Cryptic refugia vs. Tabula Rasa: Boreal trees in glacial Fennoscandia

Plant growth during the Weichselian glaciation and early Holocene in northern Europe

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Abstract

Recent studies applying innovative technologies, such as genetic analysis and carbon dating, contradict the palynological based assumption that Scots pine (*Pinus sylvestris*) and Norway spruce (*Picea abies*) vanished from Fennoscandia during the Last Glacial Maximum (c. 20,000 yrs BP) and re-colonized after the cold Younger Dryas (c. 12,000 yrs BP). Instead, those studies indicate glacial survival of boreal trees in ‘cryptic’ refugia within Scandinavia, which is still heavily debated. In this report, I try to get a better grip on the discussion if Norway spruce and Scots pine survived Weichselian glacial periods in isolated ‘cryptic’ refugia within Scandinavia, or either re-colonized Fennoscandia by post-glacial migration from eastern areas such as Russia. To this aim, climatic settings are described and an overview is given on what is already known on the distribution of boreal trees during the Weichselian glaciations and the post-glacial landscape. Several records are important to detect ancient boreal trees: pollen, macrofossils and currently DNA. Macrofossils indicate early post-glacial tree growth in the central Scandes just after the Younger Dryas, aDNA indicates the existence of a ‘cryptic’ refugium on Andøya during the Last Glacial Maximum and modern DNA analysis possibly indicates isolation of spruce in western Norway, which are all contradicted by the current interpretation of low pollen percentages. Altogether, alternative hypotheses supporting glacial survival of plants might have been overlooked and pollen interpretations need revision, which could turn the exclusion from the past into supporting evidence for the glacial survival of *P. abies* and *P. sylvestris* in Scandinavia.

Key words: boreal trees, Fennoscandia, cryptic refugia, Weichselian, glacial survival.
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1. Introduction

Changing climates influence ecosystem composition, migration and extinction of species (Pearson & Dawson, 2003; Thomas et al., 2004; Elith et al., 2006; Parmesan, 2006). Much of the debate today focuses on how current ecosystems will be influenced by a warming climate. Less focus is put on ecosystem changes that may accompany glacial periods that will inevitably affect northern Europe in the future. Put to the extremest circumstances, plants show remarkable surviving strategies during glacial periods, and their distribution during deglaciation is important for plant colonization and diversity in the post glacial landscape.

In cold periods with harsh living conditions, plant species tend to retreat to warmer regions where growing conditions are more favourable, so called refuge areas, or, if possible, survive in small patches, which requires fit growing substrates. Therefore, ice sheet cover and dynamics are crucial to give insights on swiped away vegetation and possible refugia. During the Last Glacial of Europe and northwestern Russia (110,000 – 12,000 yr BP), known as the Weichselian glaciation, climate and vegetation composition have been the focus of innumerable studies (e.g. Prentice et al., 1991; Reitalu et al., 2015; Stebich et al., 2015). During the Last Glacial Maximum (LGM), were extreme conditions prevailed c. 20,000 years BP (Hughes & Denton, 1981), ice sheet extension was reaching its maximum, covering northern Europe as well as parts of West-Russia and the British Isles (Böse et al., 2012).

Long it has been assumed that subarctic plant species, such as boreal trees Scots pine (Pinus sylvestris) and Norway spruce (Picea abies), as well as white birch (Betula pubescens) and rowan (Sorbus aucuparia), were wiped out of Fennoscandia by ice sheets and harsh conditions during the LGM (Seppä et al., 2009; Cheddadi et al., 2006; Eide et al., 2006; Giesecke & Bennet, 2004; Snyder et al., 2000; Tallantire, 1977). Palynological research indicates survival in macrorefugia in the ice free areas of Russia and central and eastern Europe (Tzedakis et al., 2013). After deglaciation at the transition from the Late Weichselian to the Holocene, re-colonization of Fennoscandia followed in a migration process taking thousands of years (Hafsten 1985), also referred to as the 'Tabula Rasa theory' (Brochmann et al., 2003; Gugerli & Holderegger, 2001). *Picea* was even thought to thrive again in Scandinavia as late as 3500 years BP (Huntley & Birks, 1983).

However, recent studies applying alternative technologies such as genetic analysis and carbon dating of macrofossils, shed doubt on the assumption that boreal trees were wiped out from Fennoscandia, and indicate early presence during the Late Weichselian and early Holocene (Kullman, 2008; Parducci et al., 2012). The aim of this report is to review the discussion on the possible glacial survival of pine and spruce by scrutinizing scientific literature, focusing on glacial plant behavior, distribution during the Weichselian glaciation and several survival options for boreal trees to get through the harsh glacial conditions of Fennoscandia. A research question was formulated:

Did Norway spruce (*Picea abies*) and Scots pine (*Pinus sylvestris*) survive Weichselian glacial periods in isolated 'cryptic' refugia within Scandinavia, or did those boreal trees re-colonize Fennoscandia by post-glacial migration from eastern areas such as Russia?

To this aim, several sub questions are discussed:

i) What were the climatic conditions of the Weichselian period, including ice-sheet dynamics and interstadial vegetation?

ii) What is already known on the distribution of boreal trees in Fennoscandia during the Weichselian glaciations and the post-glacial conditions?

iii) What implications can be deduced from the integration of year-long research?
2 Material & Methods

This review on growth of boreal trees during harsh glacial conditions in Scandinavia is totally based on an extensive network of literature, being analyzed and criticized thoroughly. The scientific literature was gained by using the search engines ‘Web of Science’ and ‘Google Scholar’, applying varying combinations of keywords such as boreal trees, glacial survival, Fennoscandia, cryptic refugia, LGM, Weichselian, Holocene, pollen, ancient DNA, macrofossil, migration rates; as well as a considerable use of cited and citing references from relevant literature.

3 Results & Discussion

3.1 The Last Glacial period in Fennoscandia

3.1.1 Climatic settings

Approximately 2.5 million years ago, Earth’s climate shifted into the Quaternary, represented by a colder period which is still persisting today (Shackleton, 1997). During the Quaternary, climate has been fluctuating extremely (Figure 1), being characterized by repetitive cycles (c. 40,000-100,000 years) alternating swiftly from a warm interglacial with temperatures similar or higher than today. This shifted into a mild early glacial, followed by a cold late glacial, abruptly terminated by rapid deglaciation, thus being the start of a new glacial cycle (Broecker & van Donk, 1970). The timing of those oscillations mainly find their origin in Earths changes in solar insolation, due to orbital changes of the Earths movement around the sun (Kukla & Gavin, 2005), although the climatic response to solar forcing is delayed by several millennia (Figure 1; Ruddiman, 2004).

The last glacial cycle lasted from 130,000 until 15,000 years BP at the start of the Holocene, and being the most recent, it is the glacial cycle most known in detail (Lisiecki & Raymo, 2005; Severinghaus & Brook, 1999). Based on marine oxygen isotope records from deep sea core samples, changes in past temperatures can be distinguished. High levels of $^1^8$O represent warm interstadials, whereas low levels of $^1^8$O represent cold stadial periods (Figure 1). The last glacial (Marine Isotope Stadium (MIS) 5 – 2), consists of two major geological time periods: the Eemian (MIS 5e) and Weichselian (5d – 2), which is divided into the Early Weichselian (MIS 5d – 5a), Middle Weichselian (MIS 4 -3) and Late Weichselian (MIS 2; Figure 1). At transitions from cold stadial to warm interstadials, temperatures reconstructed from Greenland ice-cores indicate rapid amplitude shifts from 8 to 16°C (Landais et al., 2004; Huber et al., 2006). Driving mechanisms of these rapid shifts include changes in ocean thermohaline circulation (Knutti et al., 2004), interaction between wind fields and seawater with continental and marine ice-sheets (Wunsch, 2006), and tropical processes (Clement & Peterson, 2008). Based on palynological and lithological data from Sokli, northern Finland, mean July temperatures were shown to be quite stable for Fennoscandia during the whole glaciation shifting from 16°C in MIS 5 to 13 °C during MIS 4-2 (Helmens et al., 2007ab, 2009; Helmens, 2014 and references therein), whereas winter
Figure 1. At the left the last interglacial-glacial cycle and its correlated chronostratigraphy of northwestern Europe based on stacked marine oxygen isotope records (Hättestrand, 2008; and references therein). Figure a-h is a comparison between marine- and terrestrial based records for the last 140,000 years in northern western Europe, based on compilation figures from Helmens (2014; and references therein), with (a) solar insolation during July, (b) benthic global stack δ¹⁸O with Marin Isotope Stages (MIS), (c) abundances of *N. pachyderma* with Greenland Interstadials, (d) relative sea-level changes including a grey confidence interval line, (e) stacked ice-rafted debris record, (f) ice-advances of Denmark, (g) simplified summary of glaciations, vegetation and climate for Sokli, Finland and Lake Yamozero, north-western Russia, as well as (h) a chronostratigraphy (Helmens, 2014; and references therein).
temperatures and precipitation experienced major shifts, but little detail is known on these data. Changes in winter temperatures determine Pleistocene climate variations most strongly, as well as vegetation responses (Helmens, 2014; and references therein). Extrapolation of similar current summer temperature conditions can help to estimate winter conditions. Current mean July temperatures of 13°C in Fennoscandia are accompanied by varying mean January temperatures, such as -20°C in sub-continental north western Russia, -15°C in northern boreal Finland and 0°C in maritime conditions of the Norwegian coast, and show how geographical location is of great importance (Helmens, 2014).

Sea levels almost never exceeded current levels, but fluctuated extremely. Glacial periods accompanied low sea levels, with a minimum of around 130 meters below current sea levels during the LGM (c. 20,000 yrs BP; Waelbroeck et al., 2002).

### 3.1.2 Glacial dynamics

If only the low temperatures in Fennoscandia during glaciations were the major factor limiting plant growth, survival might have still been possible. But, due to the strong decreases in winter temperatures during glaciations, ice sheets expanded covering total land surfaces and thus disable vegetation growth totally by covering growing substrates. Therefore, ice sheet dynamics during those glaciations is important to track possibilities for vegetation growth.

The record of glacial distribution over Fennoscandia shows two occurring forms: i) short periods of cooling reflected in a narrow western Scandinavian ice sheet covering the Scandes Mountains (Kleman, 1992) and ii) a Scandinavian ice sheet with a more easterly situated center, reflecting a prolonged build up during glacial conditions as the LGM. The first proposition occurred repeatedly before 800,000 yrs BP, while the easterly distributed ice sheets only started to occur after this, although details are still debated (Kleman & Stroeven, 1997). The Scandinavian Ice Sheet (SIS) seen during the LGM, began to build up 70,000 years BP (MIS 4) and was characterized by a center lying over southern Norway (Kleman et al., 1997).

The Scandinavian Ice Sheet was very dynamic, alternating between shrinking and building up during warm interstadials and cold stadials respectively, with a maximum expansion with the LGM (MIS 2, c. 20,000 yrs BP) covering the whole of Scandinavia reaching as far as central Europe (Figure 2). The ice sheet at its peaks during stadials 5b, 4, 3 and 2 (Figure 1 & 2) could have covered large areas in Norway, thus possibly disabling vegetation growth during the glacial. Presence of vegetation dated to the warm interstadials between those cold stadial, did migrate and colonized from areas which were ice-free during the stadials. Nevertheless, present-day glacial research is still performed to reconstruct more detailed glacial movement and ice-free zones, were vegetation could have survived (Wohlfarth, 2010; and references therein).
3.1.3 Vegetation history

To determine if boreal trees theoretically could have survived glacial periods with wide expansion of ice-sheets, temporal vegetation dynamics from before and after glacial can assist. Vegetation can tell a lot about climate conditions, but also climate can tell a lot about vegetation behaviour.

MIS 5c (c. 105.000 – 95.000 yr BP) - During interstadial correlated to MIS 5c, prior to the MIS 5b glaciation (Figure 2), locations close to core areas of ice sheets in northern Sweden such as Riipiharju, Takanenmännenkkö and Onttovaara were ice-free based on sediments (Lagerbäck & Robertsson, 1988) and was characterized by subarctic shrub tundra. Furthermore, it has been interpreted boreal trees, *Betula* and *Pinus*, grew in Finland near Sokli and Oulainen during the period correlated to the Swedish Brörup interstadial (Helmens et al, 2000, 2007ab).

MIS 5a (c. 85.000 – 75.000 yr BP) – During the glaciation of MIS 5b ice moved over both the previous mentioned Swedish sites as well as Finnish Sokli. The succeeding Swedish Odderade (correlated to the Finnish Maaselkä interstadial; MIS 5a) was characterized by high presence of *Betula*, but much lower *Pinus* pollen in northern Sweden (Lagerbäck & Robertsson, 1988), which is in agreement with pollen records in Sokli, Finland.

MIS 3 (c. 60.000 – 22.000 yr BP) – Prior to the long Middle Weichselian interstadial MIS 3, the glaciation during MIS 4 was described by an advancing ice sheet over Fennoscandia, covering both Riipiharju and Sokli. Ice-free conditions dominated northern Fennoscandia during the Middle Weichselian interstadial of MIS 3. It was a lengthy interstadial (c. 40.000 yrs), which left thick sediments accomplishing to extensive pollen records. It knew three major stages, two warm ones interrupted by a cold stage. During the first stage (LPAZ2) the climate became warmer and ice sheets retreated. At Sokli, *Betula* thrived (Helmens et al., 2007ab), as well at Riipiharju in northern Sweden where the landscape was open birch forest (Hättestrand, 2008). Succeeding the warm period, a cold stage (LPAZ3) arrived and ice sheets expanded with limits west of Riipiharju.
3.2 Boreal trees during the Weichselian glaciations and in the post-glacial landscape

3.2.1 Previous theory based on palynological evidence

‘Absolute disappearance and postglacial re-colonization’

3.2.1.1 *Picea abies*

For a long period, based on palynological records, it has been assumed that *Picea* was wiped out of Scandinavia entirely by glaciation during the LGM and did return in northern, central and west Scandinavia during the late Holocene, deriving from survived populations in the ice-free areas in east Europe and central Russia. *Picea* was thought to have migrated from as far as Russia to e.g. southern Norway in a period of only 4000 years. Spruce first occurred in the central Scandes ca. 2500 years ago and in southern Norway 1000 years BP (Seppä et al., 2009).

Based on previous pollen analysis, *Picea* migrated into Scandinavia via two proposed pathways (Figure 3), deriving from European Russia and the Balkans some 7000 years ago into Finland than i) dispersing to northern Fennoscandia entering Norway and Sweden (4000 yrs BP), the central Scandes (2500 years BP) and Norway (1000 years BP), as well as a second migration route ii) where *Picea* populations were founded at the south Baltic coast of Finland and dispersed to the central Swedish coast (3000 years BP), possibly with the support of the Åland Islands (Seppä et al., 2009; Eide et al., 2006; Snyder et al., 2000; Giesecke & Bennett, 2004; Tallantire, 1977).

3.2.1.2 *Pinus sylvestris*

Based on both pollen and genetic analysis Scots pine is thought to have migrated into eastern and southern Fennoscandia some 9000 years ago by two migration routes, one via central Europe to south Sweden and secondly via Russia and Finland into northern Scandinavia (Cheddadi et al., 2006). *P. sylvestris* arrived in central Scandinavia some 8000 years BP (Figure 4; Snyder et al., 2000).

Figure 3. Holocene spreading pattern of Norway spruce (*Picea abies*) in Fennoscandia, from Russia, via Finland to Sweden, indicated by isolines in approximate millennia (as in Seppä et al., 2009; based on Giesecke & Bennett, 2004). Colours indicate modern abundance of Norway spruce (m³ ha⁻¹; Seppä et al., 2009).
3.2.1.3 Pollen representation

'A weighty 1% threshold value'

For long there has been a consensus that little amount of pollen finds indicate far located pollen sources. Most palynological analysis have been conducted with this assumption that low pollen percentages indicate local absence of pollen production and find their origin in long-distance distribution. Single pollen grains of Picea could be explained by either local vegetation stands or long-distance transport, where the latter has been applied in the discussion on the spread of Picea abies in Fennoscandia (Kristiansen et al., 1988; Eide et al., 2006; Birks et al., 2012; Giesecke & Bennett, 2004). Threshold values varying from 15 to 0.5% have been used to state actual presence (Zazula et al., 2006; Latalowa & van der Knaap, 2006; Giesecke & Bennett, 2004; and references therein), but 1% is a much used robust threshold (Giesecke & Bennett, 2004). However, as macrofossils emerge on locations where pollen records were very low indicating vegetation absence, the interpretation of pollen percentages should be reconsidered. Pollen percentages are depended on the abundance of the local vegetation stand, distances, weather conditions, prevailing wind direction, the capturing substrate (i.e. slippery ice or porous soils) and pollen productivity. As to the latter, pollen productivity diminishes with low temperatures (Hicks, 2006; Barnekow et al., 2007) and low atmospheric CO$_2$ concentrations, as circumstances were during the LGM (Jackson & Williams, 2004). Therefore, threshold values should be treated with great caution and interpretation of pollen values regarding distant or local origin should be considered with care (Segerström & Stedingk, 2003; Zazula et al., 2006).

As both temperatures and atmospheric CO$_2$ concentrations during the LGM were low, arboreal productivity, including Picea and Pinus, might have strongly decreased or even...
ceased (Hicks, 2006; Barnekow et al., 2006), which makes it hard to determine what pollen percentages represent. If low percentages are revised, interpretations of many palynological studies which previously indicated no glacial and early Holocene presence of *Picea*, could be interpreted in another way. That is, spruce might have been present during the Scandinavian LGM and Younger Dryas, and many scientific statements could be revised (Kristiansen et al., 1988; Eide et al., 2006; Bjune et al., 2009; Birks et al., 2005; Seppä et al., 2009). Also, with a revised interpretation, pollen records from southern Norway support the presence of spruce during the early Holocene (Velle et al., 2005; Eide et al., 2006; Bjune et al., 2009). Nonetheless, palynological records stay a source not waterproof to erroneous interpretation. Macrofossils are of local origin and therefore are easier to interpret, but are hard to gather quick and systematically, as they are encountered by accident. Still, as macrofossils unambiguously indicate vegetation presence, this is a valuable source. Combined with palynological records, as well as genetic data, assessments about the presence and survival of boreal trees in Fennoscandia can be made.

3.2.2 Macrofossil evidence

*Another view*

The general opinion that Quaternary vegetation history was all cleared up by pollen analysis, e.g. ruling out the possibility of cryptic refugia in Scandinavia, has been challenged by finds of macrofossils. This alternative option to track paleovegetation uses macrofossils; pieces of wood long preserved in anaerobic circumstances of lakes or peat, where cones, roots or trunks are dated by $^{14}$C dating techniques. Macrofossils are thought to have a local origin, as their weight and size make transport by wind or water unlikely (Kullman & Kjällgren, 2006), although this is questioned (Eide et al., 2006). Numerous macrofossils have been found by Kullman in several areas in Fennoscandia, of which both *Picea* and *Pinus* already dated to the Late Glacial and early Holocene (Kullman, 2002, 2004, 2008). Naturally, this challenged the hypotheses based on palynological records that *Picea* and *Pinus* didn’t survive the glacial period and recolonized Sweden much later.

Figure 5. The oldest tree reported globally is a Norway spruce called ‘Old Rasmus’ and grows far above the current treeline at mountain Sonfjället, central Sweden. The oldest remnants were dated 9480 $^{14}$C-years old. In winter, the patch is more extensively snow covered than the surroundings, creating isolation from harsh conditions, which also can be seen in the abundance of *Vaccinium vitis-idae* at the patch (Oberg & Kullman, 2011).
Some notable macrofossils of Late Glacial *Pinus sylvestris* were found in the central Swedish Scandes, all located high above the current treeline. On the mountain Åreskutan (Figure 5) a piece of fossil pine was dated back to 11.720 ± 90 years BP (Kullman, 2008), 60 km south at Helagsfjället a pine fossil was dated to 11.160 ± 80 years old (Kullman & Kjällgren, 2000), and 100 km south from there at the slopes of the mountain Städjan, wood was dated to an age of 10.500 ± 60 years (Kullman, 2004). This presence of *Pinus sylvestris* during deglaciation, contradicts post-glacial re-colonization from Europe and indicates survival within Scandinavia, even in the high elevated areas of the central Scandes. In the northern Scandes in northern Lapland little megafossils are studied, but near Abisko on mountain Njulla the oldest macrofossil pine dated to 8540 ± 50 years BP was preserved in an alpine lake (Kullman, 1999).

Oldest finds of fossil *Picea abies* were done on the slopes of the mountain Åreskutan, 350 meters above the current treeline, and dated back to 11.020 ± 60 and 10.250 ± 90 years ago (Kullman, 2001, 2008) and were found on high elevation. Other, slightly younger (< 10.000 years BP) spruce fossils throughout Sweden (Kullman, 2001; Öberg & Kullman, 2011) were detected as well. *Picea* macrofossils originating from before 8000 years ago, are only detected on high elevated areas (Kullman, 2001), thus Kullman states that *Picea* did survive glaciations in micro refugia on ice-free mountain tops, so called nunataks (Kullman, 2001). Pollen analysis confirm this presence of *Picea*, but do not necessarily indicate survival on mountain nunataks (Segerström & von Stedingk, 2003). Furthermore, Late Glacial presence of birch (*Betula pubescens*) some 14.000 years BP far above the current treeline indicates tree fit growing conditions on nunataks (Kullman, 2008). These high mountainous areas were surrounded by ice sheets, being a refuge haven for pioneer vegetation and even supported genetic drift (Slatkin, 1987). After ice-melt, spruce dispersed downwards colonizing other parts of Scandinavia. In the east of northern central Sweden, *Picea* macrofossils were at most 6000 years old (Kullman, 2001). Untill now, no early Holocene macrofossils have been found in eastern Sweden. It could be interpreted that early Holocene *Picea* travelled from the western mountains, where spruce was abundant during the Holocene, to the east (Kullman, 2008). Furthermore, deglaciation is more complex than previously thought (Olsen et al., 2014; Boulton et al., 2001) and the option of ice-free nunataks acting as ‘cryptic’ refugia in the central Scandes is reconsidered (Paus et al., 2006).

The fact that Late Glacial treelines, containing birch already 14.000 years BP, and spruce and pine 11.000 years BP, were exceeding current treelines by 350 m, seems contradictory with the cold climatic conditions of the Younger Dryas period (Kullman, 2008). However, the land surface was suppressed with ca. 400 meters in the Swedish Scandes (Eronen, 2005), so that the ‘cryptic’ nunatak refugia were situated at much lower elevations. This makes the Late Glacial ‘higher’ treelines set in a cold climate less controversial.

If *Picea* and *Pinus* survived the cold Younger Dryas in microrefugia, their origin lies within Fennoscandia as they should have survived the LGM in close located areas. Scandinavia during the LGM was mostly covered by ice-sheets, but ice did not expand over the entire Norwegian coast. On the island of Andøya, NW Norway, paleo-glacialological studies did reveal ice-free conditions during the maximum extent of the Scandinavian Ice Sheet (Vorren et al., 2013; Nesje et al., 2007). Macrofossil evidence (*Betula pubescens*; 16,900 ± 170 years BP) implies survival of trees during the LGM on Andøya, which is in agreement with pollen analysis and the behaviour of glaciations (Vorren et al., 2013; Nesje et al., 2007; Kullman, 2006; Paasche et al., 2007). Thus, scientists hypothesize that Andøya functioned as a cryptic refugium and support the idea that boreal trees survived in some isolated, ice-free areas at the Norwegian coast. However, early Holocene spread of spruce is not well known, as conditions prevented the formation of suitable palynological records, due to blockages by ice, gravel and sand at unstable slopes (Giesecke & Bennett, 2004). More macrofossil finds could support the view that boreal trees where much earlier present after deglaciation than previously thought, and also confirm the reliability of the use of macrofossils.
Under harsh climatic conditions as seen during the last glacial, it is hard to propagate for pine and spruce as seedlings do not survive, especially on high elevated, alpine nunataks. However, under cold conditions both spruce and pine are able to regenerate vegetative. Caused by a harsh and windy winter climate under open taiga-tundra conditions (Lavoie & Payette, 1994), this results in crippled trees, called ‘krummholz’ (German for ‘crooked wood’; Holtmeier, 1981). Recorded clonal Picea in the Swedish Scandes demonstrate this durable survival of individuals over a period with variable climatic conditions. Öberg & Kullman (2011) found several long-living clonal spruces in the Nationalparks of Fulfjället and Sonfjället, with oldest living individuals reaching an age of 9550 and 9500 years old (Figure 5). Those clonal spruces grow in minor depressions in the alpine, exposed tundra landscape. Accumulating snow in those depressions protect the crippled spruce from cold and moist conditions (Petit et al., 2008; Öberg & Kullman, 2011). This lengthy survival up to 9500 years, including a cold period in the mid-Holocene, implies that individuals might have been able to survive glacial conditions as ‘krummholz’ on nunataks in the Scandinavian mountains, as well as in coastal areas of Norway during the LGM.

3.2.3 Genetic implications

‘Turbulent findings’

Based on Kullman’s macrofossil findings in the central Scandes and the hypothesis that Picea survived at coastal Norway, it can be suspected that Picea derived from the putative refugia should show genetic distinction from populations spread from the east due to geographical isolation in south-western Scandinavia (Birks et al., 2005; Kullman, 2002; Bucci & Vendramin, 2000). Only recently, research using modern and ancient DNA (aDNA) did some remarkable findings, indicating presence of both pine and spruce during and after the Last Glacial Maximum on the island of Andøya, northern Norway, as well as signs of spruce at Trøndelag in central Norway, dating back to the transition of the cold late-glacial and the early Holocene (Parducci et al., 2012a). The findings by Parducci and colleagues challenge the theory that Scots pine and Norway spruce were totally killed off by the ice sheets during the LGM and indicate the survival during the last glacial-interglacial cycle, including its coldest peaks, which is a climax for this edge of research.

First of all, Parducci et al. (2012a) found that a gene (mh05) of modern mitochondrial DNA (mtDNA) specific to Norway spruce showed two varieties, haplotypes A and B, throughout Europe. Haplotype A only resided within Scandinavia, with highest frequencies in the west gradually declining eastwards (Figure 6b), while haplotype B is fixed in the rest of Europe. Haplotype A finds its ancestor in haplotype B after genetic mutations. The geographical distribution suggests a colonization of spruce with haplotype B from the east and agrees with former classic patterns describing dispersal after deglaciation coming from Russian refugial and southern located areas from the Weichselian Scandinavian Ice Sheet (Giesecke & Bennett, 2004; Tollefsrud et al., 2008). Based on genetic data and fossil pollen data, it is even assumed that spruce post-glacial colonization originated from only one putative refugium (Tollefsrud et al., 2008). Additionally, another recent genetic study on mtDNA reinforces the assertion that Norway spruce has been isolated in southern Norway, as haplotypes of the nad1 gene differ for southern Norway in comparison to northern Scandinavia (Mudrik et al., 2015).

However, spruce haplotype A (mh05) is only observed in west Scandinavia (with one unremarked exception on the Åland Archipelago; Parducci et al., 2012a) and therefore appears to have dispersed from there. Haplotype A must have been present before the LGM, because models show fixation of a mutation in mtDNA, being the origin of haplotype A, requires at least 200,000 years to establish in spruce populations, excluding north Scandinavian post-glacial colonization from the east (Parducci et al., 2012a). A plausible
explanation for the distribution of haplotype A might be glacial survival in microrefugia in western Norway, where after populations expanded and later on mixed with haplotype B spruces in central Scandinavia.

3.2.3.1 Sediment record findings at Trøndelag

With western survival of spruce in mind, Parducci et al. (2012a) tried to retrieve aDNA from lake sediments hoping to find tracks of spruce and/or pine confirming their suspicions. They did this at Trøndelag. Here, ancient tracks of spruce found in lake sediments in Trøndelag, central Norway, (10,300 to 6300 years BP) indicate presence during the late glacial and early Holocene (Parducci et al., 2012a), what is in fierce contradiction with the previous pollen-based statement that spruce populations expanded only 3500 to 3000 years BP to northwestern Scandinavia (Giesecke & Bennett, 2004). Another research conducted in the Dovre Mountains, located in the central Scandes Mountains, found that both Picea and Pinus sylvestris were already present 10,000 - 9500 years BP in Rødalen (Paus, 2010). Appearance of boreal trees so early in the Holocene, could not strike temporally with migration from the east. Furthermore, local ice caps covered the area of Rødalen during the Young Dryas (ca. 12,000 years BP; Paus et al., 2015), possibly excluding the option of survival in a putative local microrefugium here, but pine could likely have migrated to central areas from the west, such as Trøndelag. As Paus et al. (2015) nowadays implement techniques using ancient sedaDNA to acquire plant species, an analysis similar to that of Parducci et al (2012a) on Pinus instead of Picea might yield relevant information. An older study conducted in the surrounding of Ålesund, central coastal Norway, (Kristiansen et al., 1988) mentions Pinus
pollen percentages of 5%, i.e. exceeding the common threshold value for local plants, but isn’t discussed further as in this period boreal trees were assumed not to be present in Norway. Therefore, they even assume long-distance transport from forests from northern Germany. However, Tallantire (1972) states that pollen percentages above 1% are indicative of local presence and a threshold value of arboreal pollen values of 0.5% (Hafsten, 1992) are stated to indicate the local presence of a tree. In this light, it can be revised that pine has been present already from 10,300 years BP onwards near Ålesund (Kristiansen, 1988), again reinforcing the statement of boreal tree growth in central Norway during the late glacial and early Holocene.

3.2.3.2 Andøya refugium - More sediment records findings

The search for ancient spruce and pine DNA was not only conducted at Trøndelag, but also on the island Andøya, northern Norway, which is known for its long, continuous sedimentary record with sediments in several lakes dated up to 26,000 years old (Parducci et al., 2012a) and is believed to have been a ice-free haven during the LGM (Nesje et al., 2007; Vorren et al., 2013). As Parducci et al. (2012a) didn’t encounter mtDNA in the Andøya sediments, they focused on chloroplast DNA (cpDNA) and macrofossils. Andøya was characterized by a polar desert or open pioneer vegetation from 22,000 years BP onwards. It was on this island, that DNA of both pine and spruce was found in lake sediments dated back to 22,000 – 19,200 and 17,700 years BP respectively. The team states that the finds of DNA in the lake sediments at both Andøya and Trøndelag likely indicate local presence of pine and spruce. The option of long-distance transport of sedaDNA is thought to be unlikely (Haile et al., 2009; Willerslev et al., 2003) and would mean that plant material, such as pollen and seeds, otherwise should have travelled impressive distances from German Holocene forests. Also, marine driftwood as source of DNA is discussed, but thought to be very unlikely as a marine transgression based on algae is dated 22,000 years BP, predating the presence of pine and spruce on Andøya, together with the high located lake sediments (Parducci et al., 2012b). Still, to exclude the option of marine driftwood is tricky, as it might be possible that driftwood strands and under extreme weather conditions could have been moved, partly over lower lying ice, to the higher located lakes.

Warming occurred around 15,000 years BP, and Sorbus aucuparia was even part of the vegetation (Parducci et al., 2012a). So, also growth conditions for Picea abies, Pinus sylvestris and Betula spp. increased between the LGM and the cold Younger Dryas.

3.2.3.3 My critical reflections on Andøya refugium

The findings of Parducci et al. (2012a) have not been recognized by all scientists. Birks et al. (2012) find their evidence unconvincing and thus disagree with the proposition that pine and spruce survived the glacial period.

First of all, the reliability of aDNA derived from lake sediments is questioned. The field of aDNA is still developing and is not fully understood yet, thus possibly leading to inaccurate interpretations. The influence of water logging on the quality of sedaDNA has not been tested thoroughly yet, but there is suspicion of variability of analyses (Hofreiter et al., 2012). This ignorance is devastating for their analysis, say Birks et al. (2012), as well as the methodology doesn’t exclude contamination, although this remains unspecified. However, Parducci et al. (2012b) are reluctant to agree and dispute the option of contamination, as methodology was very secure, using different equipment on several expeditions, two varieties of DNA markers and replicated laboratory analyses thrice.
Worrying is the undiscussed find of nettle (Urtica spp.) in one of the samples (Parducci et al., 2012a), as nettle would not have been part of a polar dessert ecosystem neither of the current ecosystems. The presence of Urtica in the sample might be due to contamination in the field or lab (modern DNA), of insecure cleaning of corer or resedimentation, although the latter is assumed to be unlikely (Parducci et al., 2012b). A strong antithesis is that, if contamination at location had occurred, not Urtica, but prominent present-day sub-arctic species as Vaccinium spp. and Calluna vulgaris should have been detected (Parducci et al., 2012a), but this could also be seen as a confirmation on contamination of the corer itself. Another explanation of presence of Urtica might be the lack in controlling the match of DNA primer with the aDNA in a sequence database, which might result in an erroneous interpretation. Further assessment of the quality of waterlogged sedaDNA is necessary to verify the hypothesis.

Secondly, doubts exist about the lack of suitable habitats for glacial survival on Andøya (Birks et al., 2012). On the one hand, scientists claim that Andøya was glaciated extensively (Lambeck et al., 2010), with some exceptions of high ice-free nunataks (Vorren & Plassen, 2002), and is associated with unfit growing conditions. However, ice conditions in western Norway fluctuated more than previously thought (Johnsen et al., 2012) and several recent studies indicate ice-free conditions on Andøya, revising previous statements of extensive ice cover (Vorren, 2015, Nesje et al. 2007). Studies indicate that the melting of the Scandinavian Ice Sheet (ca. 13,000 years BP) created a cold and dry climate during the Younger Dryas (Muschitiello et al., 2015), keeping away moist from ice mass and thus inhibiting growth and expansion of the Scandinavian Ice Sheet during the cold harsh period (Paasche et al., 2007). This could be in agreement with the existence of ice-free refugia. July temperatures during the first half of the Younger Dryas (ca. 12,000 years BP) were approximately 10°C (Vorren & Alm, 1999), enabling growth conditions of boreal trees. Birks et al. (2012) are sceptical about the absence of any Picea or Pinus pollen and are amazed by the exclusion of palynological evidence. It is suggested that this absence is in contradiction to the hypothesis of glacial survival of boreal trees (Birks et al., 2012). However, under colder climatic conditions, pollen productivity tends to decrease or even cease (Birks & Willis, 2008; Hicks, 2006; Willis & van Andel, 2004), and therefore pollen percentages are hard to interpret. Absence of pollen does not indicate absence of trees (Hicks, 2006), and trees leaving no palynological records behind are therefore called ‘silent trees’. Here, aDNA can have promising contribution, as the tiniest pieces can indicate presence of genetic material of plants otherwise being missed by pollen research. Yet, little genetic material could be originating from elsewhere, thereafter being transported over far distances. A lot of vegetation dynamical research of the last glacial-interglacial cycle has been conducted using pollen records, although not for the LGM (Tzedakis et al., 2013; and references therein). Pollen silence is stated to be nonsense based on pollen found in sediments of Lake Galichskoye, NW Russia, indicating that Pinus still produced pollen during the LGM (Tzedakis et al., and references therein), but this is counteracted by new finds the lake was distanced some 100 km from the Scandinavian Ice Sheets edge (Lunkka et al., 2001) and thus ice cover inhibiting pollen productivity cannot be compared to the case of Lake Galichskoye. Overall, DNA, macrofossils and pollen do not have to indicate the exact same vegetation, but those disciplines can act complementary (Parducci et al., 2012a), and when pollen records are lacking, aDNA is a brilliant alternative.

With the warming and deglaciation it can be expected that pollen productivity will increase. However, both Pinus and Picea pollen percentages of warmer periods never exceed those occurring during the predating LGM (Vorren et al., 2009). At the start of the Holocene, Picea pollen were even absent, however Pinus pollen were present continuously (Vorren et al., 2009). Today, no Picea grows on Andøya and is found in Norway a mere 500 km south and only a small amount of Pinus can be found on the island (Birks et al., 2012; and references therein). The climate during the LGM and Younger Dryas was harsher than today, so it is notable that boreal trees didn’t expand on the island afterwards (Birks et al., 2012). A speculating explanation could be that under warming conditions and deglaciation, migration of herbivores to those areas increases as well, foraging on the only little vegetation present
and inhibiting boreal tree pollen productivity. Vegetation composition and presence is very dynamic and local (Parducci et al., 2012a), and it would be too simple to think that vegetation populations are static. Also, it has been seen before that boreal trees are absent now where they were present after deglaciation (Edwards et al., 2014). Also it should be kept in mind that the Scandinavian Ice Sheet depressed land considerably, and land surface was lowered, making climate relatively softer at current elevated areas.

3.2.4 Migration rates

In case that boreal trees did migrate post-glacial into northern Scandinavia from putative refuge areas located in Russia, *Pinus* and *Picea* travelled far (>1500 km) to areas with early-Holocene spruce finds, like in the southern Scanes. Currently, more-and-more research is being conducted on migration rates of boreal trees (Paus, 2012; Feurdean et al., 2013; MacDonald et al., 2008; Snell & Cowling, 2015), as migration rates and corresponding migration periods do not agree with early presence of *Pinus* and *Picea* in central Sweden. The paradox of Reid, describing post-glacial colonization where plant migration rates do not support this quick colonization (Clark et al., 1998), can be applied to this situation. Therefore, migration rates might be used as evidence against post-glacial re-colonization from far located refugia.

In a virgin, barren post-glacial landscape, tree species such as *Picea* spread rapidly as isolated individuals or small populations in an 'advancing wave front' ahead of an intensive colonization (Bialozyt, 2012; Giesecke, 2005). After pioneers settled, spread is more slowly due to competition. In northern Russia, migration and colonization of *Pinus* lagged behind on *Picea* after deglaciation at the end of the Younger Dryas (13,000 – 12,000 years BP; Figure 7. Glacial behaviour of the Scandinavian Ice Sheet from the LGM (thick line) to the end of the Weichselian (Svendsen et al., 2004).
MacDonald, 2008). This could mean that *Picea* might be a faster migrant than *Pinus* in pristine and barren landscape conditions, even although *Pinus* is early-successional and *Picea* late-successional (Feurdean et al., 2013).

### 3.2.4.1 Post-YD from Russia

The Scandinavian Ice Sheet of the LGM experienced its maximum extent some 20,000 years ago and covered Fennoscandia almost entirely, with the ice sheet reaching as far as the Valdai Hills in western Russia (Svendsen et al., 2004). Gradually, a warming climate supported an ice withdrawal and an open landscape was left, ready to be slowly colonized by pioneers. The gradual warming was interrupted by a swift turn to a colder climate ca. 12.800 years BP, when a last glacial advance appeared with its Scandinavian Ice Sheet maximum reaching approximately to the Finnish-Russian border (Figure 7). Oldest macrofossils of *Picea* and *Pinus* are dated shortly after deglaciation to 11.020 and 11.720 years BP respectively (Kullman, 2008). Assuming that boreal trees were present at the glacier edges, they should have migrated at least some 1500 km to the location of early spruce and pine, the mountain Åreskutan in the Southern Scandes, in c. 1500 and 2200 years, respectively, which corresponds with expected migration rates of 1 and 0.7 km yr⁻¹. This exceeds migration rates, based on modelling with macrofossil finds, by far, as *Picea* is said to spread with an average rate of 70 m yr⁻¹ and a maximum of 300 m yr⁻¹ (Feurdean et al., 2013; Svenning & Skov, 2007). This is even far overestimated when compared to a recent study indicating a *Picea* migration rate of around 50 m yr⁻¹ (Snell & Cowling, 2015). *Pinus sylvestris* migrates with some 195 m yr⁻¹ and the fastest records indicate 515 m yr⁻¹ (Feurdean et al., 2013). As the expected migration rates exceed the recorded rates by far, it implies that the tree fossils from the early Holocene in the Scandes do not originate from post-glacial re-colonization after the Younger. So, it can be deduced that boreal trees were present within Scandinavia during the Younger Dryas. However, other factors fastening migration are not included, such as dispersal by water, wind or animals.

### 3.2.4.2 Post-YD from Norway

And what if migration rates are tested from Andøya refugium? If pine and spruce survived the LGM on the Norwegian island Andøya and possibly other coastal areas in Norway (Parducci et al., 2012a), boreal trees which settled early after deglaciation (ca. 10.200 years BP; Kolstrup & Olsen, 2012) at Åreskutan could originate from Andøya. If so, trees spread 1000 km in an estimate of 1500-2000 years, corresponding to expected rates of 500 m yr⁻¹, by far exceeding the estimated spread by Feurdean et al. (2013) of both pine and spruce. So, the disability of boreal trees to spread fast enough after the deglaciation at the end of the Younger Dryas to reach the central Scandinavian mountain range in 2000 years supports the theory of local survival in the central Scandes.
3.2.5 My alternative hypotheses regarding glacial survival

3.2.5.1 Debris-covered glaciers hypothesis

Until now, focus has been on glaciation acting as an ice sheet covering land, thus making it impossible for plants to grow in those areas. However, Fickert et al. (2007) recognized the existence of present-day debris-covered glaciers around the globe accommodating vegetation growth, from sparse pioneer vegetation to abundant conifer forests (Fickert et al., 2007). Observations of this phenomenon are recorded for glaciers in semi-arid (Karakoram, Himalayas, western Kunlun, Andes), semi-humid (Peruvian Cordillera Blanca), and humid regions (Cascade Range, Alaska, New Zealand Alps, European Alps, Daxue Range; Fickert et al., 2007), indicating that debris-covered glaciers occur irrespectively of the regions macroclimate. Dense spruce (*Picea sitchensis*) forests grow on Fairweather Glacier in Alaska (Figure 8), under similar humid conditions as seen in Pleistocene Scandinavia. Although not the same species, this might indicate that *Picea abies*, as well as other species such as *Pinus sylvestris*, could have grown on debris on top of ice sheets, opening up an additional survival strategy for boreal trees under glacial conditions. Today, no general guidelines exist on which plant species can live on debris-covered ice, so more research in the future on plant growth on soil-covered ice might be convenient.

Fickert et al. (2007) claim that the only reason for absence of plant growth on ice is due to the too high elevation, coinciding with harsh conditions, insufficient debris cover or a too mobile debris layer. On Carbon Glacier in Mount Rainier, Washington, the genera *Picea* and *Pinus* are present on the debris-covered ice (Fickert et al., 2007), as well as a high number of other plant species. So, although debris-covered ice sheets might not seem the most favourable niche, due to negative factors as a low soil temperature and a shallow mobile root horizon, it seems positive factors, such as the humus-poor, mineral-rich soils and light availability on the ice plateau, match up (Fickert et al., 2007). Furthermore, microclimate was found to be of importance for the survival of vascular plants on ice, as temperatures differed much for ice surfaces of the Carbon Glacier.

Figure 8. The debris-covered Fairweather Glacier in Alaska accommodates dense spruce (*Picea sitchensis*) forest, with individuals up to 150 years old. Note the relatively thin debris layer. U.S. Geological Survey, 2013; Tom Bean Photography.
3.2.5.2 Viability of ancient seeds

Nature always aims on survival of organisms, and plants and their seeds have shown a remarkable ability to survive extreme conditions over millennia (La Farge et al., 2013; Science World Report, 2015). Finds on ancient seeds experiencing ice ages have been proven to be viable and were regenerated (Yashina et al., 2012;). In Siberia, seeds of *Silene stenophylla* have been stored in the Late Pleistocene undisturbed permafrost for ca. 31,800 years, buried by squirrels. Seeds were brought to live into fertile, seed producing plants (Yashina et al., 2012). The viability of ancient seeds stays mystical, but the ability of lengthy survival under cold conditions might be something to consider in the discussion about glacial survival of boreal trees. Although the study of Yashina et al. (2012) regenerates seeds of a remarkable age over 30,000 years, to survive the glaciation of the LGM or Younger Dryas demands much shorter periods of several thousands of years. Seeds might have been present in permafrost conditions and could have regenerated naturally in the warming conditions shortly after deglaciation. The germination ability of Norway spruce and Scots pine has only been tested for a tiny fraction of 10 year-old seeds (Tomášková et al., 2013), but showed promising ranges up to 74% successful germination. However, nothing is known yet about ancient viability of spruce and pine seeds and this will stay an interesting speculation.

3.2.5.3 Early human impact

Never mentioned in the discussion about glacial survival of boreal trees is that in the period of deglaciation in Fennoscandia and the presence of *Picea* and *Pinus* after the Younger Dryas, early human presence is recorded. Actually, there are signs of nomadic reindeer herders in Southern Scandinavia at several points in this period as 14,000 years BP and 12,800 years BP, possibly even hunting and travelling further up north on the ice-sheet (Wygal & Heidenreich, 2014). Further north, at the Swedish coast of Bohuslän settlements from the Hensbacka-Fosna culture are dated to ca. 12,800 years BP, as well as signs from a similar culture in Boknafjord at the north Norwegian coast dated to 11,200 years BP (Wygal & Heidenreich, 2014). Although those detected humans were located far South, nomadizing individuals could have travelled considerable distances on the ice-sheet, p.e. after game. In case of such circumstances, humans could have approached the central Scandes nunataks or ice-free areas on the Norwegian coast. The chance that all small groups of hunter-gatherers are noticed by archaeologists is small, and therefore human presence cannot be excluded totally if there are no traces. Later, findings of nomadic people have been found in northern Sweden dated from 10,700 years BP onwards (Möller et al, 2013; Hörnberg et al., 2006; Bergman et al., 2004), which means they migrated there, possibly from south- and western areas of Sweden and Norway. Also, close to the Lofoten and the island Andøya, several Mesolithic hunter-gatherer camps have been found dated to 11,000 years of age (Möller et al., 2012; and references therein). So, speculating that seeds of spruce and pine might have been transported by humans, a lot of knowledge is needed before exclusion is possible. Either they could have carried seeds by accident, or perhaps deliberately as cones for the edible seeds, such can be seen still with isolated Siberian populations, or as fire starters, containing fast-burning resin, even under wet circumstances.

3.2.5.4 Marine influx

Based on revised isostatic uplift, diatoms and aquatic flora, Kolstrup & Olsen (2012) propose that parts of the Scandinavian mountains were glacio-isostatically more depressed than traditionally thought, creating sporadic waterways for sea-water from the Baltic into the lower lying mountain areas and even to the Atlantic Ocean. At some locations, it might even have been possible for Atlantic water to reach mountainous areas the other way round. If this is true, many theories on the formation of post-glacial vegetation composition and geology might have to be revised as well, and plants might have dispersed far distances by waterways.
into central Scandinavia, followed by immediate colonization and growth. However, more research is needed to verify this provoking hypothesis.

4 Implications

The assumption that Norway spruce and Scots pine disappeared from Fennoscandia due to a kilometres thick ice-sheet covering the landscape and re-entered Scandinavia only 3000 years ago has totally been based on palynological data retrieved in the last 50 years. Pollen research is a long-established discipline, and has been much applied and appreciated method, establishing a certain faith in its reliability, although interpretation can be controversial. Being embedded in basic scientific methods, opposing statements based on innovative methods might mix up the world of conservative scientists. To me, this seems the case in the discussion on the early post-glacial presence of boreal trees in Fennoscandia, where new techniques applying carbon dating on macrofossils and genetic analysis have shown results which are in conflict with those based on pollen analysis. However, it should not be assumed that palynological evidence is not reliable, but interpretation of pollen percentages should be treated with care and should not be seen as static. A great amount of studies noticed small amounts of Pinus and/or Picea pollen in western and central Scandinavia dating back to glacial and early post-glacial periods, but might have interpreted this too lightly, as long-distance transport, or more recently, contamination, influenced by the general assumption of absence of boreal trees and side-lining the possibility of inhibited pollen production due to cold conditions. At a certain stage, when the theory is established for several decennia, propagation is difficult.

In the current intense discussion, the genetic analysis of Parducci et al. (2012a) and macrofossil findings from Kullman of Pinus sylvestris and Picea abies do not agree with the studies based on pollen analysis. As pollen analysis has been settled much longer in scientific research than the others, this has determined the view on boreal trees in post-glacial landscapes. With the introduction of the new analyses, palynological research can now be criticized. This is not per sé disadvantageous as pollen analysis needs to be revised, developing the method further. Here, the incongruous findings of little pollen and the proof of local presence of boreal trees based on DNA and macrofossils force re-consideration of earlier interpretations of low pollen percentages. If low pollen amounts are interpreted as possible presence of boreal trees, all methods (palynological, genetic and macrofossil) seem to agree with one another on the presence of glacial and post-glacial boreal trees in coastal, but also mountainous areas of Scandinavia, and the methods might act complementary. The exclusion of a possibility that little pollen indicate local presence, decided the direction of development.

And that, the exclusion of possibilities, is exactly what is happening in this puzzle; going against the principles of scientific research, where the improbable is not impossible if not unproven. Not only the pollen threshold value, but so far also other potential hypotheses are totally neglected. Although improbable, no study has ruled out possible roles of regeneration of ancient seeds after deglaciation or accelerated spread due to aquatic transport land inwards, nomadizing humans or animals, such as squirrels of which 10.400 year old bones were found in a cave at the coast of west Norway (Larsen et al., 1987). It would be convenient to integrate those hypotheses into the discussion on glacial survival of boreal trees in Fennoscandia.

In order to come back to the aim of this review, I discuss the answer on the following question: Did Norway spruce (Picea abies) and Scots pine (Pinus sylvestris) survive Weichselian glacial periods in isolated ‘cryptic’ refugia within Scandinavia, or did those boreal trees re-colonize Fennoscandia by post-glacial migration from eastern areas such as Russia? No forward answer can be given, neither a confirmation or disproval. Nonetheless, in
my opinion there is no reason to discard the theory that both pine and spruce were growing in Scandinavian ice-refugia during the glacials of the late Weichselian, as has been done by the majority of scientists. The findings of a considerable amount of hard-to-find macrofossils, dating back to early glacial and post-glacial period after the Younger Dryas, together with the findings of genetic once isolated groups of Norway spruce in western Scandinavia, I grasp as a strong indication of the actual presence of boreal trees in western and central Scandinavia. But how did they come to grow there; is it indeed as Kullman proposes, that ice-free nunataks in the central Scandes offered a refugium, or was it rapid, not solely driven by natural migration, re-colonization by processes not yet fully understood?

What can be said, is that both Scots pine and Norway spruce where present in central Scandinavia shortly after the Younger Dryas. If those boreal trees came to grow there in a process only involving slow natural migration over land (no water or animal seed transport), it means that during the predating Last Glacial Maximum either those trees survived in the Scandes, or/and migrated from other peripheral refugia, such as Andøya at the Norwegian coast. The latter is confirmed by the findings on Andøya of ancient spruce and pine DNA dating back to the Last Glacial Maximum. So, to me it seems plausible that boreal trees grew on Andøya during the extreme conditions of the LGM and from there spread through central Scandinavia. Certainly, when taking into account possibilities as ice-free refugia, the existence of debris-covered glaciers in glacial Fennoscandia on which vegetation could have grown, the crippled krummholz growing forms of both pine and spruce which are able to survive harsh conditions for a long time, the regeneration of ancient spruce and pine seeds being exposed from the permafrost to a rapid warming conditions, or even human impact. And then there is the provoking hypothesis of the Scandes being much more isostatically depressed than previously thought, causing possibilities for marine influx into the mountains. There are a lot of pathways, or combinations of those, which could have created surviving strategies for boreal trees in the harsh glacial conditions of the LGM and the YD.

It should be emphasized that if boreal trees did survive glacial periods within Scandinavia, the theory that pine and spruce migrated from Russia areas need not necessarily be untrue, as migration from the east could still have taken place simultaneously. So, the focus should not be ‘Tabula Rasa or glacial survival’, but rather ‘Did glacial survival of boreal trees prevail in Scandinavia?’. Furthermore, the emphasis in this review lies specifically on Pinus sylvestris and Picea abies, but this discussion could also have wider implications for other occurring vegetation, geological processes, climatic circumstances and fauna, and vice versa.

Future research is needed to create more clearness in this dilemma on glacial survival of plants in Fennoscandia. Developing techniques such as aDNA can be a valuable tool to answer many questions and create new insights, as there remain a lot of ambiguities. Focus of further research could lie in diverging disciplines from growth phenology of plants and viability of seeds to geological substrates and their origin, as well as testing the accuracy of methods as carbon-dating to behaviour of ice-sheets. All findings in those fields could help to solve the puzzle if there has been survival of Picea abies and Pinus sylvestris during the LGM and Younger Dryas in Fennoscandia. Untill now, a bias can be noticed regarding geographical research locations. Main focus of research has been the island of Andøya, NW Norway, having played a key role in the process of glacial survival, as well as the central Scandes due to the findings of tree-macrofossils there. However, little research regarding the possible glacial survival of boreal trees is conducted in northern Fennoscandia and inland Sweden, as well as other parts of Norway. To create a more complete image and perhaps to observe significant missing links, research elsewhere is convenient.
5. Literature


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