent disintegration of snow and glacier ice have disclosed megfossils of pine and birch high above their present-day treelines in the study area (Table 2, Figures 14 and 15). Obviously, the last-mentioned interval was the warmest period of the Holocene in northern Fennoscandia, as inferred in some prior studies in the Scandes although none of these studies disclosed growth of pine trees at correspondingly high elevations, relative to the present-day situation [44,118-124]. Subsequently pine gradually lost in abundance at high elevations towards the present day, presumably ultimately forced by Earth´s orbital variations and associated summer climate cooling and decreased seasonality, which transiently allowed birch still to grow here, when summers became colder and snow disappeared later in the season [125]. The present records indicate that following 5100 cal yr BP, practically no trees of any species appear to have existed at the concerned elevational interval, i.e. 1000-1100 m a.s.l. The latter point of time may indicate the onset of the Neoglaciation, when retreating tree cover was extensively replaced by alpine tundra [12,21,45,111,126]. However, single pine megafossils, recovered in the study area date to the 13th, 15th and17th centuries when pine grew 75-100 m higher than present (Figure 16), conforming to a common pattern of Medieval high treeline establishment and warmer-than-present conditions along the entire Swedish Scandes [102]. These data invalidates claims by Sonesson and Lundberg that the pine limit has never during the late Holocene been higher than today.

Drawing on the unformitarian principle, applied to local treeline/climate relations and supported by multi-site and multi-species studies of tree-line change on videly different time scales implies that variable past treeline positions may be taken as proxy of low-frequency of palaeoclimate dynamics [8,17,19,56,125-127].

Thus, it may be inferred from the historical treeline data, presented here with a maximum 1090 m a.s.l. (Table 1), that summer temperatures in the study region culminated during the period 9500-8500 cal. yr BP. This early temperature peak is inferred also from chironomid and diatom records from the same area as the present study and concurs with various proxies in other parts of the Scandes

Figure 12: Current treeline of *Populus tremula*, Mt. Slåttatjåkka 510 m a.s.l., represented by a tree with 102 tree rings (2013) at the root collar. Photo: 2015-08-07.

Figure 13: Shrubby clone of *Populus tremula*, with numerous shoots (0.1-0.4 m high) from root suckers. This specimen was noted at this specific site in 1972, when the areal size was more restricted than the present-day situation, and the shoots were fewer and not higher than 0.1 m. Mt. Slåttatjåkka, 670 m a.s.l. Photo: 2009-08-23.

Table 2: Radiocarbon dates and site characteristics of megafossil *Pinus* and *Betula.*

Species	**Age**	**Cal yr BP**	**Sample Altitude**	**Treeline 2013**	**Relative**	**Locality**	**Coordinates**	**Lab code**
	^{14}c yr BP	**Midpoint**	**(m.a.s.l)**	**(m.a.s.l)**	**Altitude (m)**		**N lat.; E long.**	**Beta-**
Pinus	270 ± 30	1630	580	520	70	Njulla	68 21 829; 18 44780	362597
Pinus	710 ± 30	1280	610	520	100	Slåttatjåkka	68 20 435; 18 42971	358487
Pinus	370 ± 90	1485	585	520	75	Slåttatjåkka	68 20 209; 1842 649	358488
Pinus	8380 ± 80	9335	1030	520	520	Njulla	68 21 887; 18 41126	264390
Pinus	7690 ± 50	8490	1005	520	495	Njulla	68 21 861; 18,41293	284456
Pinus	7710 ± 70	8500	1090	520	580	Slåttatjåkka	68 21 474; 18,41305	284461
Pinus	8130 ± 90	9085	1000	520	500	Njulla	68 21 919; 18 41812	91498
Pinus	8380 ± 60	9400	1000	520	500	Njulla	68 21 919; 18 41812	108508
Pinus	8540 ± 50	9490	1000	520	500	Njulla	68 21 919; 18 41812	108777
Pinus	8380 ± 80	9335	1030	520	520	Njulla	68 21 888; 18 41128	264390
Pinus	7690 ± 50	8490	1005	520	495	Njulla	68 21 919; 18 41812	284456
Betula	7730 ± 70	8470	1000	890	110	Njulla	68 21 919; 18 41812	108781
Betula	4480 ± 50	5090	1000	890	110	Njulla	68 21 919; 18 41812	108506
Betula	8370 ± 80	9395	1000	890	110	Njulla	68 21 919; 18 41812	108504
Betula	5420 ± 60	6175	1000	890	110	Njulla	68 21 919; 18 41812	106368
Betula	4760 ± 50	5465	1025	890	135	Njulla	68 21 886; 18 41100	284457
Betula	6900 ± 60	7735	1015	890	125	Njulla	68 21 930; 18 41297	284458
Betula	8210 ± 70	9210	1030	890	140	Njulla	68 21 891; 18 41131	264392
Betula	8510 ± 70	9490	1030	890	140	Njulla	68 21 925; 18 41212	264391
Alnus	4590 ± 60	5255	1000	890	110	Njulla	68 21 919; 18 41812	108505
Alnus	8220 ± 90	9190	1000	890	110	Njulla	68 21 923; 18 41814	99415

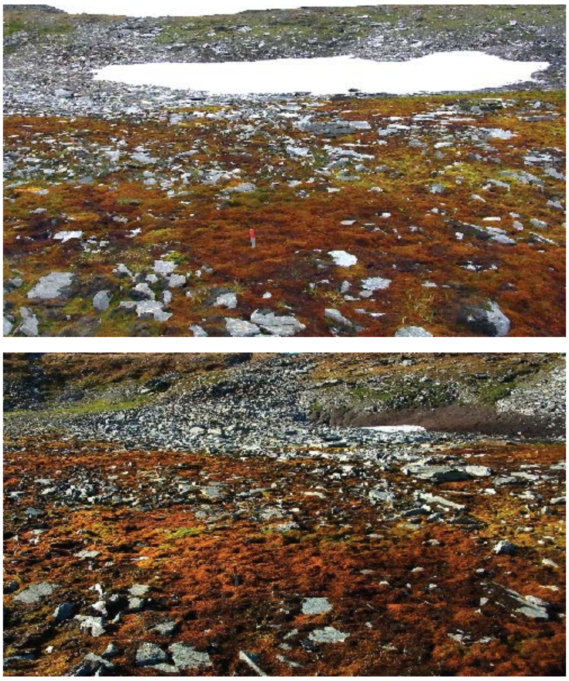

Figure 14: *Top.* Late-melting and previously long-term permanent snowpatch and its moss-covered forefield, situated in the depression between Mt. Njulla and Mt. Slåttatjåkka, 1030 m a.s.l. Within the post-Little Ice Age melt-out area, currently dominated by bryophytes, recovered megafossil birches and pines range between 9500-5300 and 9400-8400 cal. yr. BP, respectively. Photo: 2010-08-27. *Bottom.* By 2013, the snow patch had virtually disappeared, leaving a bank of "snowbed loess" (brown) with subfossil wood remains. Photo: 2013-09-03. Note the red/white wooden reference stick in the foreground. In early-august 2015, the snow patch was substantially larger than 2010-08-27.

Figure 15: Subfossil pine log emerging in a melt-out channel, 1090 m a.s.l.,Mt. Slåttatjåkka. Radiocarbon dating yielded 8490 cal. yr BP. Photo: 2010-08-29. By August 1915, the log was absent, presumably disintegrated and washed away.

although contrasting with other studies, suggesting that the Holocene thermal optimum was around the mid-Holocene [128-131].

Using a lapse rate of 0.6 °C per 100 m and a maximum pine treeline depression of about 600 m, implies that the temperature difference between the early Holocene optimum, about 9500 cal. yr BP and the present amounts to 3.6 °C, which has to be reduced by 0.6 °C, accounting for land uplift by approximately 100 m since the early Holocene and associated general cooling [132,133].

Conclusions

In the Abisko area of northern Swedish Lapland, short- and long-

Figure 16: A piece of megafossil pine wood, emerging in eroded subalpine heath on Mt. Slåttatjåkka, 610 m a.s.l., i.e. about 100 m higher than the present-day pine treeline. Radiocarbon-dating yielded 1280 cal. yr BP. Photo: 2013-09-13.

term performance of high-elevation tree cover was investigated. The main focus was on an altitudinal transect running through the treeline ecotone between the coniferous boreal forest over the subalpine birch forest and into the lower alpine tundra.

During the period 1913-2013, the treeline of birch, pine and aspen advanced by 230, 45 and 110 m, respectively. These figures conform to data from the southern Swedish Scandes, indicating that broad-scale climate warming has been the principal driver. Treeline rise by birch and aspen was mainly accomplished by phenotypic transformation of old-established krummholz into erect tree forms. Relative to the treeline, the upper boundary of closed mountain birch forest and pine forest exclaves have shifted insignificantly in elevation, although the upper stands have grown denser. This suggests that future climate warming (if becoming a reality) may not threaten the continued existence of the alpine tundra and its contained biodiversity.

Age structure analysis refutes prior claims that birch treeline dynamics mainly reflects the intensity of reindeer grazing rather than temperature variability. This study challenges recent proposals that aspen is currently spreading upslope and westwards in the birch forest belt by seed establishment of new individuals. By combination of older geobotanical records and recent observations, it is obvious that most aspen stands have existed over the entire region since long ago, mainly in the form of stunted krummholz. In response to recent warming they have attained tree size and have become a more conspicuous element of the landscape.

New tree species to the Abisko area, quite recently established in low frequency and abundance are *Picea abies* and *Larix sibirica*. These appear as young saplings of obscure origin. According to megafossil records, mixed stands of birch and pine existed near 600 m above current treeline during the early Holocene. This implies 3.6 °C warmer than present, in contrast to often advocated opinions that summer temperatures peaked in the middle Holocene. Adjusted for glacio-isostatic land uplift by c. 100 m since about 9500 cal. yr BP, the above figure has to be reduced by 0.6 °C.

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