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# Resurgence of warmth-demanding tree species and a common pending thermophilization in subalpine and northern boreal Sweden-an ecological signal of post-Little Ice Age climate improvement

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## Abstract

Largely consistent with general predictions and earlier empirical studies, it appears that post-Little Ice Age climate warming has started to affect large-scale biogeographic patterns in northern Sweden. Long-term monitoring in subalpine and adjacent regions reveals sparse spread of broadleaved thermophilic tree species. Saplings of *Quercus robur, Ulmus glabra, Acer platanoides, Alnus glutinosa* and *Betula pendula* have responded to recent climate warming by jump-dispersal in the order of 50-300 km northwards and 500-800 m upwards, relative to their natural range limits. Consistent with treeline rise by boreal tree species, the thermophilies have reinvaded regions where they grew during the warmest phase of the Holocene, 9500-8000 years ago, but were subsequently extirpated by the Neoglacial cooling. Confined to the past 20 years or so, the unique observations of recent termophilies comply with background climate data, i.e. warming of all seasons. These results may contribute to more realistic vegetation models by stressing that the distributions of certain plant species are able to track climate warming without substantial migrational lag. Hitherto, vegetation and climate evolution appear to be well within the frames of natural dynamics during the postglacial era, although mechanisms may differ.

**Keywords:** Thermophilies; Subalpine; Climate change; Biogeographic shifts; Swedish Scandes

## 1. Introduction

In a time coined by widespread concern and anxiety for proposed future climate warming, one of the most important tasks for contemporary vegetation ecology is to elucidate plant cover and landscape ecological changes over the past 100 years, following the climatic and ecological nadir of the Little Ice Age, approx. AD 1300-1900 (Lamb 1995; Grove 2004; Helama et al. 2021). During the former interval, climate change in concert with land use impacts, appears to be on the verge of turning subalpine and northern boreal ecosystems into states, unprecedented for several millennia of the Holocene (Kullman 2006a; 2010a,b, 2021a,b, 2022a; Macias-Fauria et al. 2012; Kullman & Öberg 2020, 2022; Schickhoff et al. 2022). This projection is contingent on the assumption that climate change scenarios (IPCC 2021) are borne out. In that perspective, detailed *in situ* biogeographic monitoring with a background of historical data is urgently needed.

The recent warming phase is reported to have already affected ecosystems and species in widely different parts of the world (Parmesan & Yohe 2003; Penuelas & Boada 2003; Kullman 2004a,b, 2010a; Walter et al. 2005). High mountains at high latitudes play a key role in the early detection of ecological responses to the modern climate transformation. This is due to relatively large proposed future temperature changes hereabouts and since many resident plant and animal species exist at the limit of their climatic tolerance, i.e. responsive even to minor climatic shifts. Moreover, the pristine nature of extant biological communities enables interpretation in terms of climate change.

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In the southern Swedish Scandes, summer (J.J.A.) and winter (D.J.F.) warming amount to about 1.5 °C for the period 1901-2022 (Kullman & Öberg 2022). This course of change has evoked upshifts of altitudinal (alpine) boreal treelines (trees at least 2 m tall) by maximum 200 m or slightly more, to positions that seem unsurpassed during the past 7000 years (Kullman & Kjällgren 2006; Kullman 2017a,b, 2021b). In addition, substantial upward migration of ground cover species, including herbs, sedges, grasses, ferns and dwarf-shrubs, by an average of 200 m, has occurred since the early 1950s. This course of change implies increased plant species richness on high alpine mountain summits in the Scandes (Kullman 2002, 2007a, b; Klanderud & Birks 2003; Odland et al. 2010; Michelsen et al. 2011; Felde et al. 2012). The marginal situation and volatile character of these new outposts, with particular respect to snow melt phenology, was highlighted by slight local extirpation and retreat during the cold summer of the year 2012, characterized by a short growth period and late snow melt at high alpine elevations (Kullman 2014).

It is important to stress, that the upper limit of *closed forest* has shifted upslope much less than the *treeline* during the past 100 years (Kullman 2022b), thereby contesting alarmistic model projections of a future substantial forest cover expansion and consequent major reduction of the alpine world and its constituent species in the Scandes (Moen et al. 2004).

In the above context, it has been predicted that thermophilic (boreonemoral) woody species, e.g. of the genera *Quercus, Ulmus, Alnus, Corylus, Tilia, Acer* and *Betula*, are likely to shift northwards into high-latitude and high-elevation boreal forests of Norway and Sweden, given that current climate amelioration prevails (Aas 1970; Boer et al. 1990; Dahl 1990; Holten & Carey 1992; Hafsten 1992; Angelstam & Svensson 1996; Vera 2000). These projections gain some local support from casual observations (Erkamo 1956; Aas 1970; Kullman 2002, 2003, 2006a, b).

With this background, I here report and discuss in the perspective of modern climate change, the anomalous phenomenon of recent migration of broadleaved thermophilic tree species from distant low-lying sources into the subalpine belt of the south-central Swedish Scandes. In addition, the occurrence of planted trees and saplings of species belonging to this group is documented from the coniferous *northern boreal forest* where *Picea abies* and *Pinus sylvestris* prevail as dominants at the present day (Ahti et al. 1968).

## 2. Material and methods

### 2.1. Study area

The study is located mainly to the southern Swedish Scandes and adjacent boreal tracts to the east. Climate data relevant for treeline ecotone performance are derived from Storlien/Visjövalen meterological station, 642 m a.s.l., in the mountains close to the border between Sweden and Norway (Fig. 1). The standard level temperatures for January, July and the year are -5.5, 12.3 and 2.0 °C, respectively (1991-2020). Annual precipitation amounts to c. 1000 mm/year (Swedish Meteorological and Hydrological Institute). Over the period 1901-2021 summer (June-August) and winter (December-February) temperature increased by 1.6 and 1.5 °C, respectively (Kullman & Öberg 2022).

A subalpine belt and upper treeline with dominant mountain birch (*Betula pubescens* ssp. *czerepanovii*) prevails today in the main study region. Solitary specimens of *Picea abies* and *Pinus sylvestris* occur regularly in the lower reaches of the birch belt. The treelines of *Betula, Picea* and *Pinus* are positioned approximately 950, 850 and 800 m a.s.l., with large local variation depending on site and aspect. Impact of former land use on treeline positions is negligible (Kullman 2010b, 2017a). East of the Scandes, closed semi-natural forests with dominant *Picea abies* and *Pinus sylvestris* alternate in the landscape. Early successional stages are characterized by birches (*Betula pubescens* coll. and *Betula pendula*). A comprehensive overview of the treeline ecotone and adjacent *mountain taiga* is given by different sources (Kullman 2005, 2010b; Carlsson et al. 1999; Wielgolaski et al. 2017).

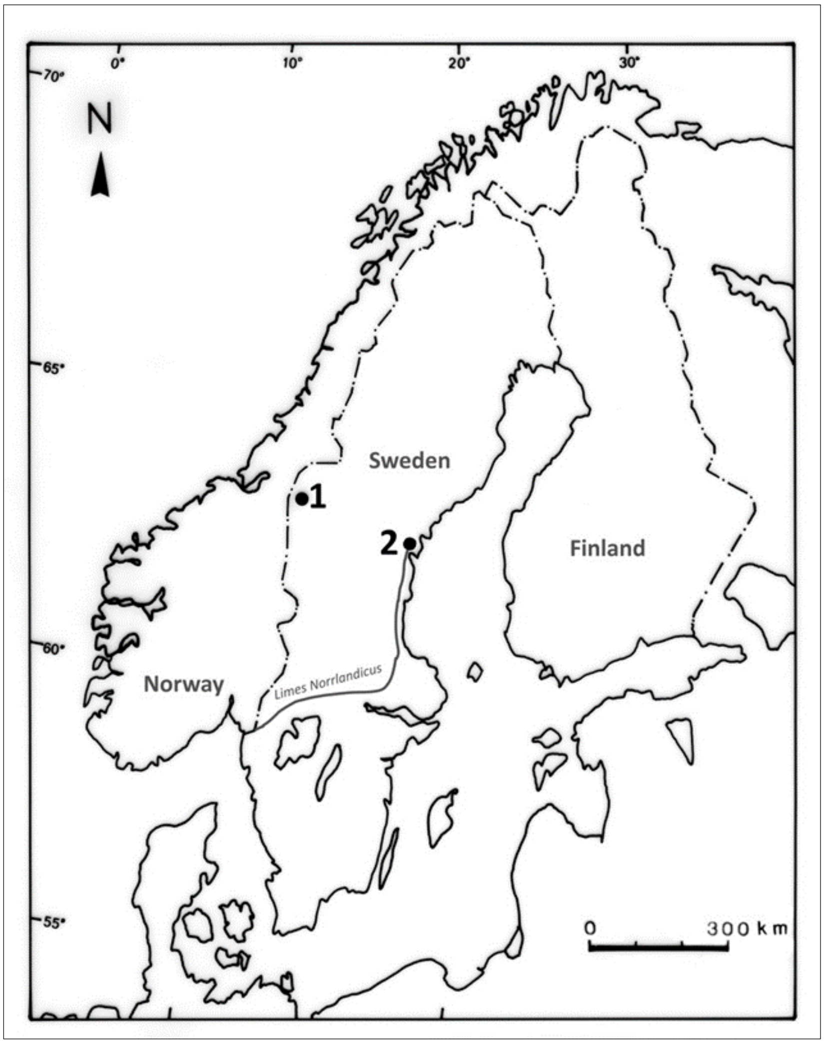


**Figure 1** Location of study sites in northern Sweden. (1) Treeline studies in the southern Scandes. (2) Mt. Skuleberget. The solid line indicates the position of Limes Norrlandicus

## 2.2. Methodological approach

The urgent need for real-world data, based on long-term systematic observations at the same locations is increasingly stressed. This is mandatory if we are to understand and tentatively foresee responses of species and communities to altered climatic conditions in the future (Holten & Carey 1992; Gitzen et al. 2012; Helama et al. 2020).

The core of the present study relies on intentional search for thermophilic broadleaved deciduous trees within a regional network of sites (permanent transects) originally intended for long-term standardized treeline monitoring in the southern Swedish Scandes (Kullman 2001). In addition to positional treeline changes, casual records of the concerned group of species are reported from outside the surveyed transects, from exploratory travels in different parts of northern Sweden.

Present-day climate-mediated distributional shifts are not just restricted to high-mountain regions, but also concern lower elevations. From a dynamic biogeographical point of view, particular focus is devoted to the northern and elevational limit of *Quercus robur*. This species most distinctly marks the so-called *Limes Norrlandicus* (Fig. 1), by tradition held as an important biogeographical transition zone in northern Sweden below the treeline, separating biota with northern and southern affinities (Fransson 1965; Gustafsson & Ahlén 1996; Sjörs 1999; Gustafsson, 2008). A northward movement of *Limes Norrlandicus* appears imminent, but is not easily detected due to human interference with the plant cover (Kullman 2012).

Precise geographical locations and altitudes are obtained with a GPS navigator. Geographical coordinates are given as degree latitude and longitude. The present paper updates and extends a previous report (Kullman 2008).

# 3. Results

## 3.1. Permanent line transects

Recent surveys of the treeline line transects have uncovered young specimens of *Quercus robur, Ulmus glabra, Alnus glutinosa*, *Acer platanoides and Betula pendula*, growing at unprecedented high elevations, well outside their previously known natural ranges and biogeographical zones in northern Sweden (Kullman 2008, 2020a). These species have their main distribution limits in the boreonemoral zones of southern and mid Sweden, hundreds of altitudinal meters below the new colonists discovered by this study. *Betula pendula* grows closer to the high mountains than other species in the group focused here, although this is the most thermophilic birch species in Fennoscandia (Holm 1994; Kullman 2005). *Quercus robur* and *Alnus glutinosa* are supposed to be newcombers, dispersed by birds and wind from the Norwegian side of the border, just like the situation inferred for the early postglacial time, based on robust megafossil data (Kullman 2020a). Table 1 accounts for these records and their appearance. Photographs are given as Figures 2-7.

All recovered specimens are of low stature and judged to be quite young, and recently established at their growing sites. There is nothing in their growth habitus, e.g. multiple stems or stools, to suggest that they have been growing at their present sites for lengthy periods as suppressed individuals.

Particular focus of search was on thermally favored mountains, renowned for a rich flora with southern affinities, as documented by competent botanists during the early- and mid-20th century (Smith 1920, 1957; Kilander 1955). These localities contained spots with this kind of flora and are assumed to be isolated remnants of a generally richer flora prevailing more extensively during the warm early-Holocene (Smith 1951; Kullman & Öberg 2019). Examples of these species are *Ajuga pyramidalis, Anthriscus sylvestris, Milium effusum, Ranunculus platanifolius, Cotoneaster scandinavicus, Anthyllis vulneraria* ssp. *lapponica* (Fig. 8).

**Table 1** Location and size of thermophilic trees species recovered in the subalpine birch forest belt

| Species | Locality | Altitude (m a.s.l.) | Coordinates | Height (m) |
|---|---|---|---|---|
| *Acer platanoides* | Åreskutan | 905 | 63° 24.732´N; 13° 04. 689´E | 0.3 |
| *Acer platanoides* | Storsnasen | 630 | 63° 13.946´N; 12° 25. 653´E | 0.3 |
| *Acer platanoides* | Enafors | 530 | 63° 16.670´N; 12° 21.436´ E | 0.4 |
| *Acer platanoides* | Tandövala | 770 | 60° 50.186`N; 13° 10. 479´E | 0.2 |
| *Acer platanoides* | Alsberget | 710 | 64° 39.896´N; 17° 35.891´E | 0.3 |
| *Alnus glutinosa* | Storsnasen | 705 | 63° 12.290´N; 12° 23.682´E | 0.3 |
| *Alnus glutinosa* | Handöl | 530 | 63° 15.410´N; 12° 26.677´E | 1.3 |
| *Betula pendula* | Storsnasen | 680 | 63° 13.845´N; 12° 25.477´E | 1.1 |
| *Betula pendula* | Tandövala | 770 | 60° 50.195´N; 13° 10.498´E | 0.5 |
| *Betula pendula* | Städjan | 1020 | 61° 54.940´N; 12° 52.845´E | 0.4 |
| *Betula pendula* | Städjan | 935 | 61° 54.585´N; 12° 53.082´E | 0.3 |
| *Quercus robur* | Predikstolen | 1055 | 62° 52.758´N; 12° 24.099´E | 0.2 |
| *Ulmus glabra* | Åreskutan | 970 | 63° 24.751´N; 13° 04.675´E | 0.4 |
| *Ulmus glabra* | Laptentjahke | 990 | 63° 08.348´N; 12° 25.551´E | 0.2 |

**Figure 2** Left. Sapling of *Quercus robur* established in meadow vegetation disturbed by reindeer trampling. The site is only 15 altitudinal meters below the birch treeline, which has shifted upslope by 175 m since early-20th century (Kullman & Öberg 2009). This individual was first discovered in 2005, when it was accompanied by another sapling. It still prevailed in 2008, showing some growth since 2005, although one individual had died. Mt. Predikstolen, 1055 m a.s.l. Photo: 2008-07-04. Right. The steep and thermally favorable and species-rich S-SE-facing slope of Mt. Predikstolen (1476 m a.s.l.). Photo: 2008-07-04

**Figure 3** Left. Young sapling of *Ulmus glabra,* recently established right at the birch treeline in a steep and warm mountain slope, where many plant species attain their highest regional stations (Kilander 1955). Mt. Laptentjahke, 990 m a.s.l. Right. Overview of the slope where *Ulmus* grew, in the upper part of the scree slope. Photos: 2005-06-16

**Figure 4** Tiny specimens of *Acer platanoides* growing in ericaceous boreal vegetation close to summit of lowfells with tree cover invading onto prior treeless alpine tundra. Left. Mt. Tandövala (province of Dalarna), 770 m a.s.l. Photo: 2010-06-15. Right. Mt. Alsberget (province of Lapland, 710 m a.s.l. Photo: 2006-09-08

**Figure 5** *Betula pendula*, our most warmth-demanding birch species, is currently advancing up to the pine forest limit and even further, far higher than previously ever recorded. Left. Handölan Valley (Province of Jämtland), 680 m a.s.l. Photo: 2017-09-12. Right. Mt. Städjan (Province of Dalarna), 1020 m a.s.l. Photo: 2004-05-22

**Figure 6** *Alnus glutinosa* is a newly establishment in the lower subalpine birch forest, where it previously grew by the early Holocene thermal optimum, more than 8000 years ago. Handölan River Valley, 705 m a.s.l. Photos: Left. 2019-10-02. Right. 2020-08-22. Source: Kullman 2020a

**Figure 7** A recently seed-sown sapling of *Ulmus glabra,* growing in a steep south-facing slope within the subalpine birch forest, about 300 altitudinal meters above the nearest possible natural parent trees in the region and quite close to the birch treeline. This specimen, as well as newly established outposts of other plant species, was extirpated during the cold summer of 2012, when snow and lake-ice remained longer than for many past decades (Kullman 2014). Mt. Åreskutan, 970 m a.s.l. Photo: 2001-07-28

**Figure 8** Warmth-demanding species which reach remarkable high growing sites, interspered in trivial low-alpine vegetation on the steep slopes of Mt. Predikstolen, i.e. the site of the remarkable finding of *Quercus robur*. Left. *Antyllis vulneraria* (1030 m a.s.l). Mid. *Cotoneaster scandinavicus* (1030 m a.s.l.). Right. *Ajuga pyramidalis* (1050 m a.s.l.). *Anthyllis* is a late immigrant to this site, which is about 400 m higher than previously recorded in this region (Kilander 1955). Photos: 2008-07-04

### 3.2. A wider geographical context

The nearest present-day natural sites for the tree species accounted for above, are located 500-800 m lower and 50-300 km to the south. However, the exact positions of the potential (climatic) limits of tree-sized and reproducing individuals of these species are unknown. Possibly, their distribution limits have been pushed downwards and southwards by selective logging and pasturing during past centuries of the Little Ice Age (Andersson & Birger 1912; Aas 1970; Huldén 2001). This may explain why sown and planted individuals often thrive far outside their past empirical and assumed natural limits (Blomqvist 1933; Erkamo 1956). For example, *Quercus robur* grows in the form of large trees in interior parts of northern Sweden, as high as 300-500 m a.s.l. Initially, many of these putative parent specimens owe their existence to plantation trials in the warm 1930s. They have subsequently expanded in size during the past relatively warm decades, when they attained reproductive maturity. Accordingly, along the entire Bothnian coast of norhern Sweden and somewhat inland, *Quercus* and *Acer* are spreading centrifugally into seminatural rural coniferous forests (Johansson 2000; Kullman 2012), as illustrated by Figures 9-11).

**Figure 9** Mature *Quercus robur*, planted during the 1920s, 20 km east of the town of Vilhelmina (southern Lapland), 470 m a.s.l. The site is about 300 m below the treeline of birch. Photo: 2012-08-27

**Figure 10** Young sapling of *Quercus robur*, established close to the summit of Mt. Skuleberget (province of Ångermanland), 270 m a.s.l. Photo: 2011-10-01

**Figure 11** Left. Tree-sized *Tilia cordata*, planted (1930s) slightly to the west of the village Mörsil (Province of Jämtland, 350 m a.s.l.). The tree is regularly fruiting. It suffered severe dieback during the exceptionally cold winters of the 1980s, but has subsequently recovered. Right. A tiny sapling was observed in a road ditch about 100 m to the west of the putative parent tree. Photos: 2010-09-08

### 3.3. The long-term historical context

Present-day dynamics of subalpine and northern boreal forests needs to be viewed in a long-term postglacial perspective. Hitherto, traditional pollen analysis has failed to provide a realistic narrative of the early Holocene (10 000-8000 cal. a BP) subalpine landscape (cf. Kullman 2018). Robust megafossil records provide a vision of a richer tree flora than previously assumed. Boreal tree species grew patchily 500-700 m higher than their present-day equivalents, coincident with the Holocene thermal optimum and summers about 3 °C warmer than the early 21st century (Kullman 2013a, 2015, 2017b, 2021a; Kullman & Öberg 2015, 2020; Väliranta et al. 2015; Paus 2021; Vinós 2022). Concurrently, thermophilic tree species focused in this study (*Quercus robur, Ulmus glabra, Corylus avellana, Tilia cordata* and *Betula pendula*) prevailed within sections of the high-mountain landscape, presently occupied by subalpine birch forest and where saplings of thermophilies are sparsely establishing at the present day (Kullman 1998a, b, 2004b; Bang-Andersen 2006). The mere existence of these juveniles demonstrates that long-distance and elevational spread is possible in present-day climate.

## 4. Discussion

With focus on the Scandes, the prevailing post-Little Ice Age climate warming phase appears to be on the brink of evoking progressive distributional responses of thermophilic arboreal taxa. Accordingly, this paper accounts for one aspect of the ongoing qualitative restructuring of subalpine plant communities and a possible emergence of novel biogeographic zonation patterns (Kullman 2010a, b, 2019, 2022a, Kullman & Öberg 2022). In that respect, the presented records concur with projections from different parts of the world (Edwards et al. 2005; Willis & MacDonald 2011; Beck et al. 2011; Macias-Fauria et al. 2012; Normand et al. 2013). Advancement of thermophilic tree species aligns with temperature rise and significant treeline upshifts by common native boreal tree species along the entire Swedish Scandes during the present warm climate phase since about A.D. 1915, following the Little Ice Age. This regional pattern relies to a common climate-change driver (Aas 1969; Kullman & Öberg 2009; Kullman 2017a, Kullman 2021b).

In the present context, some caution is needed. Findings of widely scattered saplings of warmth-demanding tree species, well beyond their previous natural ranges, should not be overstated as predictions of future trajectories, since many recovered specimens are still tiny and prone to extirpation (Fig. 8). Moreover, it is important to consider that the current spread of thermophiles represents an utterly sparse pattern in the mountainscape. Nevertheless, these circumstances are indicative of a potential to expand their distribution, abundance and biotic richness in the case of enhanced and sustained climate warming.

The reported occurrences of boreonemoral tree species are decidedly extra-limital to their known natural distributions in Sweden. In many cases, they may share the character of escapes from cultivations in nearby lower elevations. Analogous spread is recorded for exotic boreal tree species (Kullman 2013b, 2020b). Taken together, the last-mentioned aspects add a complication to models of future high-mountains plant structure change in a frequently proposed warmer world. In that context, the need to take account of the existing pool of cultivated warmth-demanding plants in the northern landscape is obvious.

## 5. Conclusions

- Thermophilic deciduous tree species (boreonemoral) are currently spreading (still mostly saplings) to the alpine treeline ecotone and adjacent mountain forests in the southern Swedish Scandes.
- Species particularly concerned are; *Quercus robur, Ulmus glabra, Alnus glutinosa, Acer platanoides* and *Betula pendula.* They have all emerged high above and further north of their traditional natural positions in the recent past. Given that the future climate will allow them to grow into tree-size, they may approach their highest tree positions during the thermal optimum by the early Holocene, 9500-8000 cal. yr BP. Even then, they would perform within the frames of inferred natural climate and vegetation evolution of the present interglacial era.
- The obtained progressive distributional shifts comply with an initial displacement of the so-called *Limes Norrlandicus*, that is a biogeographic transition zone in northern Scandinavia, separating biota with northern and southern affinities, respectively.
- In many cases, the origins of the newly thermophilies are cultivated trees further south, although beyond the natural distribution limits. This implies that models of future arboreal evolution will have to account for such outposts as dispersal nodes in a future warmer climate.
- The current records are consistent with more general and ongoing treeline rise and restructuring of the plant cover in subalpine and upper boreal forests, in response to post-Little Ice Age climate warming (all seasons) since the early 20th century. That would be a resurgence to a stage that last prevailed during the Medieval Climate Optimum, 600-700 years ago, in many respects beneficial to society as well as nature.

## Compliance with ethical standards

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### *Disclosure of conflict of interest*

No conflict of interest to be disclosed.

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