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Importance of air and soil temperatures for bioclimatic delimitations in Norwegian mountains

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Abstract

Distribution limits of plants in relation to climatic variables have long interested ecologists. High latitudes and altitudes house distribution limits of forests, treelines, treeline ecotones and vascular plants in alpine and Arctic areas, which are all considered to be climatically sensitive. Separation of Arctic, alpine and boreal biomes have mostly been defined by forest distribution limits. The biomes are bioclimatically defined, consequently it should assumed that they are defined both in terms of biota and climatic variables. Temperatures (air and soil) have been considered as one of the most important factor in limiting tree growth and determining the position of treeline; beyond treelines we come across open areas usually dominated by heath communities. Earlier studies have focused on air temperatures and rarely included measured soil temperatures. Recent studies have however, shown that plant distribution limits are often better explained by soil than by air temperatures. Also, soil characteristics are highly affected by temperature variables.

The main focus of this thesis has been to study vegetation, air and soil temperature conditions with increasing latitude and altitude in southern and northernmost birch forest limits in Norway. The forest limit position in northernmost Norway has been used as the main criteria for including the narrow coastal heath fringe in the Arctic biome. If this criteria is useful, it should be assumed that the forest limit is climatically defined. In addition, coastal heaths of northernmost Norway have been an issue of debate since decades on whether it belongs to Arctic biome. Data on temperature and soil properties have been collected from the northernmost coastal heaths along with adjacent heaths located south of polar treeline, and compared with Arctic heaths from Bear Island and Spitsbergen. Plants and plant communities found growing on high mountain summits often represent limits for plant distribution, we have studied relationships between air- and soil temperatures and plants at summits from south to north Norway. We have also tried to answer if we could use air temperatures as proxy for soil temperatures.

Norway along with adjoining Islands spanning from 57 °N to 81 °N latitude; with its undulating and rugged topography, high mountains (0 - 2469 m) and huge fjords, offers a perfect study area. For this study, sampling was conducted in alpine treeline ecotone, forests, forest limits, treeline and treeless heaths. Data on vegetation communities, soil temperature, air temperature, soil properties (only for Paper II and III), tree-ring (only for Paper II) and topography have been gathered. Study plots (2 X 2 m) were randomly selected in homogeneous vegetation stands for data collection. Air temperatures at 2 m height above ground were interpolated from gridded temperature dataset. Soil temperatures were obtained by using temperature data-loggers dug down at 10 cm below ground in each plot.

The southern limits of birch forests are located at low elevations near coastal areas and the elevation increase as we move inland. Warmer temperature conditions are recorded in coastal areas as compared to inland areas. The temperature conditions in northernmost birch forests located far north are slightly warmer than the southern forests. Additionally, the temperature conditions from northernmost forests were comparatively warmer than other such transitional zones. From our results it was clear that these northernmost forests are not limited by temperature but rather due to presence of Barents Sea, wind and topography.

We studied these northernmost coastal heaths along with heaths located immediate south of treeline, heaths from Bear Island and Spitsbergen. Our results suggests that based on vegetation, temperature and soil properties; heaths south and north of treeline were similar and it is unjustifiable to group them in to two separate zones.

Study of air and soil temperatures of vegetation plots on 19 mountain summits revealed that air temperature is generally a poor proxy for soil temperature in cold areas, except during July. From our results it was clear that vegetation composition and lichen cover influenced soil temperatures; lichen abundance and degree of soil frost were strongly correlated.

Keywords: Air temperature, alpine, alpine treeline ecotone, Arctic, birch, forest limit, growing season temperature, growing season length, July temperature, soil properties, soil temperature, treeline, tree rings.

List of papers

This thesis is based on the following four research papers and will be referred to in the text by their Roman numerals:

Paper I

Gauri Bandekar, Gro Skeie, Zdenek Dvorak, Arvid Odland (2017). Vegetation, soil- and air temperature studies within alpine treeline ecotones of southern Norway. Oecologia Montana, 26: 19-32.

Paper II

Gauri Bandekar, Arvid Odland (2017). Ecological characterization of northernmost birch forests and treeline ecotones in Norway. Phytocoenologia, 47 (2): 1-14.

Paper III

Gauri Bandekar, Live Semb Vestgarden, Andrew Jenkins, Arvid Odland. Bioclimatic gradients and soil properties of coastal heaths from North Norway to Spitsbergen (Svalbard). (Submitted to Polar Biology: Under review)

Paper IV

Arvid Odland, Gauri Bandekar, Inger Hanssen-Bauer, Sylvi M. Sandvik (2017). Relationships between vegetation, air and soil temperatures on Norwegian mountain summits. Geografiska Annaler: Series A, Physical Geography, 1-14.

Papers summary

Paper I

Gauri Bandekar, Gro Skeie, Zdenek Dvorak, Arvid Odland (2017). Vegetation, soil- and air temperature studies within alpine treeline ecotones of southern Norway. Oecologia Montana, 26: 19-32.

Abstract

Alpine treeline ecotone (ATE) is the transition zone between closed forest and the treeless alpine zone. The main objective of this study is to investigate air and soil temperatures within ATE from seven different areas which have previously been described to be climatically limited. The study areas include a gradient in oceanity, wherein forest limits have been mapped to vary from below 800 m to higher than 1100 m. In ATE, soil temperatures were measured using data loggers at the depth of 10 cm in the top soil layer and gridded air temperatures (2 m above ground) were obtained from the Norwegian Meteorological Institute. Kruskal-Wallis test showed statistically significant differences between the study areas, with higher summer temperature values in the oceanic influenced areas. Seven vegetation communities were categorized by TWINSPAN analysis; gradient in vegetation was explained with soil- and air- temperature frost sum, growing season soil temperature and growing season length (calculated using soil temperature). The current ATE position could be significantly explained by growing season length (air and soil temperature), temperature frost sum, and duration of the frozen soil period. The results suggests that temperatures may not be critical for current ATE altitudinal positions in oceanic areas.

Keywords: *Betula pubescens*, growing season length, growing season temperature, heat sum, July temperature, vegetation communities

Paper II

Gauri Bandekar, Arvid Odland (2017). Ecological characterization of northernmost birch forests and treeline ecotones in Norway. Phytocoenologia, 47 (2): 1-14.

Abstract

The northernmost birch forests in the world are found along the coast in Finnmark (Norway) and are used to delimit boreal biome from the alpine/Arctic biome. These forest limits near Arctic and alpine biomes are assumed to have bioclimatic characterization. The current paper focuses on quantifying ground vegetation, estimating age, distribution and ecological conditions in 28 selected birch forest stands. Another key objective of this study was to investigate whether these forests are temperature limited. We also wished to determine if there were any significant differences in ecological conditions between forest, scattered trees and shrub plots. Soil and air temperatures were measured within selected stands and soil samples and tree cores were collected. The results showed the field layer to be dominated by *Empetrum - Cornus - Vaccinium*, *Polytrichum - Cornus* and *Cirsium - Viola* types; the gradients between these types being explained by pH, July temperatures and thaw days. Based on the tree-ring data, the age of the trees was estimated to be 11 - 77 yrs. Elevated levels of calcium were evident in some of the study plots. We found no differences in temperature conditions and soil properties between forests, scattered trees and shrubby stands (with the exception of potassium concentration). The overall temperature conditions in present study were warmer than in other northern limit of birch forests. This suggests, that forests are probably not limited by temperature conditions, but more likely limited by strong wind, topography and absence of land further north. However, more data will be needed to confirm this claim.

Keywords: air temperature; birch age; birch distribution; growing season length; soil properties; soil temperature

Paper III

Gauri Bandekar, Live Semb Vestgarden, Andrew Jenkins, Arvid Odland. Bioclimatic gradients and soil properties of coastal heaths from North Norway to Spitsbergen (Svalbard). (Submitted to Polar Biology: Under review)

Abstract

In the far high north of the Norwegian mainland in the county of Finnmark, boreal forest is replaced by heaths. This northernmost treeline has been equated with the boundary between the boreal and Arctic biomes (heaths north of this treeline are referred as Arctic). To deepen the knowledge about these heaths and to justify if heaths north of treeline belong to Arctic; data on vegetation, temperature and soil properties were collected from coastal heaths in Finnmark both south- and north of the northernmost treeline, and below and above the altitudinal treeline. In addition, we collected data from unequivocally Arctic areas such as Bear Island (only temperature data) and Adventsdalen, to quantify latitudinal and altitudinal gradients in heath vegetation from north Norway to Adventsdalen. As expected there was a clear trend in climatic variables along the axis Finnmark - Bear Island - Adventsdalen. Vegetation analysis using TWINSPAN classification, identified five vegetation communities, two on Adventsdalen and three in Finnmark and established a clear vegetation difference between the two areas which could be explained by maximum average air temperature, average annual air temperature and soil frost sum. In contrast, heath communities north and south of the treeline in Finnmark were not distinguishable in terms floristic composition, air temperature, soil temperature or soil properties. Neither was there any clear distinction between high and low-altitude plots. Furthermore, temperature measurements were not consistent with the presence of permafrost, a hallmark of Arctic heaths. We conclude that the previously-used division of heaths in Finnmark into boreal, alpine and Arctic biomes is not justified.

Keywords: alpine, Arctic, air temperature, soil properties, soil temperature,

Paper IV

Arvid Odland, Gauri Bandekar, Inger Hanssen-Bauer, Sylvi M. Sandvik (2017). Relationships between vegetation, air and soil temperatures on Norwegian mountain summits. Geografiska Annaler: Series A, Physical Geography, 1-14.

Abstract

Geographic variations in air and soil temperatures are dependent on several biotic and abiotic factors. Air temperature has mostly been used to characterize thermal conditions for plant life, and studies of bioclimatic gradients. From a biological point of view, it is also essential to know to what extent soil temperature is coupled with air temperature. In this study, we have quantified the deviations between soil and air temperatures along gradients in latitude, altitude, and possible effects of the vegetation. Sixteen different temperature variables were estimated from 49 vegetation plots on 19 mountain summits along the high mountain range in Norway, ranging from 230 to 1780 m a.s.l., and from 59°N to 71°N. Soil and air temperature variables were estimated from the study plots during one year. All air and soil temperature variables were significantly correlated, but the rate of explanation was mostly relatively low (37.0–60.0%), except during the growing season. Start of the growing season, determined by air or soil temperatures, could deviate by 38 days mainly due to effects of frozen soils. Vegetation composition, especially the lichen cover, had a major impact on soil temperature, Dwarf shrub cover increased significantly with increasing July temperature. Lichen abundance and degree of soil frost were strongly correlated and explained a major part of the variation in soil temperatures. The study indicates that air temperature is generally a poor proxy for soil temperature in cold areas, except during July.

Keywords: Latitude, altitude, plant functional types

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Abbreviations

Avg	Average annual temperature (°C).
Avg(Jul)	Average July temperature (°C).
Avg(Jan)	Average January temperature (°C).
GSST	Average soil temperature during the growing season (°C).
GSAT	Average air temperature during the growing season (°C).
STHS	Heat sum for soil temperature (dd - Degree days)
ATHS	Heat sum for air temperature (dd)
STFS	Frost sum for soil temperature (dd)
ATFS	Frost sum for air temperature (dd)
SGS	Start of growing season (day of the year)
GSL	Growing season length (number of days)
Smelt	Snowmelt (day of year)
ThD	Thaw days (number of days)
SF	Soil frozen period (number of days)

Contents

1 Introduction

The main objective of this thesis is to gain thorough understanding of air and soil temperature conditions in forests, treeline ecotones and in treeless areas of Norway. Temperatures have been considered as the most important factor limiting tree growth at higher latitudes and altitudes (Körner 1998b, Holtmeier 2003). Substantial knowledge about temperature data is mainly restricted to air temperatures (Körner 2003, Holtmeier 2009). Measures of soil temperature below ground at treeline ecotones and in treeless areas is rare (Anschlag et al. 2008). As such, the temperature conditions can be explained/quantified in terms of average annual temperatures, temperatures during the warmest month, heat sums, frost sum, growing season temperature and growing season length.

Earth has been divided into climatically controlled regions based on the characteristic plant and animal life; these regions are referred as biomes (Walter 1980, Zlotin 2002). In Norway, heterogonous topography along with strong oceanic influence gives rise to distinct regional variation in vegetation (Ahti et al. 1968). Presence of permafrost at high latitudes have been used to define the Arctic biome (Brown et al. 1998).

In Norway, biomes have frequently been separated at high latitudes and altitudes: i.e. boreal, and treeless Arctic and alpine biomes (Moen 1999). Separations between boreal, alpine and Arctic biomes have primarily been based on the distribution limit of birch forests (alpine and Arctic/polar treelines), which are generally assumed to be associated with an average warmest month temperature of 10 °C (Brockmann-Jerosch 1919, Köppen 1919, Körner 1998a). Criteria for the delimitation of the zones within the boreal and alpine biomes in the north-western Europe follow mainly Ahti et al. (1968) and recently revised Moen (1999). The distribution of the plants further rely on both temperatures and precipitation (Moen 1999). The latitudinal north to south gradient of Norway has been separated into five vegetation zones (Ahti et al. 1968, Moen 1999). Another approach uses oceanity - continentality gradient to categorise vegetation from west to east in to vegetation sections see references in Ahti et al. (1968) and (Moen 1999). The three dimensional approach to categorise vegetation along latitude, longitude and altitude (usually referred to as belts) are a common approach (Ahti et al. 1968, Walker 2010).

1.1 Boreal, alpine and Arctic biome

1.1.1 Boreal zone

Boreal zone is subdivided in to southern boreal zone, middle boreal zone and northern boreal zone occupying 12 %, 20 % and 28 % of total Norwegian landmass respectively. The southern boreal zone is characterised by presence of spruce, pine, and mixture of deciduous woodland mostly dominated by thermophilous vegetation. It is spread over Helgeland, Tronheimsfjord, Møre, Romsdal, Rogaland, south eastern Aust-Agder and central Norway rarely reaching 500 m a.s.l. Middle boreal zone dominated by Norway spruce, Scots pine, birch, grey, alder and aspen, and is distributed in south-east and east Norway in Hedmark County, in Trøndelag, Nordland and towards west coast. The upper limit of the middle boreal zone lies at 800 m a.s.l. in southern Norway, decreasing northwards to below 130 m a.s.l, and towards the west coast (below 300 m a.s.l). Northern boreal zone forms an uppermost and northernmost zone reaching ca. 1200 m a.s.l in Jotunheimen in central Norway, < 500 m a.s.l. towards south west to almost sea level in coastal areas of Finnmark (Moen 1999, Aas and Faarlund 2001). The warm north Atlantic currents raise the forests in Fennoscandia above 70 °N, whereas in Canada cold currents suppress treeline at 55 °N (Callaghan et al. 2002b).

In Scandinavia, *Betula pubescens* forms latitudinal and altitudinal treelines (Bohn et al. 2000, Bylund and Nordell 2001, Wielgolaski 2001). In Fennoscandia, mountain birch is considered a subspecies of *Betula pubescens* Ehrh., spanning from southern Greenland to the central Kola Peninsula (Väre 2001, Wielgolaski and Nilsen 2001, Jónsson 2004, Karlsson et al. 2004, Aune et al. 2011a). We have not distinguished between different *B. pubescens* subspecies in this study. Probably both subsp. *pubescens* (*B. odorata* Bechst.) and subsp. *czerepanovii* ((N.I Orlova) Hämet-Ahti, (formerly subsp. *tortuosa* (Ledeb.) Nyman) are common, however, according to Lid and Lid (2005) it is not always possible to separate between these two in most parts of the country.

1.1.2 Treeline ecotone

The boreal zone is delimited at high latitudes and altitudes globally (Sveinbjörnsson 2000). This delimitation is usually referred to as treeline (definition in Table 1). Treelines are a global phenomenon, dominated by different tree species World-wide. Treelines are conspicuous boundaries, which rarely end abruptly; rather it is a zone wherein a decrease in tree populations is evident and is referred to as treeline ecotones (Callaghan et al. 2002a, Holtmeier 2009, Körner 2012) (definition in Table 1). The lower limit of treeline ecotone is referred as forest limit (definition in Table 1).

Usually, as trees approach the treeline a decrease in tree growth and height is seen; in some cases giving rise to stunted growth forms referred to as shrubs (Callaghan et al. 2002b, Holtmeier and Broll 2005, Körner 2012). The harsh environmental conditions beyond treelines delimit the tree growth, survival and reproduction leading to decrease in tree height and canopy cover (Holtmeier 2009). The treeline ecotone can be either narrow or wide, and is generally classified in to 4 forms i.e. diffuse, abrupt, island and shrubs (definition in Table 1) (Harsch and Bader 2011). The type i.e. diffuse or abrupt depends on the local climatic differences, substrate and land use (Holtmeier 2009).

Latitudinal and altitudinal variation gives rise to complex climatic and environmental conditions thus making it difficult to identify the single factor responsible for treeline formation (Berdanier 2010). In Norway, *B. pubescens* forms higher treelines owing to its high frost tolerance (Sakai and Larcher 1987). Also, it is assumed that *B. pubescens* forms high treelines due to relatively low heat demands. The northernmost limit of the transition zone is limited by environmental factors (e.g. wind, snow, cold temperatures), and human influence (Payette et al. 2002). These limits have undergone many shifts since last glacial period (Payette et al. 2002).

Current treeline positions are assumed to be a reflection of the past climatic conditions (Richardson and Friedland 2009). Treelines can be both latitudinal and altitudinal and are referred to as Arctic/polar and alpine treelines respectively. The major difference being alpine treelines are restricted by elevation while the Arctic/polar treelines might not be necessarily restricted due to elevation often representing a limit between the boreal (the taiga) and the

Arctic (tundra) biomes (Payette et al. 2002). Alpine treelines have been studied to a greater extent than the polar treelines (Sveinbjörnsson et al. 1996).

Highest treelines are found in northern subtropics, from there they decrease towards equator and high latitudes (Körner 1998a, Holtmeier 2003). Particularly, an elevational increase of 130 m latitude^{-1} is evident from high latitudes to subtropics (Körner 1998b). In north America, treeline elevation decreases at the rate of 83 m latitude^{-1} and in Northern Europe (46.5 - 61.5 °N), the treeline decreases at the rate of approximately 75 m latitude^{-1} (Peet 1988, Körner 1998a, Odland 2010). Likewise, a decrease in treeline elevation is observed as we move from inland to coastal areas (Sveinbjörnsson 2000). In Norway, the treelines almost come to sea level in northernmost part of the country whereas the treelines are relatively constant between 32 °N - 20 °S (Berdanier 2010).

1.1.3 Alpine and Arctic biomes

Unfavourable environmental conditions result in latitudinal and altitudinal tree limits, beyond this limit short stature vegetation dominate. Several definitions and criteria are developed to categorize these treeless areas in to various zones. In this thesis, the alpine and Arctic biomes have been defined in Table 1. The differences in Arctic and alpine vegetation can be reflected through the winter temperatures and precipitation (Oksanen and Virtanen 1995). Typically, the ecological differences arise as Arctic areas are cold with less precipitation as opposed to alpine areas with mild winters and more precipitation (Virtanen et al. 2016). Major difference is brought about by the amount of seasonal solar radiation received in Arctic and alpine areas regulating temperature and in turn influencing ecosystem structure and function (Ernakovich et al. 2014). Early insolation in alpine areas brings about increase in air- and soil temperatures, early snow melt, onset of growing season and plant growth as compared to Arctic areas (Billings 1973, Ernakovich et al. 2014). The amount of insolation received during growing season is almost similar in Arctic and alpine ecosystems, however, major differences are observed in annual insolation. The amount of sunlight received is more in alpine areas as compared to Arctic, because Arctic ecosystems receive sunlight for 24 hours (during summer) with reduced intensity due to proximity to poles (Ernakovich et al. 2014). Therefore, soil temperatures remain higher in alpine areas than in Arctic areas although air temperatures are seen to be similar during growing season in both these ecosystems (Ernakovich et al. 2014).

Alpine areas are common throughout the globe (total alpine area = 4 million km^2 i.e. 3% of land surface) and occupying highest positions in tropical and sub-tropical areas (Körner 2003). The alpine zone in Norway occupies approximately 32 % of total land area and is subdivided in to 3 zones i.e. low alpine zone, middle alpine zone and high alpine zone (Moen 1999). The low alpine areas are exclusively dominated by willows, *Vaccinium* species and junipers (Moen 1999). Middle alpine zone has sparse woody species (except *Empetrum nigrum* and *Vaccinium vitis-idaea*), it is mainly dominated by sedges, herbs and snow patch communities. Discontinuous distribution of vegetation is common in high alpine zones with fewer vascular species and bryophytes (Moen 1999).

Arctic zones are categorised as areas north of polar treeline (Elvebakk et al. 1999, CAVM-Team 2003, Walker et al. 2005). This polar treeline has been mapped and described circumpolarly in Northern hemisphere (Walker et al. 2005, MacDonald et al. 2008). Based on this criteria northernmost part of mainland Norway together with Bear Island and Svalbard have been categorised as Arctic (Elvebakk et al. 1999, Moen 1999, Walker et al. 2005). The Arctic zone is subdivided in to 5 subzones (i.e. subzone E to A from south to north) based on the dominant vegetation and summer temperatures (Walker et al. 2005). Based on this method of Arctic delimitation the northern most areas of mainland Norway are assumed to be Arctic and are referred as southern Arctic zone/subzone E (Elvebakk et al. 1999, Moen 1999, Walker et al. 2005). Towards this edge on mainland Norway, the classification of Arctic and alpine becomes increasingly challenging (Körner 2003). For decades, it has been discussed if the northern parts of Fennoscandia should be included in the Arctic or not (Sjörs 1963, Ahti et al. 1968, Eurola 1974, Hustich 1979, Elvebakk et al. 1999, Moen 1999, Virtanen et al. 2016).

Bear Island and Adventsdalen (Spitsbergen) have been included in subzone C (Walker et al. 2005), subzone D intermediate in position between subzones E and C is missing in Norway due to location of Barents sea between two landmasses and unavailability of land. Svalbard Archipelago consists of Subzones C (frequently dominated by *Cassiope tetragona, Dryas*

Octopetala), subzone B (dominated by *Luzula nivalis, Luzula confusa*) and Subzone A (dominated by *Papaver dahlianum, L. confusa*) (Elvebakk 2005, Walker et al. 2005).

An alternative approach of division of Arctic in the form of elevational belts have led to 6 belts from subzone e - a (down to up) (Walker 2010). Each belt is spanning approximately 333 m vertically and is associated with a difference of 2 °C temperature decrease (Walker 2010).

1.1.4 Migration

Glaciation resulted in movement of Arctic and alpine plants towards south and at low elevations (Birks 2008). Birks (2008) and references therein suggest presence of Arctic plants near London, southern Sweden and Denmark. Arctic and alpine vegetation closely followed the changes occurring in climate and environment; and moved back to their present location during warm interglacials (Birks 2008). Deglaciation was soon followed by pioneer plants such as *Saxifraga cespitosa, Papaver sect.,* Scapiflora and Gramineae around 13000 yr BP, this vegetation was considered analogous to low-alpine communities (Birks et al. 1994). Birks (2008) and references therein describe the spread of plants from northern Europe, Siberia and North America to Svalbard as the temperature here was 2 °C higher than present (8000 years ago). Later, as the soils matured this vegetation was replaced by dwarf shrubs and tall herb vegetation eventually followed by *Betula* trees (Birks et al. 1994).

The temperature increase in Scandinavia began in Holocene leading to end of Weichselian Ice age, this resulted in melting and shrinking of ice sheets, and was followed by tree migration (Payette et al. 2002). Birch migrated in Norway after the last glacial period approximately 12000 B.P. from Denmark and North Sea continent to south western part of Norway (Ahti et al. 1968, Aas and Faarlund 2000, Payette et al. 2002, Wielgolaski 2005). After 10,000 - 9,000 BP birch spread throughout Norway replacing the glaciated areas (Aas and Faarlund (2001) and references therein). Birch migrated rapidly into the northernmost parts of Norway ca 10,100 – 9,380 cal yr BP from south Norway or from the east along the Barents Sea coast (Aas & Faarlund 2001; Birks et al. 2012). However, after ca. 9,380 cal yr BP the density of birch woodland forests started decreasing (Birks et al. 2012). Pine dominated Finnmark after ca. 9,000 cal yr BP. Historically, pine trees were growing at high elevation owing to the prevalence of dry continental climate and strong insolation, however, over the years the climate shifted to more oceanic climate leading to position of birch limit above pine forest limit (Payette et al. 2002). Literature has revealed the changing limit of treelines with climate; forest limits for pine and birch in Norway and Sweden were 150 - 200 m higher than at present owing to a warm period (commencing in the late 19th century i.e. 1930 - 60) (Aas 1969, Grace 1989, Aas and Faarlund 2000, 2001, Wielgolaski 2005). Birch established as pioneer forest species due to long migration time gap of other species (Eronen and Zetterberg 1996).

1.1.5 History

Treeline studies started as accidental observations from regional studies where the researchers provided general information on how the forests ended at certain altitudes (Holtmeier 2003). Holtmeier (2003) and references therein, suggested that the treeline research is around 200 years old although systematic treeline research is only 150 years old. On the other hand, few researchers believe treeline research is much more ancient and began in Swiss Alps in 16th and 17th century (Troll 1973, Richardson and Friedland 2009, Körner 2012). Many researchers began to find out the plausible reasons for the treeline (Brockmann-Jerosch 1919, Holtmeier 2003). Few researchers suggested that the climatic treeline might be an outcome of reduced thermal conditions (Holtmeier 2009). Since there are many factors such as altitude, latitude, wind and snow which could affect the thermal conditions; further work on identifying the causes began. While some researchers believed in mass elevation effect, which affected the treeline position. Substantial work began on the temperature conditions, to find out the possible climatic variables responsible for treelines see Holtmeier (2009). Relationships were established between the treelines and temperature during the growing season, amount of warmth required during growing season, temperatures during the warmest month and other temperature variables (Sveinbjörnsson 2000, Körner 2012).

According to Körner (2003), research on alpine plants is almost century old, the author also describes the early compilation on the altitudinal variation of vegetation which was conducted in 1555. Researcher Kerner (in 1869) conducted experiments of transplanting alpine plants at treelines and researcher Naegeli (during mid-19th century) conducted an experiment of providing alpine plants with favourable climate (Körner 2003). Sadly, both the experiments failed and resulted in a new insightful possibility that the alpine plants might be genetically adapted. Bonnier in 1800s went on to conclude that environment led to a morphogenetic changes in these plants (Körner 2003).

Remarkable increase in temperatures over northern latitudes have been observed since 19th century, global mean surface air temperatures have risen by 0.3 - 0.6 °C; with a prominent increase by 0.2 - 0.3 °C in last 40 years (Nicholls et al. 1996, Serreze et al. 2000). In Scandinavia, an increase in mean temperatures by 0.75 - 1.5 °C is observed since 1901, especially the period from 1930 - 50 and after 1980 was warm (IPCC 2013, Elmhagen et al. 2015). One of the earliest studies involving change in distribution of plants and animals in relation to climate warming was conducted in northern Finland in 1956 (Erkamo 1956, Crawford 2003). In this study, the plants showed the affinity to migrate towards east rather than north; due to extension of warm oceanic climate from east (Crawford 2008a). Later, based on 22 years of satellite data collection, it was observed that 15 % of the Arctic showed effects of warming, out of which almost 50% was due to increased temperature influencing growing season length and photosynthetic activity (Crawford 2008a). Recently, studies on influence of temperatures on favouring expansion of shrubs in alpine and Arctic areas have been rigorously studied (Crawford 2008a, Naito and Cairns 2011).

1.1.6 Factors affecting birch distribution

Although treelines are a global phenomenon, the factors responsible for position of treelines may vary from one area to another or whether it is locally or globally studied. For instance, in regional studies usually the topography plays an important role in determining the treeline position (Crawford 2005, Holtmeier 2009). There are several factors limiting birch growth at high latitudes and altitudes, in this section we will emphasize only the important ones. For example mass-elevation effect (massenerhebung) causes treelines to be distributed at high elevations due to prevalence of favourable environmental conditions (Holtmeier 2009). Other factors such as aspect and slope can also control the position of treelines (Holtmeier 2009). Abiotic environmental factors such as temperature, precipitation, snow cover, frost damage, soil properties, wind, light and CO_2 partial pressure are important in deciding tree limits (Kullman 1979, Grace 1988, Aas and Faarlund 2000, Wielgolaski 2001, Payette et al. 2002, Sveinbjörnsson et al. 2002, Holtmeier 2003, Wielgolaski et al. 2004, Holtmeier and Broll 2005, Anschlag et al. 2008, Holtmeier 2009, Richardson and Friedland 2009). Equally important are biotic and anthropogenic factors such as grazing, insect infestations (e.g. geometrid moths), land use, agriculture and deforestation which have resulted in the birch occupying the current positions (Wardle 1974, Wielgolaski 1999, Järvinen 2001, Wielgolaski 2001, Tenow et al. 2007, Holtmeier 2009, Richardson and Friedland 2009, Hofgaard et al. 2013). Cold Arctic air masses are also considered as one of the reasons for current forest-tundra limits (Krebs and Barry 1970). Apart from these external factors it is noteworthy to know that species forming treelines can be an outcome of reduced reproductive regeneration, reduced seed production and dispersal and growth form (Holtmeier 2003).

Temperature variables are considered most powerful in explaining treelines, however, the variation cannot be explained by just single factor such as average temperatures (Körner 1998b, a, 2003, Körner and Paulsen 2004, Holtmeier and Broll 2005, Holtmeier 2009). Temperatures can be related to the treelines in terms of following commonly used variables such as growing season length, growing season temperature, heat sums, frost sums and temperature during the warmest month.

Harsch and Bader (2011) and (Körner 1998a) have described and discussed mechanisms which could explain the temperature driven transition from forests to alpine life zone; these are stress hypothesis, disturbance hypothesis, reproduction hypothesis, carbon balance hypothesis, growth limitation hypothesis, dieback and seed mortality.

1.2 Air and soil temperature

Temperature is assumed to be a fundamental factor deciding the location of treelines (Tranquillini 1979, Körner 1998b, Jobbágy and Jackson 2000). Bioclimatic zonation at high elevations and latitudes have previously mainly been related to air temperature data (Tuhkanen 1984, Moen 1999, Walker 2010, Jorgenson et al. 2015), and possible effects of soil temperatures have hardly been studied. Temperature directly or indirectly affects vegetation (Sveinbjörnsson et al. 2002). Usually an increase in altitude and latitude is followed by decrease in temperature (Sveinbjörnsson 2000, Richardson and Friedland 2009). Temperature increase have been evident globally with rapid changes occurring at high latitudes and altitudes (Solomon et al. 2007).

Körner (1998a) and references therein briefly discussed how the temperatures experienced by the tree crowns are nearly similar to air temperatures. Then again, soil temperatures under the trees remain close to air temperatures, contrary to high soil temperatures under treeless soils caused due to radiative warming (Körner 1998a).

Studies have shown strong influence of air temperatures in limiting tree growth. Tree growth is strongly limited at seasonal mean air temperatures lower than 5.5 - 7.5 °C (Körner 1998a, 2003). At high latitudes and altitudes, where the forests are replaced by dwarf shrub vegetation, study of soil temperatures becomes eminent (Graae et al. 2012). In World-wide study of treelines a mean soil temperature of 6.7 °C during the growing season is common (Körner and Paulsen 2004). The soil temperature heat sum (dd) above a certain threshold plays a crucial role in the bud break and start of growing season above ground. The heterogeneity of treeline ecotones increases as we move from global to local scale, thus, making the study at local scales far more complex (Holtmeier and Broll 2005, Holtmeier 2009). In regional studies, the variables such as altitudinal temperature gradient, growing season length, seasonal variations in climate play a crucial role (Holtmeier and Broll 2005). The growing season lengths range 12 months at treelines near equator, whereas, it comes down to 2.5 months in Arctic and alpine treelines (Körner 1998a).

Soil temperatures are assumed to be more correlated to elevation than air temperatures (Scott et al. 1997, Sveinbjörnsson 2000). Soil temperatures measured in root zone i.e. 10 cm is indispensable for proper growth and survival of plants (Holtmeier 2009). Soil temperature in turn are influenced by plant cover, wind, solar radiation, snow cover and soil physical properties (Holtmeier 2009). According to (Gehrig-Fasel et al. 2008) growing season temperatures are considered powerful indicator for treeline position. A temperature (air and soil) threshold of 5 °C is used to mark the beginning of growing season; below this threshold the biological activity is seriously affected (Skaugen and Tveito 2004, Holtmeier 2009). For instance, temperatures lower than 5 °C tend to retard the growth and nutrient uptake processes in *Betula* seedlings at Arctic and alpine treelines (Karlsson and Nordell 1996, Körner 1998a). However, there have been situations wherein soil temperatures did not decrease with elevation for e.g. in case of Njulla in Sweden highest soil temperatures were recorded at treelines and lowest in Abisko valley. Land use pattern of an area has a possibility of effecting soil temperatures due to changes brought about in vegetation structure (Hecht et al. 2007).

With increase in altitude one might be forced to think that temperature conditions in the alpine areas might be quite severe for the alpine plants. Interestingly, this is not the case as the alpine plants are assumed to be genetically adapted forming cushions, temperature approximately 2 cm above ground and between these cushion canopy can reach up to 27 °C (Körner 2003). Adiabatic lapse rates of annual atmospheric temperature means ranges from 0.8 k 100 m^{-1} decrease in elevation in coastal areas to 0.4 k/100 m of decrease in elevation in inland areas (Körner 2003). Likewise, Arctic plants are well adapted to survive at low temperatures. The mean July temperatures can range from 1 - 12 °C (lower temperature are recorded at high latitudes) (Walker et al. 2005).

According to Chapin (1983) and references therein, optimum temperature for photosynthesis in Arctic plants is 15 °C, this temperature optima is low as compared to other vegetation groups. This low photosynthetic optima is achieved by Arctic plants due to presence of large number of rate - limiting RuBP carboxylase enzyme (Berry and Björkman 1980, Chapin 1983). Along with temperature, length of growing season plays a crucial role in regulating the productivity in tundra plants (Chapin 1983). For instance at Barrow, an increase of 10 days (i.e. 12%) in growing season length brings about an estimated 55 % increase in annual Carbon gain (Tieszen 1978).

1.3 Soil properties

According to Bylund and Nordell (2001) and references therein, birch can exist wide range of soil conditions. Although, phosphorus plays a pivotal role in plant metabolism, it is noteworthy to mention about low phosphorus concentration in Arctic and boreal soils (Crawford 2008b). In Arctic areas, negligible input of minerals in soil from chemical weathering is recorded because chemical weathering is inhibited at low temperature (Chapin 1983, Crawford 2008b).

According to Chapin (1983) and references therein, precipitation and nitrogen fixation are major sources of nutrient input in Arctic ecosystems. In Arctic, the rate of both these aforementioned processes is low as compared to temperate ecosystems, hence, more internal nutrient recycling is observed (Chapin 1983).

Arctic landscapes are frozen for most of the year. The soil is frozen from 25 – 90 cm down, and it is impossible for trees to grow. The presence of continuous permafrost degrades into discontinuous permafrost in the southern part of the zone (Richardson et al. 2007). The depth of the active (seasonally frozen) layer of the soil during the growing season depends on summer temperatures and varies from about 80 cm near the treeline to about 40 cm in polar deserts.

Differences in the main soils within the actual latitudinal / altitudinal gradients have previously been separated into three main categories: tundra soils in Svalbard, mountain or highland soils in the Scandinavian alpine areas, and podzols or spodosols in the boreal forest (Jones et al. 2009)

1.4 Literature review

Historically, latitudinal and altitudinal boundaries of boreal forests have been considered to be thermally driven (Crawford 2008b). It was long established according to Köppen`s Rule that the limit of tree growth was associated with the mean temperature of 10 °C during the warmest month (Köppen 1931). Alpine treelines are also assumed to coincide with 10 °C mean air temperature during warmest month (Brockmann-Jerosch 1919, Daubenmire 1954, Körner 1998a). Although, research on treelines has been going since decades, there exists major drawbacks such as use non-standard definitions World-wide, methodology and protocols used in locating and mapping of these treelines which have been causing difficulties in bridging the knowledge gap (Callaghan et al. 2002a, Richardson and Friedland 2009).

In certain studies (Körner and Paulsen 2004) growing season soil temperatures are given importance; whereas in other studies changes in treeline are linked to winter warming (Harsch et al. 2009). According to Körner and Paulsen (2004), sub-arctic and boreal treelines are related to 6 - 7 °C soil temperature during the growing season. Temperatures measured at treeline correlate well with the treeline positions when temperatures < 5°C are excluded (Ohsawa 1990, Körner 1998a). A growing season length of 100 - 120 days is common for alpine treelines (Odland 2011).

Global warming negatively effects these high latitude and altitude ecosystems, studies at 20 sites indicate predicted increase in above freezing air temperatures roughly over a month by year 2070 (Christensen et al. 2013). The influence of temperature on Arctic and alpine ecosystem will be different, and so their response mechanisms will differ (Ernakovich et al. 2014). These short statured plants from Arctic and alpine areas share a lot in common, for instance they are well adjusted to the extreme temperature conditions due to their morphology, with their shoots and roots being in close association to ground where maximum heat accumulation occurs (Körner and Paulsen 2004, Ernakovich et al. 2014).

European alpine areas are associated with mean ground growing season temperature of 5.7-11.6 °C and growing season length of 106 - 203 days (Körner et al. 2003). Mean July temperature of 8.4 °C was observed in the alpine areas of central Norway (Körner et al. 2003).

The growing season lengths are very crucial for high latitude Arctic areas, an increase in growing season lengths is observed since 1980s at a rate of > 3 days per decade (Xu et al. 2013a). The growing season length (days with temperature > 5 °C) was ca. 202 days with average annual temperature of 1.9 °C in dwarf shrubs in sub-Arctic Finland (Anschlag et al. 2008).

1.5 Main questions to be addressed in this thesis

1. Air and soil temperature comparisons between coastal birch limits in southern and northernmost Norway
    - What are the main ecological characteristics of the birch limits in southern and northern Norway?
2. To study the ecology of the northernmost birch forests and treeline ecotones of Norway
    - Are northernmost birch limits temperature limited?
3. Boreal, alpine and Arctic heath communities are common in Norway

  - What are the main floristic and ecological differences between heath vegetation south- and north of the northernmost limit of boreal forest on mainland Norway; and their comparison with heaths on Bear Island and Adventsdalen (Spitsbergen)?

4. Previous studies have shown that plant growth can be strongly associated with soil temperatures than with air temperatures
    - An essential question is therefore if air temperature variables can be used as proxies for soil temperatures.
    - To quantify response and effect of different plant functional types with temperature conditions.
5. The overall focus of the present study has been to suggest answers to the following important questions
    - Do heath vegetation north of northernmost treeline in Norway be classified as belonging to the Arctic biome?
    - Which environmental variables can be used to verify the above conclusion?

1.6 Scope

Treeline ecotones forms a transition zone between the boreal and tundra biomes and these transition zones are sensitive, thus making its proper understanding very important to deepen the study on the boreal and tundra biomes. Shifts in the position and extent of ecotone will influence the feedbacks, eventually influencing climate at regional and global scales (Betts 2000, Callaghan et al. 2002b, Aune et al. 2011a). The study of alpine and Arctic treeline ecotones are crucial in terms of global climate, biota and human settlement (Callaghan et al. 2002a). It is very important to study the condition in current boundaries to be able to predict the future changes (Sveinbjörnsson 2000). The environmental conditions in the boreal forests, alpine / Arctic zone and in the transition zone between the two i.e. in treeline ecotone are totally different (Holtmeier 2003, Holtmeier and Broll 2005). Certain studies suggest the treelines will shift with climate change. Most assume global warming and increasing temperatures will favour the tree growth and lead to encroachment of shrubs and eventually forests in alpine and Arctic zones. In contrast, there have been situations wherein the boreal forests from west Siberia have retreated south replacing current positions with bogs (Crawford et al. 2003). Lloyd and Fastie (2002) suggested that increase in growth of tree at the margins of boreal forest with climate warming is unjustifiable.

Trees, Arctic and alpine plants are long lived and their current distributions are reflection of past climates. With warming it is predicted that many of the cold adapted species will either shift towards north in search of favourable climate or get extinct from competition by shrubs. Hence, it is very crucial to study about current plant distributions and their ecology in order gain knowledge how these vegetation communities may react to changes in temperature.

1.7 Terminology

Table 1: Definitions of terminologies used in the context of this study.

Term	Definition	Reference
Tree	Tree is defined as the upright woody plant with height ≥ 3m; irrespective of its ability to reproduce.	(Körner 1998a, Berdanier 2010, Körner 2012)
Forest	Forest is defined as a continuous occurrence of trees where the distance between individuals does not exceed 30 m.	(Aas and Faarlund 2000)
Forest limit	The uppermost boundary of the closed forests (tree height ≥ 3 m) is termed as forest limit.	(Sveinbjörnsson et al. 1996)
Treeline	Beyond forest limit we come across a transition zone comprising of scattered groups of trees or single trees (tree height ≥ 2 m) and the edge of this zone is called treeline.	(Chiu et al. 2014)
Treeline ecotone	The transition zone between forest limit and treeline is called as treeline ecotone.	
Shrubs	The shrubby forms are usually polycormic with height ≤ 2 m, probably formed due to	(Holtmeier 2003)

	harsh environmental conditions (e.g. wind exposure).	
Monocormic	Single stemmed trees.	(Crawford 2008b)
Polycormic	Multiple stemmed trees.	(Tenow 1996)
Alpine treeline	High altitude treelines.	(Körner 1998a, Holtmeier 2009, Richardson and Friedland 2009)
Arctic treeline	High latitude treeline, particularly northernmost limit to tree growth beyond which tundra dominates.	(Crawford 2008b, Holtmeier 2009, Richardson and Friedland 2009)

2 Study areas, data collection and statistical analysis

2.1 Study areas

Norway is an elongated landmass with narrow shape having rugged and undulating coastline, located between 57 - 81 °N and 4 - 32 °E in Northern Hemisphere. Mainland Norway along with the adjoining major islands such as Svalbard and Jan Mayen covers an area of 365,146 Km^2 (http://www.ssb.no/). The long Norwegian coastline faces the Norwegian Sea on west and Barents Sea towards north. The ruggedness of the coastline can be explained by the presence of large number of fjords. Although, Norway is positioned at higher latitudes, it has a comparatively warmer climate due to warmth brought about by North Atlantic current. The Norwegian landmass is dominated by mountains with peaks higher than 2,100 m, the highest mountain range is the Jotunheimen mountain range (2469 m) located in the south central Norway. The topography is heterogeneous with highest mountains located in central Norway and the mountain height decreases in all directions (Aas and Faarlund 2000, Odland 2015). Gradients in temperature and precipitation from north-south, west-east and with altitude give rise to dominance of different vegetation communities.

The study area covers boreal, Arctic and alpine biomes in Norway. Altogether, 204 plots were established to in this study. Location of study areas is shown in Figure 2.1.

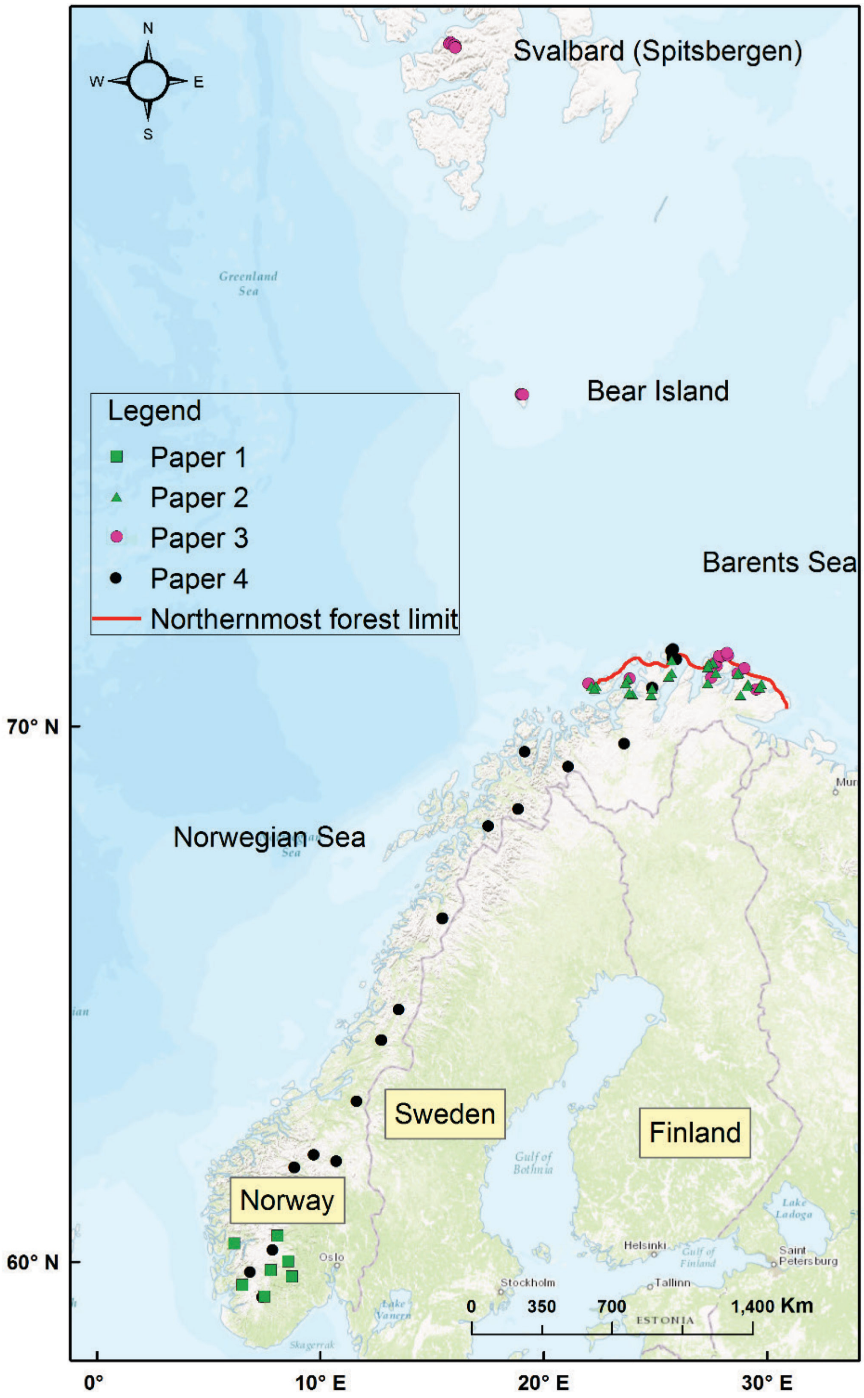

Figure 2.1: Map of sampling location

Paper I:

The tallest mountains are found in south central Norway with forest limits reaching roughly about 1200 m; from here mountain heights decrease in all directions. We used random sampling method in birch treeline ecotones along the elevational and oceanity gradient. Sampling was conducted in Kvam, Suldal, Hol, Vinje, Hjartdal, Valle and Tinn in south central Norway. The highest treelines are formed by the *Betula pubescens*. Altogether, 98 plots were established in alpine treeline ecotones, on north and south facing aspects. Sampling was conducted in alpine treeline ecotones keeping three criteria in mind: selection of highest alpine treeline ecotones in a region, decrease in tree size with altitude and no anthropogenic influence. Figure 2.2 shows the sampling areas from southern Norway.

The bedrock in these areas was mainly composed of gneiss, granite and quartzite which is hard and acidic. The soils are either podzols or leptosols (Jones et al. 2005). Precipitation ranged from 747 mm in inland areas to 2832 mm in oceanic areas during normal period 1961-1990.

Figure 2.2: Photos of sampling areas (a) Valle - south facing, (b) Valle - north facing and (c) sampled plot on Valle south facing aspect (Plot no U1S, 1071 m a.s.l.)

Paper II:

Random sampling was conducted in coastal areas in Finnmark County, in localities such as Magerøya, Kvaløy, Porsangerhalvøya and Varangerhalvøya (Figure 2.3). Arctic and alpine treelines are found to coexist in Finnmark, marking the limit of boreal forests on Norwegian landmass up north. These northernmost forests and the forest limits are usually found in valleys or on inward slopes along the coast of Finnmark. The mountain heights rarely reach 400 m a.s.l. The forest limits are dominated by polycormic, monocormic forms or shrubs.

Although, *Pinus sylvestris* and *Betula pubescens* are major forest forming species the later forms the highest and northernmost forest limit in Finnmark. Soils in Finnmark are classified as lithic Leptosols and Podzols (Jones et al. 2005). The bedrock in the study area consists of Cambro-Silurian sedimentary rocks, gneiss and limestone (Moen 1999). Annual precipitation is mostly lower than 800 mm yr^{-1}. In all 28 plots were sampled in forests, forest limits, treelines and shrubs in northernmost Norway.

Figure 2.3: Photos of sampling areas. (a) Forest limit (Plot No. 7, 109 m a.s.l.) in Hammerfest, near lake Jansvannet, (b) Forest limit (Plot No. 5, 79 m a.s.l.) in Kvalsund and (c) Treeline (Plot No. 8, 38 m a.s.l.) in Hammerfest

Paper III:

Studies were conducted in Finnmark County (70 - 71 °N, 21 - 29 °E), Bear Island (74 °N, 18 - 19 °E) and Adventsdalen (78 °N, 15 - 16 °E) in Spitsbergen (Svalbard), ca. 10 km east of Longyearbyen (Figure 2.*1*). Overall, 23, 5 and 9 plots were established in Finnmark, Bear Island and Adventsdalen (Figure 2.4). In Finnmark, coastal heaths dominate south and north of northernmost treeline, also heaths are common below and above altitudinal treelines. The heaths south of treeline are usually referred to as alpine (above treeline) or boreal (below treelines). Heaths north of treeline are referred to as Arctic and included in subzone E (Elvebakk et al. 1999, Moen 1999, Walker et al. 2005). Bear Island and Adventsdalen belonging to Arctic areas are included in subzone C (Walker et al. 2005). The soil type in Finnmark and Adventsdalen is shallow leptosol or podzol and cryosol respectively (Jones et al. 2005, Jones et al. 2009). Soil with peat deposits are common on Bear Island. The amount of precipitation received decreases with latitude; for instance, coastal heaths in Finnmark, Bear Island and Adventsdalen receive 650 mm yr^{-1}, 371 mm yr^{-1} and 210 mm yr^{-1} of precipitation respectively.

Figure 2.4: Photos of sampling areas. (a) Heaths on (Plot No. 7, 109 m a.s.l.) at site Hammerfest, (b) Heaths on Bear Island (Plot No. 26, 17 m a.s.l.) and (c) Heaths on Svalbard (Plot No. 32, 25 m a.s.l)

Paper IV:

Sampling was carried out on mountain summits above treeline in treeless areas, so as to include the Scandinavian mountain range where the forest limits reach their highest elevations along a latitudinal gradient from 59 °N to 71 °N. The elevation above the forest limit varied between 60 and 805 m. Total 19 summits were sampled with 2 - 4 plots established on each summit. The selected summits lie along an inland transect where the climate is mostly weakly oceanic (Moen 1999), except for some of the northernmost summits. On each summit, annual precipitation along the north-south transect varies mostly between 1000 and 1500 mm yr^{-1}.

Figure 2.5: Photos of sampling areas. (a) Mountain summit Solvågtind (Plot No. 10 (a-d), > 1500 m a.s.l.) in North Norway and (b) Nordre Knutshø summit in central Norway (Plot no 5a, 1688 m a.s.l.)

2.2 Data Collection

2.2.1 Vegetation data (Paper I-IV)

Random sampling method was chosen for vegetation data collection. Ground vegetation data was collected by establishing a 2 x 2 m quadrat in homogenous vegetation refer Figure 2.6. All the vascular plants and cryptogams were identified and their abundance was recorded as percentage cover. The nomenclature follows Lid and Lid (2005) for vascular plants; and cryptogams were identified according to Frisvoll et al. (1995) and Holien and Tønsberg (2006). In case of sampling of vegetation plots for Paper II, in birch forests, forest limits and treelines ecotones, additional data on three-layer analysis was conducted for each quadrat which included canopy cover of *Betula pubescens* (%), combined dwarf shrub, herb, pteridophyte and graminoid cover (%) and bryophyte cover (%).

Figure 2.6: Field layer vegetation plot sampling in (a) treeless coastal area in Sørøya, Finnmark (Paper III, Plot No. 2, 188 m a.s.l.) and (b) in birch forest limits in Kvalsund, Finnmark (Paper II, Plot No. 5, 79 m a.s.l.)

2.2.2 Air and soil temperature (Paper I-IV)

Soil temperature was measured with a LogTag TRIX 8 temperature data logger (LogTag recorders limited, Auckland, New Zealand) buried at a depth of 10 cm in topsoil layer. Air temperature was inferred for each plot at 2 m above ground, from the 1 km^2 resolution gridded data of the Norwegian Meteorological Department. Air and soil temperatures were logged daily at 01:00 and 13:00 in order to obtain a measure of daily average temperatures respectively. The variables with their units of measurement are presented in Table *2*

Table 2: Overview of soil and air temperature variables, with abbreviations and measurement units used in the context of this study. In each plot, the following variables were estimated. (Note: Variables Avg, Avg(July), Avg(Jan) and GSL were calculated for air and soil temperatures and will be followed by (A) and (S) respectively in further analysis for e.g. Avg(A) for average annual air temperatures).

Abbreviation	Meaning and definition
Avg	Average annual temperature (°C).
Avg(Jul)	Average July temperature (°C).
Avg(Jan)	Average January temperature (°C).
GSST	Average soil temperature during the growing season (°C).
GSAT	Average air temperature during the growing season (°C).
STHS/ATHS	Heat sum for soil and air, respectively: sum of all daily average soil and air temperatures ≥ 5 °C respectively, measured throughout the study period (degree days (dd))
STFS/ATFS	Frost sum for soil and air, respectively: sum of all daily average soil and air temperatures ≤ 0 °C respectively, measured throughout the study period. (degree days (dd))
SGS	Start of growing season: measured as the day of the year when soil temperature rose to 5 °C for five consecutive days.
GSL	Growing season length: measured as the number of days between SGS and the day of the year when temperature (air and soil temperature) dropped below 5 °C during autumn.
Smelt	Snowmelt: day of the year on which soil temperature rose to ≥ 1°C
ThD	Thaw days: measured as number of days between snowmelt (Smelt) and start of growing season (SGS) (days).
SF	Soil frozen period: number of days when soil temperature was ≤ 0 °C (days).

2.2.3 Soil properties (Paper II and III)

Soil was sampled from the four corners of the vegetation plot to a depth of 5 cm in the topsoil using a 7 cm diameter steel cylinder. Samples were collected from the four corners of each quadrat and were homogenized, air dried, ground and passed through a 2 mm sieve to remove coarse materials. Extractable plant available phosphorus (P), calcium (Ca), magnesium (Mg) and potassium (K) were determined using the ammonium lactate method (Egnér et al. 1960). Soil organic matter (OM) was estimated by the loss-on-ignition method (Dean 1974), bulk density (BD) by method given in Page-Dumroese and Jurgensen (1999) and soil moisture (SM) was estimated according to ASTM D 2216 − Standard Test Method for Laboratory Determination of Water (Moisture) Content of Soil.

2.2.4 Tree height, growth form and age data (Paper II)

The tree height and growth form are pivotal for defining the boundaries (e.g. treeline or forest limit) (Callaghan et al. 2002b). Tree cores were obtained from the biggest tree in the stand; for monocormic and polycormic trees (in case of polycormic tree the largest stem was cored) (Figure 2.7). In shrubby stands, the biggest specimen was selected to obtain a stem section. Cores and stem sections were collected at 50 cm above ground. Tree diameter was measured at breast height (DBH) ca. 130 cm above the ground level. One tree was sampled per stand. The cores were mounted on a wooden support and polished with a planer. The polished core was then placed under the microscope and tree rings were counted manually. This data was used to estimate age of the stand.

Figure 2.7: Tree core sampling.

2.2.5 Topography data (Paper I-IV)

Altitude, distance from sea, aspect, slope and GPS position of each plot was recorded.

2.3 Statistical analysis

2.3.1 Vegetation data analysis

In Paper I-III, same method of vegetation classification was performed using TWINSPAN (Hill and Šmilauer 2005), which classifies samples and species hierarchically and produces a two way table of their occurrence. Taxa were assigned to pseudospecies on the basis of identity and cut levels (0, 5, 10, 20, 40 and 60). Taxa with less than 2 occurrences were excluded. Species occurrence and abundance (SOA) within the selected communities identified were expressed as SOA-values (Odland et al. 1990). Canonical correspondence analysis (CCA) was used to estimate the important temperature variables explaining floristic variation. Vegetation communities isolated using TWINSPAN and the most important temperature variables from CCA analysis were used in Detrended correspondence analysis (DCA) to estimate floristic turnover of vegetation communities with environmental variables included as supplementary data.

For Paper IV, vegetation was categorised into four plant functional types: 1. pteridophytes, graminoids and herbs (PGH), 2. Dwarf shrubs (shrub), 3. Lichens (Lic) and 4. Bryophytes (Bry). PCA method was used to determine the relationship between plant functional types and temperature. RDA was used to test to what extent the total abundances of the plant functional types in each plot could be explained by temperature variables.

2.3.2 Temperature data analysis

Temperature data analysis was conducted differently for each paper.

In paper I, correlation analysis was used to determine the strength of association of temperature variables. Since the variables were highly correlated, we used PCA and then multiple regression method to analyse temperature data. Kruskal-Wallis non-parametric multi comparison test was used to find out if there existed differences in temperature conditions between the seven study areas.

In paper II, correlation analysis was used to determine the strength of association between the temperature and topography variables. Kruskal-Wallis multi-comparison test was used to estimate differences in means of temperature variables between the plots.

In paper III, regression analysis and Mann-Whitney test was used to analyse temperature data.

In paper IV, principal component analysis (PCA), Redundancy analysis (RDA) and regression was used for temperature data analysis.

2.3.3 Soil property data analysis

In Paper II, PCA analysis was used to study the variation in soil properties among plots. One-way ANOVA was used to detect significant differences in means of soil properties relative to altitude, distance to shore and distance to CRL. Kruskal-Wallis multi-comparison test was used to determine whether there were any differences in soil properties between forest and shrub plots.

In Paper III, Two-way ANOVA and One-way ANOVA was used to analyse soil property data. A post-hoc Tukey test to confirm which of the groups were significantly different from one another.

2.3.4 Tree data analysis

In paper II, correlation analysis was used to establish relationships between tree height, age and DBH.

2.3.5 Comparison of southern and northernmost birch limits

CCA with Interactive forward selection was used to estimate the important temperature variables explaining floristic variation. Vegetation communities isolated using TWINSPAN and the most important temperature variables from CCA analysis were used in DCA to estimate floristic turnover of vegetation communities with environmental variables included as supplementary data.

3 Results summary

Main aims of this thesis have been addressed in the following four papers. A few questions were answered by combining the data from two or more papers, hence, new analysis have been conducted and new results have been presented in this section.

3.1 Paper I

Vegetation, soil- and air temperature studies within alpine treeline ecotones of southern Norway

The growing season soil and air temperatures ranged from 4.5 to 10.1 °C (with an average of 7.7 °C) and 7.9 to 11.1 °C (with an average of 9.0 °C) respectively. The average growing season length for all the seven areas, calculated using air and soil temperatures was 118 ± 10 days. Average July temperatures for all study areas was 11.8 ± 1.1 °C and 10.2 ± 1.1 °C for air and soil temperatures respectively. With Kruskal-Wallis test results we established significant differences in air and soil temperature variables when tested individually among all seven study areas. Seven vegetation communities categorized by TWINSPAN analysis were: *Avenella flexuosa - Vaccinium myrtillus - Juniperus communis* (AVJ), *Sphagnum* spp. - *V. myrtillus - A. flexuosa* (SVA), *V. myrtillus - A. flexuosa - Empetrum nigrum* (VAE), *A. flexuosa - Betula nana - E. nigrum* (ABE), *Vaccinium uliginosum - E. nigrum - B. nana* (VEB), *E. nigrum - V. uliginosum - A. flexuosa* (EVA) and *A. flexuosa - B. nana – V. myrtillus* (ABV). The gradients in vegetation were explained with soil temperature frost sum (20.5 %), air temperature frost sum (7.2 %), growing season soil temperature (6.5%) and growing season length (calculated using soil temperature) (5.3 %).

The alpine treeline ecotone position in south Norway could be significantly explained by growing season length (soil temperature), growing season length (air temperature), duration of soil frozen period, soil temperature frost sum and air temperature frost sum by 35.1 %, 28.7 %, 19.7 %, 9.1 % and 7.5 % respectively. The results suggest that temperatures may not be critical for current alpine treeline ecotone altitudinal positions in oceanic areas.

3.2 Paper II

Ecological characterization of northernmost birch forests and treeline ecotones in Norway

The growing season length ranged from 107 - 132 days with an average growing season air temperature of 9.5 ± 0.5 °C. Likewise, average growing season soil temperature was 9.4 ± 0.6 °C with a growing season length of 105 - 147 days. Average July air and soil temperature were 12 ± 0.9 °C and 11.1 ± 1 °C respectively. The results showed the field layer to be dominated by *Empetrum - Cornus - Vaccinium*, *Polytrichum - Cornus* and *Cirsium - Viola* types; the gradients between these types being explained by pH (15.6 %, $p = 0.002$), July air temperatures (6.4 %, $p = 0.002$) and thaw days (4.9 %, $p = 0.024$). Based on the tree-ring data, the average age of the trees was estimated to be 11 − 77 yr. The tree height and DBH were strongly correlated ($r = 0.845$, $p < 0.001$), whereas, age of the trees showed a weaker correlation with the DBH ($r = 0.563$, $p = 0.002$) and tree height ($r = 0.653$, $p < 0.001$). A one-way ANOVA analysis, showed decrease in pH levels (df = 2, $F = 3.96$, $p = 0.036$) with increasing distance from sea in forest and scattered tree plots. Comparison of forest/scattered tree ($n = 23$) and shrubby ($n = 5$) plots, using Kruskal-Wallis multi comparison test showed significant results only for potassium concentration (df = 1, $p = 0.02$). Elevated levels of calcium were evident in some of the study plots. The overall temperature conditions in present study were warmer than in other such northern limit of birch forests.

3.3 Paper III

Bioclimatic gradients and soil properties of coastal heaths from North Norway to Spitsbergen (Svalbard)

Air and soil temperatures conditions decrease with latitude i.e. from Finnmark to Adventsdalen, with Bear Island in the intermediate position. Vegetation analysis using TWINSPAN classification, identified five vegetation communities, two on Adventsdalen and three in Finnmark and established a clear vegetation difference between the two areas which could be explained by maximum average air temperature (17.2 %, $p = 0.002$), soil temperature frost sum (7.3 %, $p = 0.002$), growing season length calculated using air temperature (6.5 %, $p = 0.002$), soil moisture (5.4 %, $p = 0.002$) and air temperature frost sum (4.3 %, $p = 0.006$). The five vegetation communities were *Salix herbacea* - *Carex bigelowii* (SC) (snowbed); *E. nigrum* - *S. herbacea* (ES); *E. nigrum* - *B. nana* - *Ptilidium ciliare* (EBP); *D. octopetala* - *C. tetragona* - *Poa arctica* (DCP) and *Alopecurus magellanicus* - *Sanionia uncinata* (AS). Mann-Whitney test results suggested that in Finnmark, medians of soil property values were similar for plots north and south of treeline at both high and low altitudes. In Finnmark, heath communities north and south of the treeline were not distinguishable in terms floristic composition, air temperature, soil temperature or soil properties neither there was any clear distinction between high and low-altitude plots.

3.4 Paper IV

Relationships between vegetation, air and soil temperatures on Norwegian mountain summits

Average July air- and soil- temperature ranged from 6.7 - 11 °C and 5.4 - 11.6 °C respectively. All air and soil temperature variables were significantly correlated, but the rate of explanation was mostly relatively low (37 - 60 %), except during the growing season. Start of the growing season, determined by air or soil temperatures, could deviate by 38 days mainly due to effects of frozen soils. Vegetation were categorized in to four functional groups 1. Pteridophytes, graminoids and herbs, 2. Dwarf shrubs, 3. Lichens and 4. Bryophytes. PCA was used to extract most important temperature variables which could explain the vegetation composition. PCA axis 1, was correlated with high soil temperature variables such as average annual soil temperatures, July soil temperatures and soil temperature heat sum. Vegetation composition, especially the lichen cover, had a major impact on soil temperature, and dwarf-shrub cover increased significantly with increasing July temperature. Lichen abundance and degree of soil frost were strongly correlated, and explained a major part of the variation in soil temperatures. RDA results suggests that average annual soil temperature (15.4 %), growing season length (calculated using soil temperature)(14.3 %) and soil temperature heat sum (5.6 %) were significant in explaining total abundances of plant functional types in each plot. The study indicates that air temperature is generally a poor proxy for soil temperature in cold areas, except during July.

3.5 Ecological differences between the coastal southern and northern birch limits

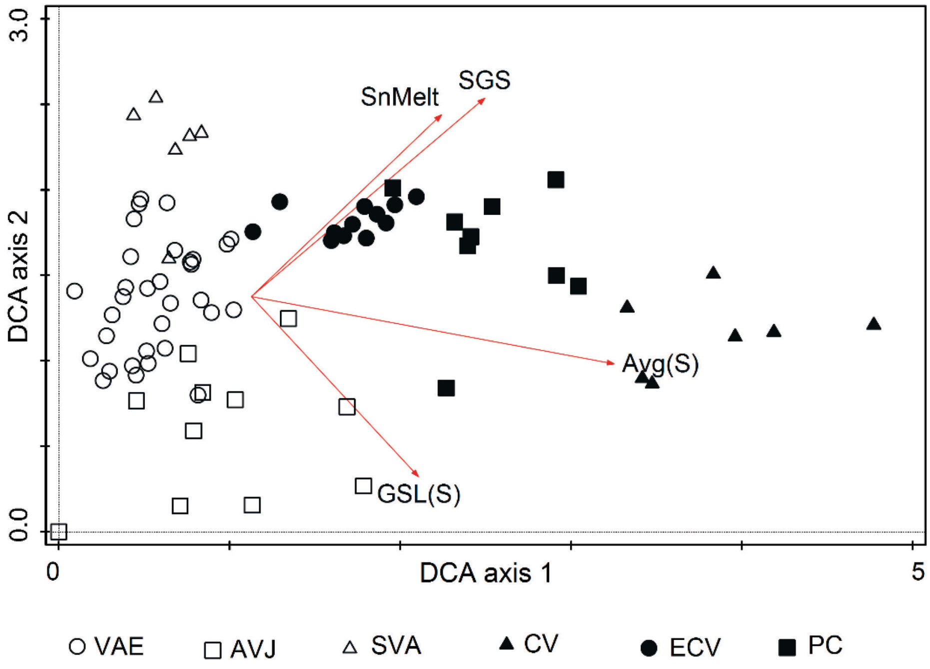

Figure 3.1 DCA diagram of relative plot positions based on vegetation groups (classified by TWINSPAN) and significant temperature variables (obtained from CCA-Interactive forward selection analysis). The vegetation communities dominant in the southern Norway alpine treeline ecotones are *Vaccinium myrtillus - Avenella flexuosa - Empetrum nigrum* (VAE), *Avenella flexuosa -Vaccinium myrtillus - Juniperus communis* (AVJ) and *Sphagnum spp. - Vaccinium myrtillus - Avenella flexuosa* (SVA). The vegetation communities dominant in northern Norway birch occurrences are *Cirsium - Viola* type (CV), *Empetrum - Cornus - Vaccinium* type (ECV) and *Polytrichum - Cornus* type (PC). (Total variation = 3.78). Temperature variables along with units of measurement are explained in Table 2.

CCA (with interactive forward selection) was conducted using vegetation and temperature data for coastal birch limit plots from southern and northernmost Norway. Total variation of 3.78 with the explanatory variables accounting for 14.6 % of variation. The eigenvalues and explained variation for axis 1 and 2 were 0.328/8.69 and 0.103/11.41 respectively. The forward selection results show start of growing season (SGS) to be most significant factor explaining 4.5 % (p = 0.002), closely followed by average annual soil temperature (Avg (S)) explaining 4.4 % (p = 0.002), followed by growing season length (GSL(S)) (3.5 %, p = 0.002) and snow melt day (2.2 %, p = 0.008). DCA diagram (Figure 3.1) shows distribution of plots belonging to 6 vegetation groups derived from TWINSPAN analysis and most significant environmental variables extracted from CCA. The vegetation types are fairly well separated on DCA axis 1. The gradient length and eigenvalues for DCA axis 1 and 2 were 4.77/0.643 and 2.54/0.239 respectively. The main gradient in vegetation i.e. DCA axis 1 separated plots with high soil temperature variables i.e. north Norway plots from south Norway plots. On DCA axis 2, plots with late snowmelt day and start of growing season were located towards upper part of DCA diagram. From Table *3* and Figure 3.1, we see that the values of calculated temperature parameters is slightly higher in northern birch limits as compared to southern birch limits.

Table 3: Average temperature variables from southern and northernmost birch occurrences in Norway. Standard deviation values are written in brackets. Temperature variables along with units of measurement are explained in Table 2

Variables	**Units**	**Suldal**	**Kvam**	**Finnmark**
Avg (S)	(°C)	2.6 (0.5)	3.5 (0.4)	3.9(0.4)
GSST	(°C)	6.3 (0.5)	8.6 (0.6)	9.4(0.6)
GSL(S)	(days)	133 (12)	123 (8)	128.7(10.9)
Avg(Jul)(S)	(°C)	11.4 (0.5)	10.8 (0.7)	11.1(1.0)
STHS	(degree days)	805 (110)	1143 (127)	1202.3(153.3)
STFS	(degree days)	-141 (133)	-45 (59)	-217.4(60.7)
SF	(days)	178 (12)	183 (11)	173.9(41.7)
SnMelt	(DOY)	135 (6)	139 (4)	147.6(11.5)
ThD(S)	(days)	9 (7)	7 (6)	7.4(5.8)
SGS	(DOY)	144 (7)	147 (6)	155.0(9.8)
Avg (A)	(°C)	1.8 (0.6)	3.0 (1.1)	2.5(0.7)
GSAT	(°C)	8.6 (0.5)	9.3 (0.9)	9.6(0.5)
GSL (A)	(days)	127 (10)	140 (20)	118.9(5.9)
Avg(Jul)(A)	(°C)	11.4 (0.7)	12.3 (1.3)	12.0(0.9)
ATHS	(degree days)	1212 (136)	1421 (274)	1230.5(90.1)
ATFS	(degree days)	-763 (66)	-544 (140)	-524.8(156.9)

4 Discussion

Here we will discuss the methodological considerations and results in relation to the main aims of the thesis.

4.1 Methodological considerations

We faced several challenges while selecting study areas, sampling techniques and data analysis methods due to the complexity of these ecosystems (treeline ecotones, alpine and Arctic), topography and environmental conditions related to it. Treelines and forest limits are rarely strict lines, they usually are transitions from tree to shrub forms. Major complications arise due to usage of different criteria World-wide in defining these ecosystems; especially treeline ecotones, as there are no universally accepted definitions to define forest limit and treeline (Jobbágy and Jackson 2000, Callaghan et al. 2002b, Körner 2012, Chiu et al. 2014). According to Körner (2012), terminologies like treeline are approximations, and defining them precisely does not matter as long as the terms are consistently used. Mainly because of large species diversity and environmental conditions at elevational limit of tree growth, it is impossible to narrow down to a single definition to cover all circumstances (Daubenmire 1954, Tuhkanen 1993, Walsh et al. 2003). Unlike Körner (2003), we have defined the upper limit of the ecotone to the treeline and not at the tree species line.

Another concern involved selection of particular method to measure temperatures at the forest limits, treelines and within the treeline ecotone (Körner 2012). For instance, few researchers prefer measuring temperature using midpoint of the treeline ecotone while others prefer data collection at an elevational gradient from forest limit to treeline (Daubenmire 1954). Some researchers on the other hand prefer collecting average temperature data from several locations between the uppermost limits of trees and forest limit. In this study, we chose to measure temperature at forest limits, treelines and within the ecotone by random sampling method. In this study, soil temperature is measured at 10 cm depth in the top soil layer because this is the rooting zone of the vascular plants and most commonly used criteria (Körner and Paulsen 2004).

After obtaining temperature data, the main concern was the treatment of this data to obtain temperature variables which describe growing season length, growing season temperature, heat sum, warmest month temperature, etc. The threshold used for defining these temperature variables have varied in several studies as there is no universally accepted threshold for defining these variables. As discussed in Körner (2012), temperature thresholds are mostly approximations because zero activity in certain cases may be achieved abruptly or gradually. This causes complications in selection of a particular temperature threshold. Several methods used in the measurement of data and their analysis have added complexity and rendered data incomparable to the existing studies.

To maintain consistency in the entire study, a threshold of 5 °C was chosen to mark the beginning of the growing season as there is very little biological activity below this temperature (Karlsson and Nordell 1996). Another reason for choosing this 5 °C threshold is because it is commonly used in the literature (Körner 1998a, Skaugen and Tveito 2004, Weijers et al. 2013).

4.2 Importance of air and soil temperatures

In general, global warming and changes in temperature conditions are most effective towards high latitudes and altitudes. Altitudinal and latitudinal gradients offer perfect scenario to study effects of climate at relatively short and long distances respectively (Graae et al. 2012). Temperature decreases with altitude and latitude, and it is one of the crucial factor that have been used in bioclimatic studies. It is challenging to identify individual effects of air and soil temperatures on vegetation owing to influence of other environmental factors such as solar radiation on temperature (Gehrig-Fasel et al. 2008). Studies involving temperature manipulations are conducted to find out the effects of varying temperatures on biotic and abiotic processes (Graae et al. 2012). Temperatures can affect photosynthesis, nutrient uptake, respiration and growth in plants (Grace 1989, Karlsson and Nordell 1996, Sveinbjörnsson et al. 2002, Holtmeier 2003, Körner 2012). Low temperatures can hinder biological activity of plants (Karlsson and Nordell 1996).

At higher latitudes, short stature vegetation is in close association with the ground thus making soil temperature an indispensable factor in vegetation studies (Graae et al. 2012). Soil temperatures have strong influence on both root growth and above ground metabolism (DeLucia 1986, Day et al. 1991, Körner 1999). Relationship between air and soil temperatures is influenced by the vegetation cover, snow layer duration and albedo (Odland and Munkejord

2008). Air temperatures are often found to be higher than soil temperatures during spring and summer, but in late summer and autumn soil temperatures are highest.

Treelines are known to be highly correlated with the temperature variables among all environmental variables (Grace 1989, Körner 1998b, Aune et al. 2011a). Environmental conditions are unfavorable above treelines, limiting tree growth at higher altitudes and latitudes resulting in formation of alpine and polar treelines. The mean growing season air temperature from treelines of Swiss Alps ranged from 8 - 8.8 °C (Gehrig-Fasel et al. 2008). Temperature effects trees by having negative influence on normal growth of trees leading to limiting tree growth at high altitudes. Above treelines, we do find scattered tree seedlings growing, however, these tree seedlings rarely grow to form trees (Körner 1998a). According to Karlsson and Weih (2001), mean growing season soil temperature of 12 °C is required for seedling establishment. Consequently, high elevation occurrences of high trees devoid of seedlings may indicate that these were established during previous warm periods. Temperature data from southern and northernmost forests in Norway suggests that these forest limits do not coincide with the 10 °C isotherm as the temperature condition during study period are higher than this value. The sub-Arctic birch forest limit in Northern Sweden (at 680 m) and the Arctic treeline in Siberia have mean temperature of 10.5 °C and 11.2 °C during the warmest month respectively (Körner 1998a).

Trees found at the treeline experience temperatures closer to ambient air temperature, whereas, heath vegetation communities above treeline experience warmer climate due to temperature decoupling by the canopy (Grace 1989, Körner 1998a, Körner et al. 2011, Körner 2012). Cold adapted plants are resistant to low temperature extremes. Aerodynamic decoupling by shrubs helps in maintaining warmer temperatures than surrounding air temperatures; and creating their own microclimate thus causing these dwarf shrubs to survive at high elevations (Grace 1989). Negligible plant growth is observed between temperature range of 0 - 5 °C in vascular plants, hence temperature of 5 - 6 °C is termed as zero point of plant growth and development (Körner 2016).

4.3 Ecological conditions in alpine treeline ecotones of southern Norway

Growing season temperatures reported in southern alpine treeline ecotones were higher than those reported in Körner and Paulsen (2004). This discrepancy can be explained by the low threshold values of 3.2 °C used by Körner for estimation of the growing season length. The growing season lengths in our study decreased from the coastal areas (123 - 140 days) to inland areas (106 - 114 days). Growing season lengths between 100 - 150 days have been reported for alpine treelines (Holtmeier 2003, Körner and Paulsen 2004, Odland 2011). Average growing season temperatures are lower in our studied southern treeline ecotones when compared with other such alpine treeline ecotones. In current study, all treeline ecotones showed average July temperature higher than 10 °C. It should however, also be taken into account that temperatures during the actual study periods were higher than during the normal period.

In this study, seven vegetation communities were identified and their differences were significantly explained by soil temperature heat sum, air temperature frost sum, growing season soil temperature and growing season length. This was mainly related to the differences in oceanic and the continental areas. Our results indicate that growing season length (calculated based on air and soil temperature), soil frozen days, air temperature frost sum and soil temperature frost sum provide best explanation for the current alpine treeline ecotone position.

Our results suggested that temperature conditions within the ATEs were the warmest along the coasts and decreased toward inland areas. Particularly, high air and soil temperature heat sums, longer growing season lengths and high temperatures were observed in coastal areas. This indicate that alpine treeline ecotones have not reached their potential temperature limit. This may party be an effect of relative low mountain height, influence from the ocean, or both; indicating that alpine treeline ecotones are hardly climatically limited in oceanic areas i.e. Kvam and Suldal.

4.4 Ecology of northernmost birch forests. Do we have climatic treelines in northernmost Norway?

The tundra - taiga interface is one of the largest vegetation transition zone spread across the globe for more than 13,400 km, separating the boreal and Arctic biomes (Callaghan et al. 2002b). This transition zone occupies around 5 % of total vegetated landmass in Northern hemisphere (Harding et al. 2002). Along the interface, changes occur in tree distribution and vegetation communities along with variation in temperature, precipitation and snow depth and duration (Callaghan et al. 2002b). This transitional boundary is associated with a mean July soil temperature of 7 °C at a depth of 10 cm (Körner 1998a).

The northernmost birch occurrences in Finnmark have been a topic of debate since decades, however, not many ecological studies have been reported for the birch distribution limits. It is very difficult to distinguish between Arctic and alpine treelines in certain regions (Jobbágy and Jackson 2000). According to Salisbury and Ross (1992), when temperatures are concerned latitude compensates for altitude, for instance treeline elevation decreases by roughly 78 ± 10 m latitude^{-1} (Odland 2015).

The mountain heights in Finnmark are low and forest stands were found up to 207 m a.s.l. Most of the forest stands were found growing in sheltered sites protected from strong winds. Monocormic and Polycormic forms including multi-stemmed trees up to 10 m and multi-stemmed individuals 1.5 - 2 m were commonly found in our study area. Stands with average height of 6 m and age ca. 11 - 70 yr were common in our study area. High tree ages found in this study indicate that there hardly have been any recent northward advance of birch forests since last century. Tree age estimated from tree rings in Finnmark is high as compared to tree age from other such transitional zones from northernmost Europe (Kullman 1979, Sonesson and Hoogesteger 1983, Jónsson 2004).

Three major floristic communities were identified *Empetrum - Cornus - Vaccinium* type, *Polytrichum - Cornus* type and *Cirsium - Viola* type. In the current study, *Empetrum - Cornus - Vaccinium* dominated soils were slightly acidic but rich in potassium, phosphorous and organic matter. Those soils dominated by *Cirsium - Viola* type were alkaline and rich in Calcium. Plots dominant with *Polytrichum - Cornus* type had nutrient- poor soils. Soil pH decreased with increasing altitude and distance from coastline.

Average growing season length of 105 - 134 days in the northernmost birch forest limits are in the agreement with other such transitions zones (Veijola 1998, Blinova and Chmielewski 2015, Bandekar et al. 2017). Annual air temperature, growing season temperature and average July temperature in the present studied birch stands were higher than at birch limits in Abisko (north Sweden), Murmansk area, Iceland, Greenland or southern Norway (Böcher 1979, Berglund et al. 1996, Hecht et al. 2007, Wöll 2008, Aune et al. 2011b, Bandekar et al. 2017). This suggests that the northernmost birch forests are hardly climatically limited.

Birch occurrences were mostly limited to sheltered areas due to undulating rugged topography (too steep, rocky or exposed), and prevalence of strong winds in the coastal and high altitude regions in Finnmark. Another reason might be lack of land in certain areas where forest limits were close to Barents Sea. Climatic treelines have bioclimatic characterization and are used as reference lines to which other mountain biota can be related (Körner et al. 2011). Since, these forests are probably not climatically limited, they should not be used as a criterion to separate between boreal and Arctic biomes.

4.5 Vegetation, air and soil temperature comparisons between southern and northernmost birch limits in Norway

In this section, we will describe and discuss the conditions from birch limits belonging to oceanic areas in southern (Paper I) and northernmost (Paper II) Norway. Data on the northernmost limits of birch forests is rare, hence, an attempt is made to compare the environmental conditions and explain how they vary from southern birch forests. As discussed earlier separation of northernmost birch treelines in to Arctic or alpine treelines is difficult, hence, we have just averaged the temperature conditions for all sampling plots.

In alpine treeline ecotones of south Norway (Paper I), the floristic variation in ground vegetation communities was small and dominated by the oligotrophic and mesotrophic boreal species. In the northernmost limit of birch forests (Paper II), there was a large vegetation variation, with species characteristic for both moist eutrophic soils and shrub-dominated oligotrophic heath vegetation. From the results it was clear that dominant dwarf vegetation communities in Paper I and II were different from each other. The vegetation in northern Norway in general was characterized by higher soil temperature conditions as compared to southern Norway.

According to the results of Körner and Paulsen (2004), mean growing season soil temperature in the sub-Arctic boreal and boreal was 6.4 °C and 6.6 °C respectively. Similar temperature values (ca. 6.6 °C, 650 m a.s.l.) during growing season were recorded at birch treelines of northern Sweden (Karlsson and Weih 2001). A difference of 3 days in growing season length was observed between sub-Arctic boreal and boreal (Körner and Paulsen 2004) further suggesting that treelines are temperature driven and are associated with common temperature conditions. On the contrary, it was interesting to note that temperatures in the northern limits of birch forests were slightly warmer than the birch forest limits found in southern Norway (Paper I and II). The treeline ecotone in the most oceanic areas was found close to sea level although the temperatures during warmest month were greater than 10 °C. This suggests that temperatures might not be limiting factors for tree growth in these areas. This indicates that oceanic forest limit in southern Norway and northern Norway have not reached their potential climatic limits.

4.6 Comparison between ecological conditions in the coastal heaths of North Norway, Bear Island and Adventsdalen, Spitsbergen. Do we have Arctic heaths on mainland Norway?

Heath vegetation often dominates the Arctic, the boreal and alpine biomes, however, vegetation composition, air-and soil temperatures, and soil conditions can be highly different. An important criteria for separation of the Arctic biome from the Boreal and Alpine biomes is the extensive permafrost distribution in Arctic. Permafrost cover is continuous in Arctic and it decreases or becomes discontinuous as we move south (Brown et al. 1998). During summer, the top active layers of permafrost thaw in Arctic leaving the ground soggy (in flat terrain) while the alpine soils are better drained. This can particularly explain high soil moisture values at high latitudes and altitudes. Warming during growing season will cause soil moisture in alpine areas to decrease while in Arctic areas it is predicted to increase (Xu et al. 2013b).

Studies such as Young (1971) and Karlsen et al. (2005) suggests vegetation based methods can be used for mapping local climatic conditions and vice versa. Heaths north of treeline on mainland Norway were different from their Arctic counterparts on Bear Island and Adventsdalen (Spitsbergen). According to (Eurola 1974), in Fennoscandia Arctic vegetation is commonly found on calcareous substrates. This can be possibly explained by the presence of acidophilous communities dominant on mainland Norway and calciphilous communities dominant on Adventsdalen.

In our study, high calcium concentrations were recorded at low elevation plots in Adventsdalen, this can partly explain the dominance of calciphilous vegetation. Soil organic matter content was thrice as much higher in Finnmark as compared to Adventsdalen. Decrease in potassium, magnesium, phosphorous, soil moisture, bulk density and organic matter content with increase in altitude could have occurred due to high frost sum values and large number of days with frozen soil at high altitudes. Soil chemical properties are similar in both the vegetation zones on Mainland Norway.

Temperature conditions varied with latitude with differences being more prominent at high elevations as compared to low elevations. Bear Island, allocated to the Arctic subzone C, lies in an intermediate position in terms of temperature variables as opposed to Adventsdalen, which is also allocated to the Arctic subzone C. The average July air temperatures from our study in Subzone E, Bear Island and Adventsdalen are in range of previously measured temperatures in Walker et al. (2005).

Earlier studies have excluded heaths north of treeline in Norway and Kola Peninsula from the Arctic zone due to the dominance of large number of southern (boreal) species in this zone (Ahti et al. 1968, Aleksandrova 1980, Tuhkanen 1984, Yurtsev 1994). According to Hustich

(1960), areas not defined by temperature - limited forest limit have been described as "pseudo tundra" or "pseudo-Arctic". Pseudo- Arctic vegetation in Scandinavia, Iceland and Greenland has physiognomic appearance of tundra but it should be included in the boreal zone. Nowhere in Fennoscandia is there truly regional Arctic vegetation at sea level, and that the oceanic sea-level heaths largely belong to mainly wooded northern boreal zone (Ahti et al. 1968, Eurola 1974, Böcher 1979, Haapasaari 1988).

Our main question here is do heath vegetation north of northernmost treeline in Norway be classified as belonging to the Arctic biome? Discussions and investigations for decades, however, have led to unsettled decision on whether the treeless coastal heaths of northernmost Norway are Arctic or not (Sjörs 1963, Ahti et al. 1968, Eurola 1974, Hustich 1979, Elvebakk 1999). Several definitions used to define and delimit Arctic have further added to the confusion. In areas strongly influenced by oceanic climate it is very difficult to separate Arctic and boreal biomes (Elvebakk 1999). In Norway, the northernmost treeline which has been used to delimit the Arctic biome is strongly influenced by anthropogenic factors over the years (Ahti et al. 1968, Elvebakk 1999). Usage of this treeline as the main factor to delimit Arctic regions might not be satisfactory. As can be seen from our earlier results this northernmost treeline is not climatically limited (Paper II), thus making it an unreliable criteria to define transition between Arctic and boreal biome.

Studies such as (Walker et al. 2005) have shown temperature conditions and vegetation characteristics as the main criteria to categories vegetation zones. If these two variables are to be used as sole criteria then our results suggests that the heaths south – and north of treeline should not be treated as separate zones as they have fairly similar vegetation, growing season temperature, growing season length and heat sums based on both air and soil temperature. The soil properties also remain unchanged south of and north of treeline. Therefore, it is not ecologically justifiable to separate these heaths in to different biomes.

4.7 Variation in temperature conditions from south to north Norway at mountain summits. Can air temperatures be used as a proxy to soil temperatures?

Studies involving air and soil temperature decoupling at alpine and Arctic communities are gaining importance (Körner 2003, 2007, Scherrer and Körner 2010). Soil temperatures on these remote mountain summits are rarely being included in the earlier literature.

Usually, air temperatures are used as a proxy to determine soil temperatures, but recent studies have shown that soil surface temperature can have remarkable fine-scale variation, with temperature differing by several degrees over distances less than one meter (Scherrer and Körner 2010, Wundram et al. 2010, Graham et al. 2012, Suvanto et al. 2014). Although, soil temperatures closely follow variation in air temperature with a delay of 3 - 4 hours (at 10 cm depth); air temperatures used in the estimation of soil temperature are usually obtained from the gridded temperature data sets often ranging at spatial resolution of Kilometres square while ecological processes vary at scales of mm to meters (Körner and Paulsen 2004, Graae et al. 2012). Question remains how precisely we can estimate soil temperatures from air temperatures? Few studies such as Toy et al. (1978), Brown et al. (2000), Gehrig-Fasel et al. (2008) have managed to successfully estimate soil temperatures from air temperatures; however, each study has its own limitations and drawbacks.

Temperature is well correlated and decreases with altitude (Graae et al. 2012). At low elevations, the ground vegetation is often tall and dense and this effects relationship between air and soil temperature whereas, at high elevations vegetation density and cover decreases leaving patches of bare area. Graae et al. (2012) and references therein suggest how large climatic differences over short areas are observed due to changes in topography, wind, precipitation, surface hydrology and shade. The temperature condition at or below soil surface are critical for the dwarf shrub vegetation (Körner 2003, Graae et al. 2012). Temperature patterns in our study areas varied with the functional vegetation type, season, altitudinal and latitudinal gradient. It is therefore of interest to study to what degree air temperature variables are a useful proxy for soil temperature variables. In this study, the air and soil temperatures coupled well during the growing season. It has previously been shown that mean monthly air temperatures measured at 1.5 - 2 m above soil surface may be 5 °C colder and 10 °C warmer at soil surface (Graae et al. 2012). The mean annual air temperatures on the other hand are 3.8 lower and 1.6 higher than the soil temperatures (Graae et al. 2012).

Climate change has resulted in decrease in abundance of lichens and increased abundance of shrubs (Hallinger et al. 2010, Aalto et al. 2013). Lichens are usually associated with low soil temperatures. Although snow cover and duration was not measured in this study, we can roughly estimate the duration using measured soil temperature data. In current study, soil temperatures are much higher than air temperature values during winter suggesting presence of insulating snow cover. It takes a lot of energy to melt a wet frozen soil and a long period with frost to freeze wet soil.

PFTs are system used by climatologists to classify plants according to their physical, phylogenetic and phenological characteristics as part of an overall effort to develop a vegetation model for use in terrestrial studies and climate models (Smith et al. 1997). The dwarf shrubs are mostly ericoid, with evergreen leaves (except *B. nana* and *V. uliginosum*). This group is associated with relatively high air and soil temperatures, and is strongly negatively associated with low air and soil temperatures (Sundstøl and Odland 2017). This is also consistent with the ongoing global warming, which has been shown to result in an increase in shrub cover in both Arctic and alpine areas (Sturm et al. 2001, Hallinger et al. 2010). In this study, we observed that shrubs were well correlated with relatively high July air temperatures and lichens on the other hand were correlated with soil frost. Lichens and bryophytes are generally known to reduce soil temperatures due to high reflectivity and low thermal conductivity (Kershaw 1985, Gold et al. 2001, Porada et al. 2016). Lichen heaths have also previously been found to be associated with long periods of frozen soils (Odland and Munkejord 2008).

5 Conclusions

Based on vegetation analysis combined with data on air and soil temperatures from different parts of Norway, Bear Island and Spitsbergen, we have reached following conclusions:

- In alpine treeline ecotones of southern Norway, high soil and air temperature conditions were recorded in coastal areas, with longer growing season lengths and higher temperature variables compared to continental sites. Based on temperature comparisons, all the seven areas were significantly different from each other. Elevation of alpine treeline ecotone could be explained by the temperature variables such as growing season length (calculated using air and soil temperature), soil frozen period, air- and soil- temperature frost sum.
- In studied northernmost birch occurrences there was no difference in temperature condition and soil properties between forests, scattered trees and shrubby stands (with an exception of potassium concentration). The northernmost forests are probably not limited by temperature conditions but more likely limited by strong wind, topography and absence of land further north.
- The overall average temperature conditions in northernmost birch occurrences were slightly warmer than alpine treeline ecotones in the oceanic areas in southern Norway.
- Data on vegetation, soil temperatures, air temperatures and soil properties from heath vegetation communities both from heaths north and south of the treeline were not significantly different and consequently it would not be ecologically justifiable to separate them into different biomes. Temperature condition decrease with latitude both at high and low elevations. In terms of temperature, Bear Island lies in an intermediate position between Finnmark and Spitsbergen. Heath vegetation plots from Finnmark and Adventsdalen (Spitsbergen) were significantly different in terms of soil properties, growing season air temperature and soil frost.
- Soil temperatures can be highly influenced by the surface vegetation composition. A lichen vegetation cover is associated with low soil temperatures. Air and soil temperatures were strongly coupled during growing season and weakly coupled during the winter. In alpine areas, soil temperatures should not be extrapolated from air temperature data during the winter.

6 Future perspectives

Global warming is a phenomenon that is causing the temperatures to increase, this increase in temperature is more prominent at high latitudes (Aune et al. 2011a). According to (Skaugen and Tveito 2004), Norway is predicted to have a 200 - 300 dd (calculated based on 5 °C threshold) increase in temperature for period 2012 - 50. According to Callaghan et al. (2002b) and references therein the temperature in the Arctic has increased by 2 - 4 °C in summer and 1 - 5 °C in winter. Increase in temperature may lead to advance or retreat of treelines (Callaghan et al. 2002b, Aune et al. 2011a). Treelines are assumed to be reflection of past climatic conditions and are changing over time. Given the unpredictable response of the treelines, the effects of warming will most likely cause changes in the alpine and Arctic areas. Species extinction, habitat loss and competition from other species especially the southern species are a few of the consequences that alpine and Arctic plant species might face (Sala et al. 2000, Birks 2008, Elmhagen et al. 2015).

This thesis includes studies about the sensitive treeline ecotones from south Norway (Paper I), Paper II, III and IV are studies from under- represented areas of Norway and will contribute to deepen the understanding of these complex ecosystems. Detailed data on dominant vegetation communities, air- and soil- temperature conditions, tree ring data (Paper II) and soil properties (Paper II and III) have been given in this study. Since, the climate change can bring about multiple changes in these ecosystems we need to document current distribution and environmental conditions to understand the future dynamics. This study can further be extended by monitoring these sensitive ecosystems, collecting longer temperature datasets and including more environmental variables for a thorough understanding of these ecosystems and how they will react to changes in temperature.

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Paper I

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Vegetation, soil- and air temperature studies within alpine treeline ecotones of southern Norway

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Abstract. The alpine treeline ecotone (ATE) is the transition zone between closed forest and the treeless alpine zone. The main objective of this study is to investigate air and soil temperatures within the ATE from seven different areas which have previously been described to be climatically limited. The study areas include a gradient in oceanity, wherein forest limits have been mapped to vary from below 800 m to higher than 1,100 m. In the ATE, soil temperatures were measured using data loggers at a depth of 10 cm in the top soil layer and gridded air temperatures (2 m above ground) were obtained from the Norwegian Meteorological Institute. The Kruskal-Wallis test showed statistically significant differences between the study areas, with higher summer temperature values in the oceanic influenced areas. Seven vegetation communities were categorized by TWINSPAN analysis and gradients in vegetation were explained using the soil- and air- temperature frost sum, growing season soil temperature and growing season length (calculated using soil temperature). The current ATE position could be explained by growing season length (air and soil temperature), temperature frost sum, and duration of the frozen soil period. The results suggest that temperatures may not be critical for current ATE altitudinal positions in oceanic areas.

Key words: Betula pubescens, growing season length, growing season temperature, heat sum, July temperature, vegetation communities

Introduction

Treelines are one of the most visible distribution limits in nature, appearing as a distinct line from a distance. However, when observed closely, there is usually a gradual transition from the uppermost limit of closed forests (forest limit) to the edge of scattered single/groups of trees (treeline) and to the treeless alpine zone (Ching-An *et al.* 2014; Körner and Paulsen 2004). This transition zone is often referred as the alpine treeline ecotone (ATE) (Kullman 2012; van der Maarel 1990).

ATE is spread over the world from the equator to high latitudes, at different elevations. The vast number of definitions proposed (Holtmeier 2003; le Roux 2009) indicate that such limits are in most cases spatially complex and represent a continuum of variation due to several environmental factors. Consequently, the vertical extension of ATE can be variable when different areas are compared (Broll *et al.* 2007; Heiskanen 2006; Holtmeier 2003). Slope angle and aspect have fundamental effects on the amount of radiation received and temperature conditions in ATE (Barry 1992). In general, south-facing slopes receive far more direct radiation than north-facing slopes (Barry 1992; Larcher and Wagner 2010). Thus, ATE is often forced at lower elevations on north facing slopes and it may therefore be assumed that the temperature conditions within the ATE on south and north-facing slopes should be equal despite occurring at different elevations.

It has previously been assumed that ATE has a bioclimatic characterization and can therefore be used as a reference for altitudinal positions of other spatial data. (Holtmeier 2003; Jobbágy and Jackson 2000; Nagy 2006; Paulsen and Körner 2014). The ATE has also been assumed to be sensitive to effects of climate change (Cairns *et al.* 2007; Körner 2012; Paulsen *et al.* 2000). Several studies have been performed to find general causal relationships for the treeline ecotone altitudinal limits on local and global scales (Aas and Faarlund 2000; Holtmeier 2003; Körner and Paulsen 2004; Müller *et al.* 2016). Factors including air temperature, soil temperature, mountain elevation, snow layer duration, edaphic factors, wind, latitude, slope, aspect, precipitation and degree of continentality have all been used to explain controlling effects on ATE (Elliott and Cowell 2015; Fang *et al.* 2014; Fang *et al.* 2012; Grace 1989; Kjällgren and Kullman 1998; Körner and Paulsen 2004; Müller *et al.* 2016; Paulsen and Körner 2014; Wöll 2008; Zhao *et al.* 2015; Zhao *et al.* 2014). Equally important is the influence of grazing, insect infestation and land-use in regulating the distribution of trees at high elevations (Cairns *et al.* 2007; Cairns and Moen 2004; Hecht *et al.* 2007; Tenow *et al.* 2007).

Among all, air and soil temperatures have been assumed to be the most important abiotic factors determining ATE altitude both in Scandinavia and globally (Holtmeier 2003; Körner and Paulsen 2004;

Moen *et al.* 2008; Müller *et al.* 2016). The slowing of tree growth that occurs with an increase in altitude has mostly been explained in terms of length of the growing season, growing season temperature and snow layer duration (Heikkinen 2005; Karlsson and Weih 2001; Körner and Paulsen 2004; Müller *et al.* 2016; Paulsen *et al.* 2000; Wieser and Tausz 2007). The growing season is considered to be the time of the year when environmental conditions are favorable for plant growth. Changes in growing season lengths have a profound influence on species composition and ecological functioning beyond forest limits (Pudas *et al.* 2008).

South-central Norway houses one of the tallest mountain ranges in Scandinavia i.e. the Jotunheimen mountain range (2,469 m a.s.l.) and has forest limits ranging above 1,200 m a.s.l. (Dahl 1998; Heikkinen 2005; Odland 2015). These highest forest limits then decrease in all directions. Aas and Faarlund (2000) and Moen (1999) have proposed a map consisting of the highest forest limit elevations in Norway. Treelines or forest limits that we observe and measure in nature should, however be defined as empiric limits because we cannot define them as climatic until temperature measurements have been performed.

Given the importance of temperature in treeline research, this study focuses on air and soil temperature conditions within the ATE in south Norway and its relation to other ATEs. Since variation in topographical features over short distances on the Norwegian landmass have led to subsequent climatic variations, an attempt is made to explain the current ATE position using temperature variables. This study quantifies vegetation communities in ATE and attempts to find a correlation with measured temperature data. The pattern of treelines in Norway as mapped on the iso-line map (Moen 1999) describe the treelines as climatically limited, thus suggesting similar temperature conditions in these ATEs (Körner and Paulsen 2004). The main aim is to investigate whether or not the studied ATEs are climatically limited as one could assume that there should be no significant differences between the areas

Material and Methods

Study areas

This study was conducted between 59.3° N - 60.1° N in south central Norway. We selected seven areas in Norway as shown in Fig. 1 and Table 1, representing both oceanic and continental areas (vegetation sections according to Moen (1999)). The bedrock in these areas was mainly composed of gneiss, granite and quartzite; which are hard and acidic. The soils are either podzols or leptosols (Jones *et al.* 2005). To truly understand the environmental factors responsible for ATE position, treelines obviously influenced by human activities were omitted from the study. Hence, ATE which were disturbed by logging, insect infestation, mechanical disturbance (e.g. avalanche tracks), fires or land-use were omitted. All forest areas in southern Norway are, however, grazed by reindeers and other herbivores.

Data collection

Sampling plots were selected between the forest limit (tree height ≥ 3 m) and uppermost occurrences of scattered single/groups of trees (tree height ≥ 2 m) i.e. treeline, both on north and south-facing slopes (Fig. 2). Altogether 98 plots of 2 x 2 m dimension were established in homogenous vegetation within ATE. Birch (*Betula pubescens* (ssp. *czerepanovii* (N.I.Orlova) Hämet-Ahti)) is the dominant tree species at high elevation forest limits in Norway (Heikkinen 2005; Moen *et al.* 2008). In every area, we selected at least five plots on south and north facing aspects. A few data loggers were lost and as temperature data could not be recovered, these plots were omitted from study.

In homogeneous stands, vegetation plots were randomly selected. All vascular plants and cryptogams were identified, and their abundances esti-

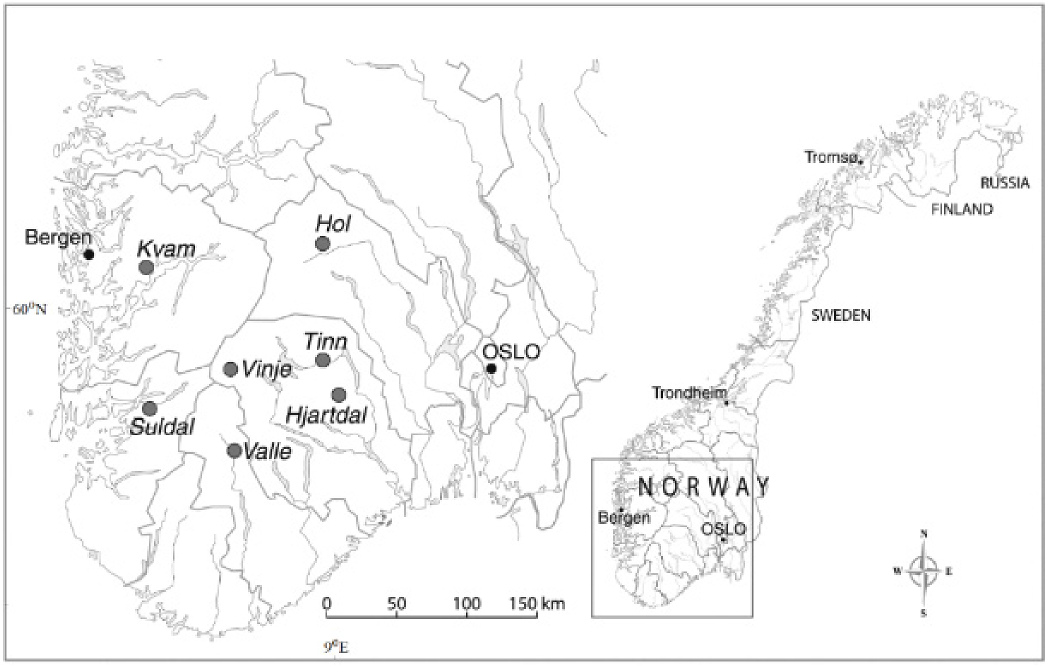

Fig. 1. Sampling areas in Southern Norway 1. Kvam, 2. Suldal, 3. Vinje, 4. Hol, 5. Tinn, 6. Hjartdal, and 7. Valle.

Area	Site description	Alt	DC	Slope	Number of plots		Diff N/S	Diff T/F	Lat	Long	P	Section**	FL
					N	S							
Suldal	Near Sandsa lake	765 ± 52	42	12 ± 11	4	4	94	36	59.4 N	6.4 E	2,299	O3	
Kvam *	Close to the Hardangerfjord	736 ± 53	47	22 ± 13	16	25	32	50	60.4 N	6.1 E	2,832	O2/O3	700-800 (Aas and Faarlund 2000)
Hjartdal	On Lifjell mountain	1,054 ± 31	162	12 ± 7	5	4	16	76	59.6 N	8.8 E	1,020	O1	1,060 (Økland and Bendiksen 1985)
Valle	Near lake Store Bjørnevatn	1,083 ± 30	96	22 ± 8	6	5	42	50	59.3 N	7.5 E	1,170	O1	1,000 -1,100 (Aas and Faarlund 2000)
Vinje	Includes two sub-areas in Vågsli and Rauland	1,065 ± 58	112	18 ± 11	5	8	68	44	59.8 N	7.6 E	1,067	OC	1,070-1,100 (Aas and Faarlund 2000; Odland and Munkejord 2008)
Hol	Near Ustevatn lake	1,097 ± 35	136	9 ± 2	4	4	51	52	60.5 N	7.9 E	747	OC	1,085 (Aas and Faarlund 2000)
Tinn	On eastern part of Hardangervidda mountain plateau.	1,124 ± 34	159	14 ± 5	4	4	55	41	60.1 N	8.5 E	795	OC	1,110 (Aas and Faarlund 2000)

*The 41 sites in the Kvam municipality represent nine different sub-areas, but due to similarities in the climatic conditions these were grouped together. **O3 = highly oceanic section, O2 = markedly oceanic section, O1 = slightly oceanic section and OC = indifferent section.

Table 1. Average characteristics of the study areas. Alt = Average altitude of the ATE in m a.s.l. ± standard deviation, DC= Distance to coastline (Km), Slope (measured in degrees) ± standard deviation, N = north facing, and S = south facing aspect, Diff N/S = average difference between the ATE on north and south facing slopes (m), Diff T/F=difference between the treeline and forest limit (m), Lat = Latitude, Long = Longitude, P = annual precipitation for normal period 1961-1990 (mm), Section = vegetation section according to Moen (1999) , FL = Forest limits (m a.s.l.) reported from previous studies.

mated as percentage cover. Distance to coastline (from the west coast of Norway) is defined as the nearest distance between sample plot and the coastline and is obtained using Arc GIS 10.4 software. GPS position, aspect, and altitude of plot have been collected using a Garmin GPS device. Slope was measured in degrees. Average precipitation for the normal period was obtained from the nearest meteorological station.

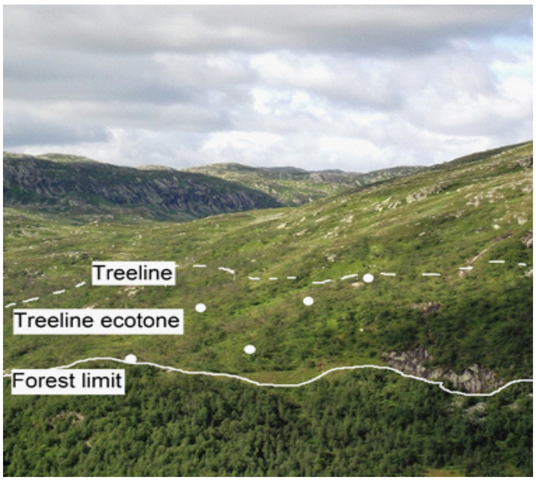

Fig. 2. Sampling plots within ATE located on the south facing aspect in Valle (59.3° N, 7.5° E). Five randomly sampled plots (2x2 m) at varying altitudes are represented in white circles.

In each plot, soil temperature was measured using data loggers, placed at a depth of 10 cm in the top soil layer. The TRIX 8 temperature data logger (LogTag recorders limited, Auckland, New Zealand) with < 0.1° C resolution for temperature ranges of -40° C to +40° C was used to measure soil temperatures. Temperature was measured twice daily at 1:00 and 13:00, and a daily average was estimated. Continuous soil temperatures were recorded from 2012 to 2013. Gridded, interpolated air temperature data was obtained from Norwegian Meteorological stations (2 m above ground), and this data was also obtained for 1:00 and 13:00 hours during 2012 to 2013.

From the daily temperature averages several temperature variables were estimated for each plot as defined in Table 2. The variables such as start of growing season (SGS) and date of snow melt (Snmelt) were calculated using day of the year (DOY) (where 1.01.2013 was taken as day 1 and 31.12.2012 as last day) to form a continuous dataset.

Statistical methods

Correlation analysis was conducted to measure the strength of association between measured temperature variables (air and soil), distance to coastline and altitude. Due to high association of predictor variables in our study, multiple regression analysis cannot be used directly to predict dependence of predictor the variable on the response variable (Abdul-Wahab *et al.* 2005; Mc-

Abbr.	Definition
Avg	Average annual temperature (° C).
Max	Maximum annual temperature (° C).
GSST	Growing season soil temperature (GSST) is defined as average soil temperature during the growing season (° C).
GSAT	Growing season air temperature (GSAT) is defined as average air temperature during the growing season (° C).
SGS	Start of growing season (SGS) given as day of the year (DOY) when temperature (air and soil) rose to 5° C for 5 consecutive days.
GSL	Growing season length (GSL) is measured as the number of days between SGS and the DOY when temperature (air and soil) dropped below 5° C.
Avg (Jul)	Average July temperature (° C).
STHS/ATHS	Soil temperature heat sum (STHS) and air temperature heat sum (ATHS) is the sum of all daily average soil and air temperatures (≥ 5° C) respectively, measured throughout the study period (Degree days (dd)).
STFS/ATFS	Soil temperature frost sum (STFS) and air temperature frost sum (ATFS) is the sum of all daily average soil and air temperatures (≤ 0° C) respectively, measured throughout the study period. (Degree days (dd)).
SF	Soil Frozen period (SF) is the number of days when soil temperature was ≤ 0° C (Days).
Snmelt	Snowmelt (Snmelt) is DOY when soil temperature exceeded 1° C.
ThD	Thaw days (ThD) is measured as number of days between snowmelt (Smelt) and start of growing season (SGS).
SWI	Summer warmth index (SWI) is the sum of mean monthly temperatures greater than > 0° C (Walker 2005; Young 1971)

Table 2. Overview of soil and air temperature variables, with abbreviations and measurement units used in the context of this study. In each plot, the following variables were estimated. (The variables Avg, Max, Avg (Jul) and GSL were calculated for air and soil temperatures and will be followed by suffix (A) and (S) respectively).

Adams *et al.* 2000). Therefore, we chose principle component analysis (PCA) to reduce errors due to multi-collinearity in further data analysis, and separated the associations to form independent principle components (Abdul-Wahab *et al.* 2005). For PCA, all the data was Log_{10} (x+5) transformed and standardized. Air and soil temperature frost sum values have been used as positive values for all analysis. A PCA was conducted using only the temperature variables; output generated from PCA were then used for two separate analysis. First, PC scores from PCA analysis were used as independent variables and ATE altitude as a dependent variable in stepwise multiple regression (also called as principle component regression (PCR)). This analysis helped in eliminating the non-significant independent/predictor variables and retaining the most important ones.

Secondly, PC loadings obtained from PCA analysis were rotated using varimax rotation. PCA analysis explains the same amount of variation before and after the varimax rotation. However, varimax rotation helps with better results interpretation as each variable tends to have high loadings on one (or few) factors (Hervé 2003). Based on the highest loading value we can select a variable on each PC to obtain information on the most important variable.

In the third step, we obtained the subset of independent or predictor variables by selecting the PCs with the highest standardized coefficient (from results of step 1), and variables associated with corresponding PCs (from results of step 2) and used these as independent variables for model fitting. The model fitting is conducted by using the above derived subset of variables as a predictor and ATE altitude as a response variable in multiple regression analysis. Finally, the multiple regression analysis generates a regression equation which could be used in prediction of ATE position. The individual contribution of each variable is calculated using standardized coefficient values, assuming all the variables together explain 100% of variation (Zhao *et al.* 2015).

The Kruskal-Wallis non-parametric multi comparison test was used to find out if differences existed in temperature conditions between the seven study areas.

Division of vegetation into communities (clusters), was achieved by using the TWINSPAN program (ter Braak and Šmilauer 2012). For the analysis, 6 cut levels were used (0, 5, 10, 20, 40 and 60) and species with less than 2 occurrences were excluded from the analysis. The relative species occurrence and abundance (SOA) values were calculated based on the formula given in Odland *et al.* (1990). A canonical correspondence analysis (CCA) with interactive forward selection (holm correction) was applied to find out which temperature variables best explained the floristic gradients. The Detrended correspondence analysis (DCA) was used to estimate the floristic turnover or compositional change along the main gradient as assessed by standard deviation (SD) units detrending by segments. The significant explanatory variables derived from CCA were included as supplementary variables. Species abundance data measured as percent cover was square-root transformed and temperature variables were Log_{10} (x+5) transformed for gradient analysis. Down-weighting of rare species was done in the CCA and DCA analysis. Bryophytes and lichens were identified to only genera level while *Betula pubescens* were selected as supplementary variables in the CCA and DCA analyses. The statistical analyses were conducted using Minitab-17 (2010), R-software (2014), WinTWIN and Canoco5 (ter Braak and Šmilauer 2012).

Results

Topography and temperature conditions at ATE

As can been seen from Fig. 3a), ATE altitude increases with increasing distance from the coastline (r = 0.886, p = 0.000). For all study areas combined, average forest limits were located at 949 m a.s.l and treelines at 977 m a.s.l. Slope inclination was steepest on south facing aspects (19° ± 13), followed by north facing aspects (16° ± 9). The altitudinal limit of ATE varied between from 603 m a.s.l in the westernmost oceanic areas to 1,177 m a.s.l. in the inland areas. Fig. 3b) shows that treelines were situated at higher altitudes on south facing aspects; average differences between north and south facing aspects are given in Table 1. The highest differences in elevation were observed in Suldal (94 m) and the lowest in Valle (16 m), and the average difference was 51 m ± 26 for all study areas. In analysis performed on combined effects of slope inclination and aspect on ATE position, no specific trends were found. The average vertical extent i.e. the difference between treeline and forest limit altitude of the ATE was 50 m ±12 (Table 1).

The average annual air temperature (1.1° C ± 2.1) was lower than the soil temperature (3.0° C ± 0.7) across all sampling areas. In all study areas, average annual air temperature recorded on south fac-

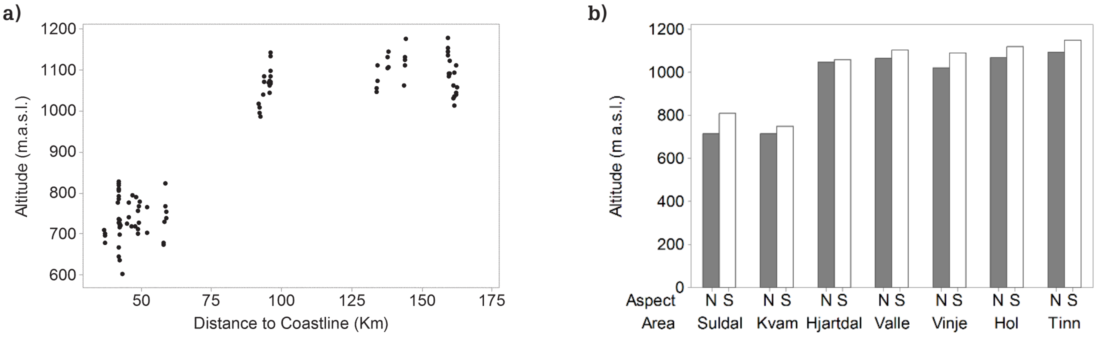

Fig. 3. a) Positions of the study plots in relation to altitude and distance to coastline. b) Bar graph showing altitudinal differences between plots on north (N) and south (S) aspects within and between the study areas.

Variables	Suldal	Kvam	Hjartdal	Valle	Vinje	Hol	Tinn
Avg (S)	2.6 (0.5)	3.5 (0.4)	3.0 (0.5)	2.8 (0.5)	2.7 (0.4)	1.7(0.3)	2.6(0.2)
Max (S)	14.5 (0.8)	14.3 (1.2)	12.3 (1.6)	11.5 (0.8)	12.6 (1.7)	11.9 (1.8)	11.6(0.7)
GSST	6.3 (0.5)	8.6 (0.6)	7.3 (0.6)	8.3 (0.5)	7.5 (0.5)	5.6 (0.5)	6.5 (0.2)
GSL (S)	133 (12)	123 (8)	124 (6)	111 (15)	108 (8)	106 (8)	115 (5)
Avg (Jul) (S)	11.4 (0.5)	10.8 (0.7)	10.1 (1.1)	9.2 (1)	9.6 (1)	9.2 (1.0)	9.3 (0.3)
STHS	805 (110)	1143 (127)	858 (135)	888 (159)	841 (123)	530 (72)	701 (39)
STFS	-141 (133)	-45 (59)	-21 (30)	-50 (78)	-42 (72)	-137 (54)	-10 (26)
SF	178 (12)	183 (11)	183 (50)	206 (15)	206 (16)	211 (14)	197 (18)
SnMelt	135 (6)	139 (4)	137 (4)	144 (3)	141 (5)	140 (2)	143 (4)
ThD (S)	9 (7)	7 (6)	9 (3)	16 (13)	14 (7)	22 (7)	13 (5)
SGS	144 (7)	147 (6)	146 (2)	159 (13)	154 (7)	162 (7)	156 (5)
SWI (S)	39.6 (3.3)	45.4 (3.9)	40.7 (5.4)	35.0 (4.6)	35.8 (4.1)	31.3 (2.5)	37.2(2.0)
Avg (A)	1.8 (0.6)	3.0 (1.1)	0.4 (0.4)	-0.4 (0.1)	-1.1 (0.3)	-2.2 (0.6)	-0.3 (0.2)
Max (A)	16.6 (0.6)	17.5 (1.2)	16.5 (0.6)	15.7 (0.1)	15.8 (0.7)	15.2 (0.3)	15.4(0.3)
GSAT	8.6 (0.5)	9.3 (0.9)	9.4 (0.5)	9.0 (0.1)	8.7 (0.5)	8.9 (0.4)	8.2 (0.3)
GSL (A)	127 (10)	140 (20)	128 (2)	114 (1)	109 (5)	113 (4)	109 (4)
Avg (Jul) (A)	11.4 (0.7)	12.3 (1.3)	12.6 (0.6)	11.6 (0.1)	11.3 (0.6)	11.5 (0.4)	10.8 (0.3)
ATHS	1212 (136)	1421 (274)	1301 (80)	1082 (21)	1025 (83)	1061 (65)	972 (52)
ATFS	-763 (66)	-544 (140)	-1260 (44)	-1371 (0)	-1565 (53)	-2009 (139)	-1227 (31)
SWI (A)	44.0 (4.4)	51.1 (9.1)	43.9 (2.9)	37.6 (0.6)	36.1 (2.4)	36.8 (2.2)	34.0 (1.5)

Table 3. Average air and soil temperature variables from the ATE in the study areas. Common air and soil temperature variables have been represented by suffix (A) and (S) respectively (e.g. Avg = average annual temperature (° C), Max = maximum temperature (° C), GSL = growing season length (days), SWI = summer warmth index, Avg (Jul) = average July temperature (° C)). The other variables such GSST= growing season soil temperature (° C), STHS = soil temperature heat sum (dd), Snmelt = snow melt day (DOY), ThD= Thaw period (days), SGS = start of growing season (DOY), SF= soil frozen days (days), GSAT= growing season air temperature (° C), ATFS= air temperature frost sum (dd) and ATHS = air temperature heat sum (dd). Standard deviations are given in brackets.

ing aspects (1.4° C) was higher than on north facing aspects (0.7° C). Likewise, average annual soil temperatures recorded on south facing aspects (3.2° C) was higher than on north facing aspects (2.7° C). The growing season lengths for all study areas calculated using air and soil temperatures were 118 days (± 10), and this decreases as we move inland. Growing season soil and air temperatures ranged from 4.5 to 10.1° C (with an average of 7.7° C) and 7.9 to 11.1° C (with an average of 9.0° C) respectively. There was a weak correlation between the growing season air and soil temperatures (r = 0.277, p = 0.006). Average July temperatures were 11.8° C ±1.1 and 10.2 ° C ±1.1 for air and soil temperatures respectively. The soil heat sums reach as low as 530 dd in Hol, (the lowest heat sum value recorded among all areas). The heat sum values calculated based on air temperatures had an average of 1153 dd for all areas. The summer warmth index was approximately 40 for both air and soil temperatures. The snowmelt event occurred on DOY 140 ± 5 at all sites irrespective of the large environmental differences along major gradients, and the onset of growing season was on DOY 151 ± 9. The time period between snowmelt and start of growing season (called thaw days) increases as we move inland, i.e. increased with decreasing oceanity with an average of 11 ± 8 days for all study areas. The soil remained frozen for 192 ± 23 days. Average soil frost sums were -55 ± 78 dd; contrastingly, frost sums due to air temperature go very low reaching a value of -1,031 ± 502 dd indicating air temperatures are below 0° C for most of the winter.

With Kruskal-Wallis tests we established significant differences in air and soil temperature variables when tested individually among all seven study areas. Tests revealed that (results given in Supplement 1) maximum soil temperature, average July soil temperature, start of growing season, soil frozen period, average annual air temperature, growing season length, air temperature frost sum and summer warmth index varied strongly between the oceanic (O3 and O2 sections) and the inland areas (O1 and OC sections). Differences were evident between Kvam and the remaining six areas for variables such as average annual soil temperature, thaw days, soil temperature heat sum and summer warmth index (calculated based on soil temperatures). The remaining variables varied randomly among the study areas without displaying any specific trends between oceanic and inland areas.

Relationships between ATE position and temperature variables

The results of correlation analysis (results given in Supplement 2) indicate strong association between air and soil temperature variables. Direct use of multiple regression methods would give rise to errors in results, thus conducted PCA analysis first, using all temperature variables, and the output of analysis was obtained in two forms i.e. PCA loadings and PCA scores. The eigenvalues / explained variation for axis 1 and 2 were 0.53 / 53.1 and 0.17 / 70.5 respectively (Fig. 4). Variables such as SF,

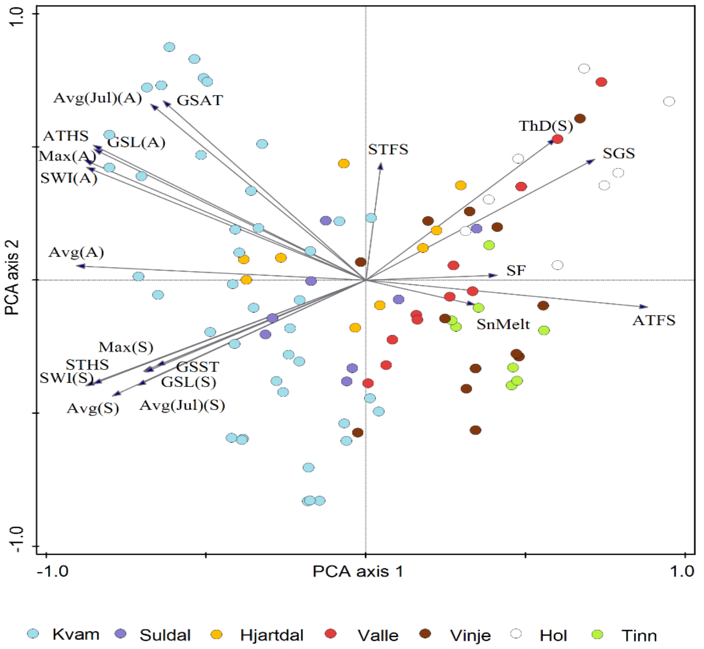

Fig. 4. PCA biplot of sample plots and temperature variables. The temperature variables are explained in Table 2.

Term	Constant	PC1	PC3	PC4	PC6	PC7	PC10
Regression coefficient	0	-0.234	0.078	0.136	-0.620	-0.174	0.105
P-value	0.000	0.000	0.006	0.000	0.000	0.003	0.049

Table 4. Results of Principle component regression analysis.

Variables	**Coef**	**SECoef**	**DF**	**p-value**	**CR**	**95% CI**	r^2_{Adj}
Constant	0.000		5				0.98
GSL (S)	1.703	0.591	1	0.005	35.1	(0.529, 2.878)	
GSL (A)	1.393	0.555	1	0.014	28.7	(0.290, 2.495)	
SF	0.954	0.351	1	0.008	19.7	(0.257,1.651)	
STFS	0.440	0.109	1	0.000	9.1	(0.223, 0.657)	
ATFS	-0.363	0.023	1	0.000	7.5	(-0.410, -0.317)	

Table 5. Results of stepwise multiple regression analysis. The model includes 98 sample plots from seven ATE areas in southern Norway. Coef = coefficient, SE Coef = Standard error of coefficient, DF = Degrees of freedom, CR = contribution rate (%) and CI = confidence interval.

ATFS, SnMelt and SGS were positively correlated with axis 1 (Fig 4). Study areas such as Kvam, Suldal and Hjartdal with oceanic influence having warm temperature conditions were positioned in the left part of the diagram.

PCA scores thus obtained were used in a stepwise multiple regression as independent variables and ATE altitude as dependent variables to find significant variables responsible for position of ATE; this is called Principle Component Regression (PCR). The results of PCR are given in Table 4, and the regression model had an $r^2_{Adj} = 0.86$. Significant results are obtained at ($p < 0.05$) for PC1, PC3, PC4, PC6 and PC7.

We conducted varimax rotation of PCA loadings (obtained from PCA analysis) to obtain the variables associated with these PCs. Varimax rotation maximizes the loadings of a single variable on each PC and ensurs zero association of that variable with subsequent PCs; thusallowing identification of the variables that contribute ito explaining the majority of the variation on that particular PC. From the results given in Supplement 3, it is clear that the first three PCs explained 80% of total variation. The first PC is loaded heavily on air temperature frost sum i.e. ATFS and average annual air temperature (Avg (A)) which together contributed 53 % of total variation. The second PC explained 18% of total variation and is heavily loaded with summer warmth index (SWI (S)). Lastly, PC 3 was heavily loaded with GSL(A) and contributed around 9% of the total variation. The variation explained by successive PCs decreases and has been mentioned in detail in Supplement 3.

In the subsequent step, we compared the output from stepwise multiple regression (Table 4) and varimax rotation of PCA loadings (Supplement 3) to isolate variables explaining the ATE position. We have selected PCs (with $p < 0.05$ from Table 4) and associated variables with high loadings on those respective PCs (Supplement 3). For instance, ATFS on PC 1, GSL(A) on PC 3, Thaw days (ThD) on PC 4, GSL(S) on PC 4, STFS on PC 6 and SF on PC 7. Finally, these selected variables were used for model fitting as independent variables (used original data) and ATE altitude as dependent variables. From the results it was clear that ATE position could be explained by GSL (S), GSL (A), SF, STFS, ATFS by 35.1%, 28.7%, 19.7%, 9.1% and 7.5% respectively (Table 5). The multiple regression analysis also yielded an equation for prediction of ATE position with respect to these selected temperature variables.

$$\text{ATE position} = 0.0000 + 1.703 * \text{GSL(S)} + 1.393 * \text{GSL(A)} + 0.954 * \text{SF} + 0.440 * \text{STFS} - 0.363 * \text{ATFS}$$

This regression model had an r^2_{Adj} value of 0.98, with the coefficients of regression being highly significant at $p < 0.05$ and normal distribution of residuals. For model validation we analyzed residuals; the residual are distributed around zero and are normally distributed (Supplement 4). There were nine outliers in the data, with data points from Kvam, Suldal and Valle area. This was because of the high temperatures recorded at these areas.

Vegetation communities and its relationship with temperature

Vegetation composition of the 98 studied plots were mostly dominated by common oligotrophic and mesotrophic boreal species. The most common species were *Vaccinium myrtillus* (98.0%), *Avenella flexuosa* (94.9%), *Vaccinium vitis-idaea* (74.5%), *Trientalis europaea* (68.4%), *Empetrum nigrum* (68.4%), *Vaccinium uliginosum* (66.3%), *Pleurozium schreberi* (60.2%) and *Cornus suecica* (51.0%). Several alpine species were frequently recorded, especially *Athyrium distentifolium*, *Eriophorum scheuchzeri, Carex brunnescens, C. bigelowii, Arctous alpinus, Salix lanata, S. glauca, S. lapponum, S. herbacea, Alchemilla alpina, Gentiana purpurea, Potentilla crantzii, Saussurea alpina, Vahlodea atropurpurea, Betula nana, Poa alpina, and Phyllodoce caerulea*. In the oceanic areas, some coastal plants were recorded, such as *Galium saxatile, Polygala serpyllifolia, Blechnum spicant*, and *Plagiothecium undulatum*.

TWINSPAN analysis was used to classify the plot vegetation, and seven communities were separated (Table 6). Seven clusters (vegetation types) were selected: *Avenella flexuosa -Vaccinium myrtillus - Juniperus communis* (AVJ), *Sphagnum* spp. - *Vaccinium myrtillus - Avenella flexuosa* (SVA), *Vaccinium myrtillus - Avenella flexuosa - Empetrum nigrum* (VAE), *Avenella flexuosa - Betula nana - Empetrum nigrum* (ABE), *Vaccinium uliginosum - Empetrum nigrum - Betula nana* (VEB), *Empetrum nigrum - Vaccinium uliginosum - Avenella flexuosa* (EVA) and *Avenella flexuosa - Betula nana - Vaccinium myrtillus* (ABV).

The results of CCA analysis with interactive forward selection showed explanatory variables accounting for 18.1% of total variation. The eigenvalues/explained fitted variation on axis 1, 2, 3 were 0.213/44.4 0.082/61.50 and 0.063/74.53 respective-

Vegetation type	AVJ	SVA	VAE	ABE	VEB	EVA	ABV
No. of plots	15	9	41	15	7	5	6
Maianthemum bifolium	21		7	1		3	3
Anemone nemorosa	13						
Galium saxatile	6		1				
Phegopteris connectilis	19	4	2				
Polygala serpyllifolia	2						
Blechnum spicant	8		9				
Calluna vulgaris	31		31			17	
Athyrium distentifolium	6	9	3				
Hylocomium splendens	28	15	31				
Eriophorum scheuchzeri		13	2				
Lycopodium annotinum	3	28	14	2			
Cornus suecica	11	35	33	11	14	3	
Nardus stricta	6	11	5			13	
Pleurozium schreberi	36	7	43	12	1	3	8
Sphagnum spp.	2	**78**	17		5	41	
Trieentalis europaea	19	19	15	17		13	11
Vaccinium myrtillus	**52**	**57**	**61**	41	29	37	**47**
Vaccinium vitis-idaea	31	11	35	38	33	3	3
Rubus chamaemorus	2	31	5		12	21	3
Gymnocarpium dryopteris	31	13	4	8			11
Juniperus communis	**41**	11	11	21	2	27	11
Avenella flexuosa	**53**	**52**	**51**	**61**	33	**43**	**72**
Vaccinium uliginosum	11	19	33	21	**62**	**43**	33
Empetrum nigrum	9	15	**47**	**51**	**62**	**47**	22
Arctous alpinus			2		12		
Carex bigelowii		2	4		2	11	3
Geranium sylvaticum	9					3	14
Solidago virgaurea	11	6	2	3		13	17
Alchemilla alpine	3					3	6
Salix glauca	8	9	1	2		27	36
Gentiana purpurea		2	1	2		11	8
Potentilla cranzii						11	3
Saussurea alpine	1			1			11
Salix herbacea					5	11	
Salix lapponum	3	2	1		7	13	33
Betula nana		4	4	**58**	**43**	3	**61**
Poa alpine				1	12		6
Phyllodoce caerulea			2	3	7	3	3

Table 6. Shortened table of TWINSPAN classification of ground vegetation communities in ATE. The values given in the table are relative species occurrence and abundance (SOA) values (Odland *et al.* 1990). Only the most common species are included in the table. The following seven vegetation types have been obtained: *Avenella flexuosa - Vaccinium myrtillus - Juniperus communis* (AVJ), *Sphagnum* spp. -*Vaccinium myrtillus - Avenella flexuosa* (SVA), *Vaccinium myrtillus - Avenella flexuosa - Empetrum nigrum* (VAE), *Avenella flexuosa - Betula nana - Empetrum nigrum* (ABE), *Vaccinium uliginosum - Empetrum nigrum - Betula nana* (VEB), *Empetrum nigrum - Vaccinium uliginosum - Avenella flexuosa* (EVA) and *Avenella flexuosa - Betula nana - Vaccinium myrtillus* (ABV). No of plots = Number of plots in each vegetation type.

ly. Percentage contribution by STHS was (20.5%), ATFS (7.2%), GSST (6.5%), closely followed by GSL (5.3%), and the remaining variables with < 5% contribution are presented in Supplement 5.

Lastly, we integrated these separated vegetation communities from TWINSPAN and environmental variables selected from CCA analysis into a DCA diagram (Fig. 2). The environmental variables are

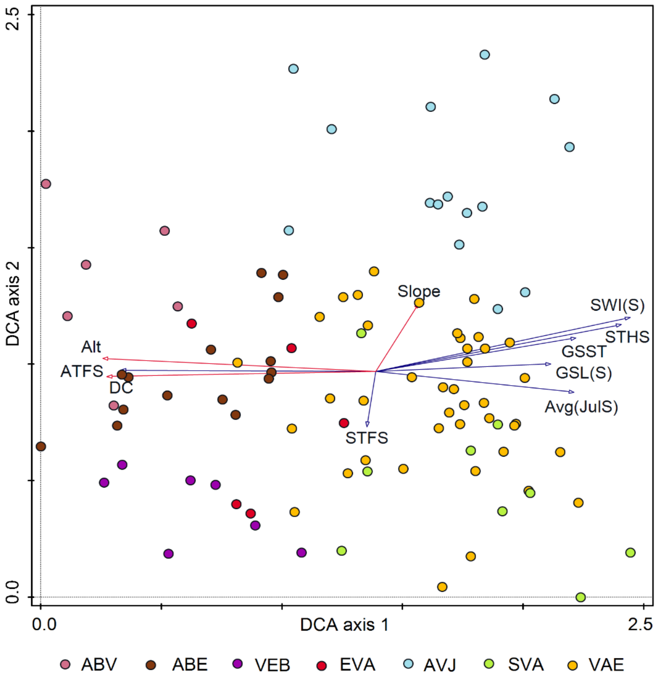

Fig. 5. DCA biplot illustrating vegetation communities classified using TWINSPAN and temperature variables chosen using CCA. 1. *Avenella flexuosa - Betula nana - Vaccinium myrtillus* (ABV), 2. *Avenella flexuosa - Betula nana - Empetrum nigrum* (ABE), 3. *Vaccinium uliginosum - Empetrum nigrum - Betula nana* (VEB), 4. *Empetrum nigrum - Vaccinium uliginosum - Avenella flexuosa* (EVA), 5. *Avenella flexuosa -Vaccinium myrtillus - Juniperus communis* (AVJ), 6. *Sphagnum spp. - Vaccinium myrtillus - Avenella flexuosa* (SVA) and 7. *Vaccinium myrtillus - Avenella flexuosa - Empetrum nigrum* (VAE). The temperature and topography variables are introduced as supplementary variables in DCA analysis. The temperature variables are explained in Table 2. Alt = altitude (m a.s.l.), DC= distance to coastline (km) and slope (degree).

used as supplementary variables in the DCA analysis (relative differences between the studied plots are shown in Fig 5).

The eigenvalues/gradient length on DCA axis 1, 2, 3 were 0.293/2.44, 0.221/2.33 and 0.166/2.45 respectively. The floristic gradients are relatively equal on DCA axis 1 and 2. On DCA axis 1, the gradient in vegetation communities from left to right changes from *Avenella flexuosa - Betula nana - Vaccinium myrtillus* (ABV) to *Vaccinium myrtillus - Avenella flexuosa - Empetrum nigrum* (VAE), *Avenella flexuosa - Vaccinium myrtillus - Juniperus communis* (AVJ) and *Sphagnum - Vaccinium myrtillus - Avenella flexuosa* (SVA). Vegetation communities rich in *Betula nana* growing in well drained and nutrient poor conditions were placed towards left; whereas, *Empetrum nigrum, Juniperus communis* and *Vaccinium myrtillus* dominated communities associated with oceanic conditions were located towards right on DCA axis 1. On DCA axis 2, the vegetation on the lower part of the axis was dominated by *Vaccinum uliginosum* and *Sphagnum* spp. while *Avenella flexuosa* and *Juniperus communis* were most dominant in the upper part. The floristic gradient on PCA axis 2 represents a gradient from wet soil condition to dry, exposed ridges or heath communities.

Discussion

Floristic variation

The study plots selected from the ATE within seven study areas show relatively small variation in floristic composition (ca. 2.5. SD units as measured by DCA), but there was a gradient from continental to oceanic areas, and from dry to moist soil conditions. The limited variation is partly because most of the sample plots have a large number of species in common, which is characteristic for oligotrophic forest communities. The vegetation types show variations in soil moisture (high moisture in SVA, EVA and low moisture in VEB). Typically, alpine species were common close to the treeline, previously described as subalpine forest communities in Nordhagen (1943).

TWINSPAN separated seven vegetation communities along two main DCA axes (Fig 5). Firstly a gradient from continental to oceanic climate in which gradual changes from ABV dominated to VAE, AVJ and SVA dominated communities were observed. This gradual change can be characterized by higher temperature and precipitation conditions. The second gradient showed a gradual change from dry, exposed ridges to moist meadows. The majority of variation was explained by growing season temperatures, although variables such as ATFS and STFS were also significant in explaining the current vegetation communities.

Alpine treeline ecotone (ATE)

In this study, ATE was defined differently than in Körner (2012), wherein the upper limit of the treeline ecotone has been drawn at the tree species limit. The reason behind this alternative method of defining ATE is that in Scandinavia, birch saplings are frequently found 300 - 500 m higher than the treeline (Dalen and Hofgaard 2005; Kilander 1955; Kullman 2001; Kullman 2010) and we have not found the species to be a useful criteria for determining the treeline, as the tree seedlings found above treeline do not develop into trees (Körner and Paulsen 2004). According to Aas and Faarlund (2000), forest and treelines are theoretical lines, drawn through the uppermost forest projections and isolated single/groups of trees respectively. The studied ATE in the oceanic areas (Kvam and Suldal) lie 300 - 400 m lower than in the inland area (Table 1). Similar patterns have also been found in earlier studies (Aas and Faarlund 2000; Moen 1999; Odland 1996). Average differences in elevation between forest limit and treelines at all study sites were less than 50 m (Table 1). According to Körner (2007), a variation of 50 m in elevation represents generally a 0.3° K difference in air temperature which is acceptable in ecological studies. In the current study, average difference between forest limits in north and south facing slopes were generally less than 50 m (Table 1) which correlates with most previous studies (Kjällgren and Kullman 1998; Nordhagen 1943).

Daubenmire (1954) suggested that where alpine timberlines were concerned, he would use the mid-point of the area between the timberline and the tree limit, even though some studies use the highest point of occurrence of trees or continuous forests. Due to this, comparisons between different study areas were difficult, and it has been suggested that an average of several local measurements between the uppermost trees and uppermost forest stands (within the ATE) should be used. Comparisons between distribution limits from different geographic areas should be based on average data as local measurements are often strongly modified by topographic or edaphic factors (Bekker *et al.* 2001; Broll *et al.* 2007; Fries 1913; Heiskanen 2006; Malanson *et al.* 2001).

Role of temperature on ATE position and comparison with other studies

Treelines are associated with a minimum July temperature of 10° C (e.g. Grace (1989) and Körner (1998)). In this study, average ATE July temperatures were mostly higher than 10° C in all areas. Present study agrees with previously stated knowledge regarding treeline temperatures being higher in oceanic areas than in inland areas. This is probably a result of both an oceanic climate and relatively low mountains in coastal areas (e.g. Fang *et al.* 2012; Holtmeier 2003; Odland 1996; Zhao *et al.* 2014).

The World-wide treeline study (Körner and Paulsen 2004) found that climatic treelines were associated with a seasonal mean ground temperature of 6.7° C ± 0.8, ranging from 5.5 to 7.5° C. This discrepancy between our study and Körner and Paulsen (2004) was probably due to the growing season being estimated from a lower soil temperature threshold of 3.2° C, measured at 10 cm soil depth. Körner and Paulsen (2004) established that the ground temperatures in climatic treeline sites do not increase beyond 15° C, and this presumption appears to be applicable to the current study wherein the warmest oceanic areas (Kvam and Suldal) experienced maximum soil temperatures below 15° C. High average daily temperatures caused early thawing of frozen soil resulting in lower thaw days, speedy attainment of the threshold temperature (5° C) and longer GSL in highly oceanic areas. The growing season lengths (calculated by air and soil temperatures) estimated in this study varied between 106 to 115 days in the continental areas, and from 123 to 140 days in oceanic areas. Globally, the variation in growing season length has mostly been found to range from 100 to 150 days measured for alpine treelines (Holtmeier 2003; Körner and Paulsen 2004; Odland 2011).

The soil temperature during growing season in our study is lower than birch forest limits in Iceland (8 - 11° C) and in Mount Njulla, Sweden (11.1° C) (Davis *et al.* 1991; Hecht *et al.* 2007). Our results are similar to forest limit studies in North Sweden where a growing season temperature of 6.6° C was recorded (Karlsson and Weih 2001). Average growing season temperature and temperature during the warmest month (July) found in the current study are lower than the northernmost birch forests of Norway (Bandekar and Odland 2017).

In general, the ATEs in the oceanic areas were associated with higher air and soil temperature heat sums, longer growing season, and higher temperatures (Table 3, Fig. 4). This indicated that the ATE have not reached their potential temperature limit. This may partly be an effect of relative low mountain height, influence from the ocean, or both; indicating that ATE may not be climatically limited in oceanic areas i.e. Kvam and Suldal.

The study shows that there were significant differences between the ATE, particularly between the oceanic and continental areas. Results of multiple regression analysis suggest that on a regional scale ATE are controlled by a subset of variables i.e. GSL (S), GSL (A), SF, STFS and ATFS provide the best explanation for the current ATE position. The majority of variation (35.1%) is explained by the GSL(S) which decreases with increasing distance to the coastline because of increasing mountain heights inland. Similar results are found in Kjällgren and Kullman (1998) where the inverse relationship between forest limits and treelines is found with increasing distance to sea.

Although this study has been conducted on regional scale, we have gathered spatially explicit regional scale data on topography and temperature variables. Unlike global scale studies on ATE, regional studies are conducted on finer scales with a specific focus on microclimate and topography (Müller *et al.* 2016). Care should be taken when generalizing the results and methods used in this study as this particular dataset cannot be considered fully representative of the entire region and the method may not be applicable to other regions of the World. However, the study can be used for expanding and deepening current knowledge of the ATE of southern Norway, as regional studies are relevant in understanding the underlying complex influence of each variable on ATE. It is clear that additional long term data sets on environmental variables will be required to stimulate further research and to have a complete understanding of this ATE phenomenon.

Conclusions

Main conclusions from the study are

- The air and soil temperature conditions are warmer in oceanic areas than in inland areas. The results suggests that temperatures may not be critical for current ATE altitudinal positions in oceanic areas.
- Average growing season temperatures were lower in studied ATEs when compared with other ATE studies.
- Seven vegetation communities were classified and could be explained with STHS, ATFS, GSST and GSL.
- Kruskal-Wallis test results showed significant differences between the temperature conditions in the studied ATEs.
- Position of the ATE could be explained with temperature variables such as GSL (S), GSL (A), SF, STFS and ATFS.

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Supplement 1. Main results of Kruskal-Wallis multi comparison test. Common air and soil temperature variables have been represented by suffix (A) and (S) respectively. For instance Avg =average annual temperature (° C), Max= maximum temperature (° C), GSL= growing season length (days), SWI =summer warmth index, Avg (Jul) =average July temperature (° C). The other variables such GSST= growing season soil temperature (° C), STHS= soil temperature heat sum (degree days), Snmelt= snow melt day (DOY), ThD= Thaw days (days), SGS= start of growing season (DOY), SF= soil frozen days (days), GSAT= growing season air temperature (° C), ATFS= air temperature frost sum (degree days), ATHS= air temperature heat sum (degree days).

Temperature variables	Observed difference	Critical difference	P value	Chi -square
Avg (S)	23.5	37.8	<0.001	58.5
Max (S)	24.9	37.8	<0.001	47.7
ThD (S)	19.9	37.8	<0.001	32.2
STFS	24.9	37.8	<0.001	26.8
GSL (S)	28.0	37.8	<0.001	44.7
GSST	29.9	37.8	<0.001	71.5
SWI (S)	24.6	37.8	<0.001	62.9
STHS	25.5	37.8	<0.001	72.4
Avg (Jul) (S)	27.1	37.8	<0.001	49.9
SnMelt	21.2	37.8	0.001	22.4
SGS	26.1	37.8	<0.001	40.9
SF	22.2	37.8	<0.001	35.5
Max (A)	27.1	37.8	<0.001	60.5
Avg (A)	30.7	37.8	<0.001	85.5
GSL (A)	27.9	37.8	<0.001	64.7
GSAT	22.1	37.8	<0.001	26.1
ATFS	30.4	37.8	<0.001	87.4
ATHS	27.9	37.8	<0.001	58.4
SWI (A)	28.6	37.8	<0.001	69.0
Avg (Jul) (A)	23.6	37.8	<0.001	31.7

Supplement 2. Results of correlation analysis. Common air and soil temperature variables have been represented by suffix (A) and (S) respectively. For instance Avg =average annual temperature (˚ C), Max= maximum temperature (˚ C), GSL= growing season length (days), SWI =summer warmth index, Avg (Jul) =average July temperature (˚ C). The other variables such GSST= growing season soil temperature (˚ C), STHS= soil temperature heat sum (degree days), Snmelt= snow melt day (DOY), ThD= Thaw days (days), SGS= start of growing season (DOY), SF= soil frozen days (days), GSAT= growing season air temperature (˚ C), ATFS= air temperature frost sum (degree days), ATHS= air temperature heat sum (degree days).

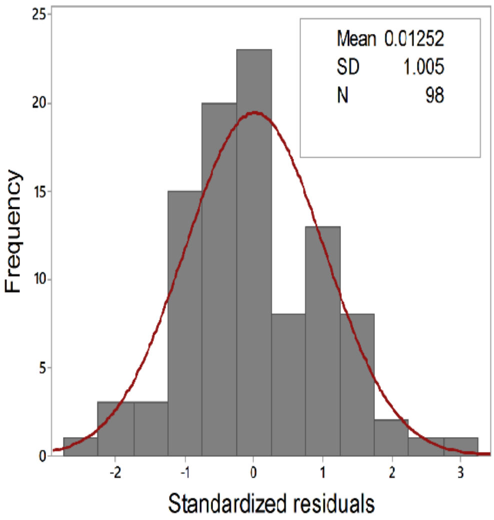
	Avg(S)	Max(S)	ThD(S)	STFS	GSL(S)	GSST	SWI(S)	STHS	Avg(Jul) (S)	SnMelt	SGS	SF	Max(A)	AVG(A)	GSL(A)	GSAT	ATFS	ATHS	SWI(A)	Ave-rage (July)	Alt	DC
Max (S)	0.562**																					
ThD (S)	-0.665**	-0.509**																				
STFS	-0.522**	0.172	0.287*																			
GSL (S)	0.566**	0.539**	-0.6**	-0.05																		
GSST	0.795**	0.558**	-0.469**	-0.23	0.275*																	
SWI (S)	0.908**	0.711**	-0.66**	-0.29**	0.754**	0.667**																
STHS	0.909**	0.688**	-0.667**	-0.22	0.621**	0.894**	0.892**															
Avg (Jul) (S)	0.589**	0.902**	-0.548**	0.037	0.67**	0.524**	0.745**	0.693**														
SnMelt	-0.071	-0.338*	-0.12	-0.387**	-0.435**	0.02	-0.34*	-0.192	-0.34*													
SGS	-0.645**	-0.615**	0.787**	0.092	-0.832**	-0.413**	-0.792**	-0.722**	-0.699**	0.444**												
SF	-0.396**	-0.193	0.069	0.188	-0.389**	-0.1	-0.48**	-0.268*	-0.21	0.415**	0.291*											
Max (A)	0.541**	0.438**	-0.32*	0.074	0.395**	0.462**	0.591**	0.595**	0.419**	-0.300	-0.415	-0.3**										
AVG(A)	0.7**	0.567**	-0.497**	-0.04	0.569**	0.58**	0.746**	0.749**	0.576**	-0.200	-0.545**	-0.4**	0.83**									
GSL (A)	0.457**	0.405**	-0.29*	0.152	0.428**	0.364**	0.546**	0.511**	0.406**	-0.300	-0.386**	-0.3**	0.95**	0.812**								
GSAT	0.264*	0.178	-0.05	0.137	0.184	0.28	0.287*	0.316*	0.177	-0.200	-0.162	-0.2**	0.84**	0.518**	0.85**							
ATFS	-0.644**	-0.579**	0.456**	-0.06	-0.524**	-0.544**	-0.72**	-0.711**	-0.56**	0.210	0.486**	0.3**	-0.82**	-0.95**	-0.8**	-0.5**						
ATHS	0.466**	0.394**	-0.28*	0.135	0.413**	0.383**	0.544**	0.519**	0.397**	-0.300	-0.385**	-0.3**	0.96**	0.792**	0.99**	0.89**	-0.8**					
SWI(A)	0.502**	0.454**	-0.32*	0.146	0.442**	0.416**	0.587**	0.565**	0.447**	-0.300	-0.412**	-0.3**	0.96**	0.837**	0.99**	0.84**	-0.86**	0.992**				
Avg (Jul) (A)	0.293*	0.179	-0.11	0.114	0.246	0.25	0.334*	0.326*	0.197	-0.200	-0.221	-0.3**	0.87**	0.557**	0.89**	0.97**	-0.53**	0.927**	0.879**			
Alt	-0.538**	-0.599**	0.442**	-0.16	-0.514**	-0.437**	-0.658**	-0.634**	-0.569**	0.250	0.485**	0.3**	-0.66**	-0.83**	-0.7**	-0.28	0.907**	-0.638**	-0.721**	-0.33*		
DC	-0.528**	-0.61**	0.48**	-0.13	-0.42**	-0.49**	-0.578**	-0.633**	-0.536**	0.140	0.442**	0.2**	-0.55**	-0.74**	-0.5**	-0.16	0.8**	-0.486**	-0.581**	-0.17	0.9**	
Slope	0.262*	0.064	-0.04	-0.06	0.061	0.33**	0.181	0.297*	0.014	0.000	-0.076	0.1	0.11	0.21	0.1	0.05	-0.24	0.084	0.105	0.024	-0.1	-0.14

** P<0.001 and *p<0.01

Supplement 3. Loadings of 22 variables on principle components rotated using varimax rotation method for 98 sample plots. Common air and soil temperature variables have been represented by suffix (A) and (S) respectively. For instance Avg =average annual temperature (° C), Max= maximum temperature (° C), GSL= growing season length (days), SWI =summer warmth index, Avg (Jul) =average July temperature (° C). The other variables such GSST= growing season soil temperature (° C), STHS= soil temperature heat sum (degree days), Snmelt= snow melt day (DOY), ThD= Thaw days (days), SGS= start of growing season (DOY), SF= soil frozen days (days), GSAT= growing season air temperature (° C), ATFS= air temperature frost sum (degree days), ATHS= air temperature heat sum (degree days).

Variable	**PC1**	PC2	**PC3**	**PC4**	PC5	**PC6**	**PC7**	PC8	PC9	PC10
Avg (S)	0.03	0.48	0.04	0.03	0.03	0.18	0.02	-0.01	-0.05	0.20
Max (S)	-0.01	0.34	0.03	0.20	0.04	-0.26	0.01	0.00	0.61	-0.06
ThD (S)	-0.02	-0.05	-0.03	-0.09	-0.25	0.05	-0.01	0.77	0.02	0.03
STFS	0.03	-0.15	0.05	-0.05	-0.03	**-0.90**	0.01	-0.01	-0.02	0.09
GSL (S)	0.00	0.07	-0.01	**-0.93**	0.03	-0.04	0.01	-0.01	0.02	0.01
GSST	-0.04	-0.04	-0.09	0.10	0.05	-0.02	-0.01	0.07	0.03	0.79
SWI (S)	0.04	0.63	0.08	-0.09	-0.07	0.00	0.01	0.01	0.02	0.00
STHS	0.04	0.15	-0.02	-0.08	-0.03	-0.04	-0.01	-0.07	-0.03	0.51
Avg (Jul) (S)	0.00	-0.20	-0.03	-0.14	-0.02	0.16	-0.01	0.00	0.78	0.03
SnMelt	0.00	-0.06	0.00	-0.05	0.91	0.04	0.00	-0.01	0.01	0.02
SGS	0.05	0.05	0.02	0.10	0.30	-0.05	0.02	0.61	-0.02	-0.05
SF	0.01	-0.03	0.03	0.00	0.00	0.01	**-0.99**	0.00	0.00	0.02
Max (A)	0.06	-0.05	0.36	0.15	-0.06	0.06	0.03	-0.07	0.01	0.05
AVG (A)	0.56	-0.34	0.18	-0.03	-0.07	0.20	0.08	-0.05	0.07	0.17
GSL (A)	0.07	0.07	**0.41**	-0.04	0.02	-0.03	-0.05	0.03	-0.02	-0.08
GSAT	-0.44	-0.16	0.36	-0.04	0.01	0.05	0.05	0.05	0.04	0.16
ATFS	**-0.57**	-0.08	-0.25	0.02	-0.04	0.06	0.02	-0.07	0.03	-0.01
ATHS	-0.03	0.03	0.40	-0.02	0.01	-0.01	0.00	0.00	0.00	-0.02
SWI (A)	0.07	0.06	0.38	0.00	0.03	-0.05	0.00	0.01	0.01	-0.03
Avg(Jul) (A)	-0.38	-0.07	0.40	-0.04	-0.01	0.07	0.01	0.00	-0.01	0.04
Eigenvalue	10.62	3.47	1.85	1.28	0.86	0.61	0.44	0.31	0.22	0.10
Proportion	0.53	0.17	0.09	0.06	0.04	0.03	0.02	0.02	0.01	0.01
Cumulative	0.53	0.71	0.80	0.86	0.90	0.94	0.96	0.97	0.98	0.99

Supplement 4. Histogram of standardized residuals obtained from stepwise multiple regression.



Supplement 5. Results of CCA analysis. STHS = Soil temperature heat sum (dd), ATFS = air temperature frost sum (dd), GSST = growing season soil temperature (° C), GSL(S) = growing season length estimated using soil temperature (days), Avg(Jul)(S) = Average July soil temperature (° C), STFS = Soil temperature frost sum (dd) and SWI(S) = summer warmth index estimated from soil temperatures.

Variable	**Explains %**	**Contribution %**	**pseudo-F**	**P-value**
STHS	7.0	20.5	7.2	0.001
ATFS	2.5	7.2	2.6	0.001
GSST	2.2	6.5	2.4	0.002
GSL (S)	1.8	5.3	2.0	0.003
Avg (Jul) (S)	1.6	4.7	1.8	0.002
STFS	1.6	4.6	1.7	0.008
SWI (S)	1.5	4.3	1.6	0.016

Paper II

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Ecological characterization of northernmost birch forests and treeline ecotones in Norway

Gauri Bandekar* & Arvid Odland

Abstract

Aims: The current paper focuses on quantifying ground vegetation, estimating age, distribution and ecological conditions in 28 birch forest stands. Another key objective of this study was to investigate whether these forests are temperature limited. We also determined if there were any significant differences in ecological conditions between forest, scattered trees and shrub plots. **Study area:** Sampling was conducted in northernmost birch forests (dominated by *Betula pubescens*) found along the coast in Finnmark (Norway). These forest limits are used to delimit the boreal biome from the alpine/arctic biome and are assumed to have a bioclimatic characterization. **Methods:** Soil and air temperatures were measured within selected stands and soil samples and tree cores were collected. **Results:** The results showed the field layer to be dominated by *Empetrum-Cornus-Vaccinium*, *Polytrichum-Cornus* and *Cirsium-Viola* types; the gradients between these types being explained by pH, July temperatures and thaw days. Based on the tree-ring data, the age of the trees was estimated to be 11–77 yr. Elevated levels of calcium were evident in some of the study plots. **Conclusions:** We found no differences in temperature conditions and soil properties between forests, scattered trees and shrubby stands (with the exception of potassium concentration). The overall temperature conditions in present study were warmer than in other northern limit of birch forests. This suggests, that forests are probably not limited by temperature conditions, but more likely limited by strong wind, topography and absence of land further north. However, more data is necessary to confirm this hypothesis.

Keywords: air temperature; *Betula pubescens*; birch forest; distribution; growing season length; Norway; soil property; soil temperature; tree age; treeline ecotone.

Nomenclature: Plant species names follow Lid & Lid (2005).

Abbreviations: ATFS = Air temperature frost sum; ATHS = Air temperature heat sum; Avg = Average annual temperature; Avg(Jan) = Average January temperature; Avg(Jul) = Average July temperature; BD = bulk density; CRL = coastal reference line; CV = *Cirsium-Viola* type; DBH = diameter at breast height; dd = degree days; DOY = day of year; ECV = *Empetrum-Cornus-Vaccinium* type; GSAT = Average air temperature during the growing season; GSL = Growing season length; GSST = Average soil temperature during the growing season; OM = organic matter; PC = *Polytrichum-Cornus* type; SF = Soil frozen period; SGS = Start of growing season; SM = soil moisture; Smelt = Snowmelt; SOA = species occurrence and abundance value; STFS = Soil temperature frost sum; STHS = Soil temperature heat sum; ThD = Thaw days

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Introduction

The northernmost occurrences of birch in the world are found along the coast in Finnmark, Norway. These coastal areas provide a suitable environment for birch forests at high latitudes due to the warming effect of the Gulf Stream. In the context of global warming, high latitude birch forests are of particular interest as future temperature changes are predicted to be greatest at high latitudes. In addition, the elevation of these forests further

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simplifies the understanding of environmental factors responsible for their occurrence (Sveinbjörnsson et al. 1996; Turner et al. 2004). Another important reason for studying these forests is northernmost birch forest limits are assumed to have bioclimatic characterization and are used to delineate the boreal and alpine/arctic biomes (Moen 1999; Walker et al. 2005; Richardson & Frieland 2009). If this is valid, then vegetation, air and soil temperature characteristics should show similarities with other areas where such transitional zones occur. The northernmost birch forests in Scandinavia, the Kola Peninsula (Russia), Petsamo Lapland, Iceland and Greenland are dominated by *Betula pubescens* Ehrh. (Kalela 1939; Crawford 2008; Aune et al. 2011). The birch forests found on the Kola Peninsula are of interest for comparison due to their proximity to the present study area, coastal influence, location above the Arctic Circle and dominance of forest-tundra communities (Ahti et al. 1968; Hämet-Ahti & Ahti 1969; Blinova & Chmielewski 2015). Comprehensive studies have been carried out on field layer, climate, soil nutrient conditions and phenology in birch forests of Kola Peninsula (Koroleva 1999, 2001; Shutova et al. 2006; Aune et al. 2011; Orlova et al. 2013; Blinova & Chmielewski 2015).

Birch migrated rapidly into the northernmost parts of Norway ca. 10,100–9380 cal yr BP from south Norway or from the east along the Barents Sea coast (Aas & Faarlund 2001; Birks et al. 2012). However, after ca. 9380 cal yr BP the density of birch woodland forests started decreasing (Birks et al. 2012). Pine dominated Finnmark after ca. 9000 cal yr BP. According to Aas & Faarlund (2001) and references therein, the forest limits for pine and birch in Norway and Sweden were 150–200 m higher than at present owing to a warm period (commencing in the late 19th century).

Birch species have been able to adapt to the extreme climates due to high a degree of polymorphism and introgressive hybridization with *Betula nana* and *B. pendula* (Thórsson et al. 2007). The resulting taxon is not clearly defined and is referred to as mountain birch; it can exist in either monocormic or polycormic forms (Crawford 2008). Mountain birch forms continuous closed forests, scattered trees (single/groups of trees) and dense shrubby stands. Birch is a pioneer species and quickly colonizes bare areas. It does not have exacting soil requirements but plentiful light is necessary for proper growth (Atkinson 1992; Aas & Faarlund 2000). It can reach up to the age of 150–200 yr (Millar 1980; Kirchhefer 1996; Aas & Faarlund 2000) and grow to a height of 1-15 m depending on the structure of the birch (Tømmervik et al. 2009). Birch treelines are usually associated with summer temperatures between 9 and 11 °C (Odland 1996; Wielgolaski & Nilsen 2001).

The distribution of forests can be limited by several environmental factors such as; air temperature, soil temperature along with the snow cover, which play a significant role in determining the position of the birch treeline (Wiegolaski 1999; Holtmeier 2003; Wiegolaski et al. 2004; Holtmeier & Broll 2005). Of particular importance are growing season length (GSL), growing season temperature and average July temperature. The 5 °C air and soil temperature threshold is commonly used to define growing season (Holtmeier 2003). Treeline is generally assumed to be associated with an average air temperature of 10 °C during the warmest month (Brockmann-Jerosch 1919; Köppen 1919; Körner 1998). Air and soil temperatures determine growth rate and biomass production, and temperature changes may facilitate insect infestation (Tenow et al. 1999). Abiotic factors (temperature, soil nutrients and moisture) and biotic factors (grazing, insect defoliation) are equally important in determining the structure and position of birch stands (Grace 1989; Tenow et al. 2007; Richardson & Friedland 2009; Hofgaard et al. 2013).The current study focuses on the ecological characterization of the northernmost birch forests and treeline ecotones. The main aims of the study were:

1. To quantify floristic differences between the stands,
2. To study the distribution and age of mountain birch,
3. To discuss whether the distribution of northernmost forests, scattered trees and shrubs are limited by air and soil temperature,
4. To evaluate patterns in soil properties relative to altitude, distance from shore and distance from coastal reference line (CRL),
5. To check ecological differences between forests, scattered trees ≥ 3 m and stands of shrubby birch ≤ 2 m.

Study area

The study area is the coastal area of Finnmark between 70 to 71° N and 22 to 29° E (Fig. 1, Table 1). Finnmark is the largest county in Norway, with a total coastline of 6844 km and mountain elevations rarely extending to more than 400 m a.s.l. Mild winters at high latitudes in Norway are favored due to warm North Atlantic currents in the Norwegian and Barents Seas (Gyory et al. 2001). These conditions favor birch forest distribution in Finnmark.

The northernmost areas (Magerøya, Kvaløy, Porsangerhalvøya and Varangerhalvøya) mostly have a narrow low lying zone between the coastal shoreline and steep slopes leading up to a mountain plateau higher than 250 m a.s.l. Forests occur only in sheltered localities some 10–30 km from the Barents Sea coastline. Towards the south-west, the lowland areas are larger, and in some valleys there is agricultural land. In sheltered fjords, forests may be found close to the seashore. The northernmost occurrences of permafrost lie in the southwestern part of the Varanger Peninsula (70° N, 25° E) above 350–450 m a.s.l. (Farbrot et al. 2008; Isaksen et al. 2008). North of the forests, there are areas of coastal heath, or steep cliffs descending directly to the sea from the plateau.

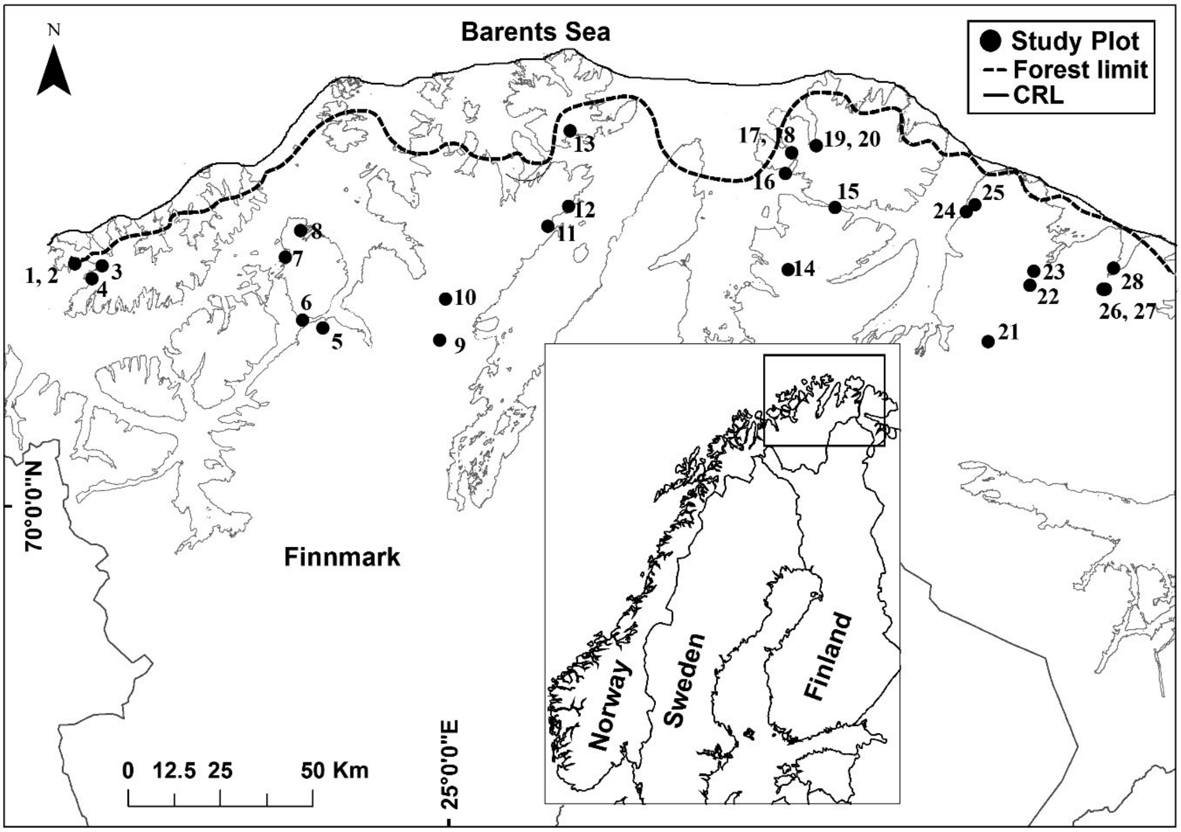

Fig. 1. Study plots in Finnmark (see also Supplement S5). The dotted line represents northernmost limit of birch forests. The forest limit is drawn from the topographic map of Norway (the forested areas were marked with green color on the topographic map of Norway (source: http://www.norgeskart.no) were bigger than 4000 m^2 and broader than 30 m). The coastal reference line (CRL) (represented with black line), is bordering the northernmost coastal area of Norway (excluding fjords).

Soils in Finnmark are classified as lithic Leptosols and Podzols (Jones et al. 2005). The bedrock in the study area consists of Cambro-Silurian sedimentary rocks, gneiss and limestone (Moen 1999). Annual precipitation is mostly lower than 800 mm yr^{-1} while the average number of days with precipitation (> 0.2 mm or more) is higher than 220 days yr^{-1} (Aune 1993). The average duration of snow cover in the lowland areas is usually less than 200 days yr^{-1} (Schuler et al. 2006).

Methods

Sampling methods

We selected 28 birch stands (Fig. 1, Table 1) in forests, at forest limits, in shrubby stands and at treelines based on the presence of natural forests. In most cases, the boreal zone does not end abruptly; rather there is a zone of transition between forest and open heath vegetation, often with scattered trees. Forest is defined as a continuous occurrence of trees where the distance between individuals does not exceed 30 m (Aas & Faarlund 2000). Forest limit is defined as the uppermost or northernmost limit of closed forest stands ≥ 3 m in height. Above the forest limit there are scattered single/groups of trees ≥ 3 m, the edge of this zone is defined as the treeline. The transition zone between forest limit and treeline is referred to as the treeline ecotone. The stands sampled comprised of monocormic or polycormic trees and dense shrubs (crippled forms). These shrubby forms are usually polycormic with height ≤ 2 m, probably formed due to harsh environmental conditions (e.g. wind exposure). For simplicity, all plots at forest limits and treeline are referred to as scattered tree plots (trees ≥ 3 m) when comparing with shrubs in further analysis. There were 23 forest and scattered tree plots and five shrubby plots.

At each site, a 2 m × 2 m quadrat with homogeneous vegetation was selected within forest and shrubby stands or, in case of scattered trees, close to single trees for field layer analysis. A three-layer analysis was conducted for each quadrat which included canopy cover of *Betula pubescens* (%), combined dwarf shrub, herb, pteridophyte and graminoid cover (%) and bryophyte cover (%). For field layer analysis, all vascular plants and bryophytes were identified and their percentage abundance estimated

Table 1. Properties of the study plots. Lat = latitude, Long = longitude, Alt = altitude, D = shortest distance between the plot and shore, D(CRL) = shortest distance between the plot and coastal reference line (CRL), A = Aspect, SL = slope, Type = forests (F), forest limit (FL) treeline (TL) and Shrub (S), Str = structure of trees (P = polycormic, M = monocormic and S = shrub), TH = tree height, Age = tree age and DBH = tree diameter at breast height.

Plot	Area	Lat (°)	Lon (°)	Alt (m a.s.l.)	D (km)	D(CRL) (km)	A	SL (°)	Type	Str	TH (m)	Age (yr)	DBH (cm)
1	Sørøya	70.7	22.2	78	0.1	11.6	SE	15	F	M,P	8	43	12
2	Sørøya	70.7	22.2	84	0.1	11.6	SE	12	S	S	2	11	2
3	Sørøya	70.6	22.3	111	0.9	11.2	NW	10	F	M	8	54	16
4	Sørøya	70.7	22.4	125	0.6	24.6	NW	3	T	M,P	4	29	10
5	Kvalsund	70.5	24	79	4.8	161.4	NE	2	FL	M,P	8	36	17.1
6	Hammerfest	70.7	23.9	65	1.7	150.4	SW	3	F	M,P	9	69	21.5
7	Hammerfest	70.7	23.8	109	1.2	82.5	SW	20	FL	M	9	43	35
8	Hammerfest	70.8	23.9	38	2	100.5	SE	1	T	M	5	37	16.5
9	Porsanger	70.5	24.9	207	11.3	220.4	N	1	F	M,P	3	25	4.5
10	Porsanger	70.7	24.9	177	9.5	186	O	20	FL	M	6	23	10
11	Porsanger	71	25.7	140	1.2	145.2	E	35	F	M	6	77	11.2
12	Porsanger	71	25.8	84	1.1	126.2	SE	35	F	M	3.5	51	8.8
13	Magerøya	71.1	25.9	30	0.3	65.9	S	35	F	M	5	34	13
14	Lebesby	70.7	27.5	181	7.9	133.5	W	2	FL	M	6.5	41	16.2
15	Gamvik	70.9	28	28	3.5	93.8	SW	3	F	M,P	9	47	19.5
16	Gamvik	71.1	27.6	27	1.4	52.3	SE	10	S	S	1.5	24	1
17	Kjøllefjord	71	27.5	68	2.6	32.7	N	3	S	S	2	27	2
18	Kjøllefjord	71	27.6	41	2.6	32.7	S	15	FL	M	6	29	10.1
19	Kjøllefjord	71	27.7	37	3.7	45.2	O	0	F	M,P	8	48	16.3
20	Kjøllefjord	71	27.7	38	3.7	45.2	N	2	F	M,P	7	44	13.4
21	Tanafjord	70.5	28.9	187	10.7	124.5	O	0	T	M	7	35	15.3
22	Berlevåg	70.9	29.2	111	10.3	70.1	E	20	S	S	2	22	5
23	Berlevåg	70.9	29.4	34	6.6	63.8	O	0	F	M,P	8	42	11.2
24	Berlevåg	70.9	28.8	58	1	39.7	SE	25	S	S	2	15	2
25	Berlevåg	70.9	28.8	94	2.4	31.8	E	20	F	M,P	4	28	7.4
26	Båtsfjord	70.6	29.8	76	5.1	53	NE	15	T	M,P	5	25	10
27	Båtsfjord	70.9	29.8	71	0.8	53	SE	5	FL	M	7	38	16.3
28	Båtsfjord	70.8	29.8	72	4.8	32.6	W	15	FL	M,P	7	42	13.6

visually (Supplement S1). Soil temperature was measured with a LogTag TRIX 8 temperature data logger (LogTag recorders limited, Auckland, New Zealand) placed at a soil depth of 10 cm. Air temperature was inferred for each site from the gridded data of the Norwegian Meteorological Department. Air and soil temperature were logged daily from Aug 2013 to Aug 2014, at 01:00 and 13:00 in order to obtain a measure of daily minimum and maximum temperatures respectively. First, we calculated daily average temperature using the minimum and maximum temperature for the day and later used these daily averages to calculate other temperature variables. The variables with their units of measurement are presented in Table 2. Variables such as start of growing season and snowmelt day were calculated using the day of the year (DOY) concept, therefore 2014-01-01 is taken as day 1 and 2013-12-31 as the last DOY to form a continuous dataset. Annual average and mean July air temperatures during the study (for July 2014) were approximately 1 °C higher than the average for the period 1961_1990 (the Normal period).

Soil samples, 5 cm deep, were taken using a 7 cm steel cylinder. Samples were collected from the four corners of each quadrat and were homogenized. In the laboratory, samples were air dried, ground and passed through a 2-mm sieve to remove coarse materials. Extractable bioavailable cations phosphorus (P), calcium (Ca), magnesium (Mg) and potassium (K) were determined using the ammonium lactate method (Egnér et al. 1960). Soil organic matter (OM) was estimated by the loss-on-ignition method (Dean 1974), Bulk density (BD) by method given in Page-Dumroese (1999) and soil moisture (SM) was estimated according to ASTM D 2216 – Standard Test Method for Laboratory Determination of Water (Moisture) Content of Soil.

Tree cores were obtained from the biggest tree in the stand; for monocormic and polycormic trees the largest stem was cored. In shrubby stands, the biggest specimen was selected to obtain a stem section. Cores and stem sections were collected at 50 cm above ground. Tree diameter was measured at breast height (DBH) ca. 130 cm above the ground level (Table 1). One tree was sampled per stand. The cores were mounted on a wooden support and polished with a planer. The polished core was then placed under the microscope and tree rings were counted manually. This data was used to estimate age of the stand.

Due to the long, undulating and rugged coastline with several fjords and islands, it was difficult to measure distance to coast directly; instead, we drew a line bordering the outermost edge of Norwegian coast and used this as a coastal reference line (CRL) (Fig. 1). Distance to coast is important when studying the distribution limit of birch because the sea plays an important role in regional climate variability (Koenigk et al. 2009). Another important measure was shortest distance to shore as the forests in the extreme north are usually positioned in sheltered sites near the shoreline, which have their own microclimate influence on these forests. Therefore, we measured both distance to CRL and distance to shore (Table 1). The shore was defined as the nearest body of water (fjords) directly connected to the sea. In addition, altitude, aspect, slope, GPS-position, height of the cored tree and tree morphology were recorded. All the vegetation plot data and environmental data are stored in the Nordic Vegetation Database (EU-00-018).

Statistical analyses

TWINSPAN analysis (Hill 1979) was conducted to separate field layer vegetation (28 sample, 59 species) into community types. The analysis was conducted by assigning cut levels of 0, 5, 10, 20, 40 and 60 (pseudospecies). Species occurring at only one site were excluded from analysis. The values obtained from TWINSPAN results were converted into species occurrence and abundance values (SOA) using the method of Odland et al. (1990).

Correlation analysis was used to establish relationships between tree height, age and DBH. For variation in

Table 2. Overview of soil and air temperature variables, with abbreviations and measurement units used in the context of this study. In each plot, the following variables were estimated. (Note: the variables Avg, Avg(July), Avg(Jan) and GSL were calculated for air and soil temperatures and will be followed by (A) and (S) respectively in further analysis for e.g. Avg(A) for average annual air temperatures).

Abbreviation	Meaning and definition
Avg	Average annual temperature (°C).
Avg(Jul)	Average July temperature (°C).
Avg(Jan)	Average January temperature (°C).
GSST	Average soil temperature during the growing season (°C).
GSAT	Average air temperature during the growing season (°C).
STHS/ATHS	Heat sum for soil and air, respectively: sum of all daily average soil and air temperatures ≥ 5 °C respectively, measured throughout the study period (degree days (dd))
STFS/ATFS	Frost sum for soil and air, respectively: sum of all daily average soil and air temperatures ≤ 0 °C respectively, measured throughout the study period. (degree days (dd))
SGS	Start of growing season: measured as the day of the year when soil temperature rose to 5 °C for five consecutive days.
GSL	Growing season length: measured as the number of days between SGS and the day of the year when temperature (air and soil temperature) dropped below 5 °C
Smelt	Snowmelt: day of the year on which soil temperature rose to ≥ 1 °C
ThD	Thaw days: measured as number of days between snowmelt (Smelt) and start of growing season (SGS) (days).
SF	Soil frozen period: number of days when soil temperature was ≤ 0 °C (days)

soil properties between the plots PCA analysis was employed. Multivariate analysis of vegetation and environmental data was performed after square-root and log-transformation of data respectively. One-way ANOVA was used to detect significant differences in mean of soil properties relative to altitude, distance to shore and distance to CRL. These factors were classified as: altitude (divided into 3 levels: low (0–100 m a.s.l.), medium (100–200 m a.s.l.), high (> 200 m a.s.l.)); distance to shore (divided in to 3 levels < 1 km, 1–10 km and >10 km) and distance to CRL (divided in to 5 levels: < 50 km, 51–100 km, 101–150 km, 151–200 km, 201–250 km). ANOVA was conducted separately for the individual forest/scattered tree data (n = 23) to determine if there were significant differences among all forest plots. Furthermore, the Kruskal-Wallis multi-comparison test was used to determine whether there were any differences in soil properties between forest (n = 23) and shrub (n = 5) plots. The forests and scattered tree plots were treated as a joint category in ANOVA and Kruskal-Wallis analysis.

A Kruskal-Wallis multi-comparison test was used to determine whether significant differences in medians of temperature variables existed between forests, scattered trees and in shrubby plots. Correlation analysis was conducted to determine strength of association of average annual air and soil temperature and topographical variables.

Next, we conducted canonical correspondence analysis (CCA) with interactive forward selection. This analysis helped to determine the most important environmental variables explaining variation in field layer composition. Lastly, detrended correspondence analysis (DCA) was combined with the vegetation classification (excluding *B. pubescens*) and the significant variables obtained from CCA analysis were introduced as supplementary variables.

The analyses were performed using Minitab 17.2.1, CANOCO 5.04 and R 3.3.1, (R Core Team, 2014). Parameters are reported as arithmetic means ± one standard deviation.

Results

Vegetation types

A total of 58 species were recorded in our study including 31 herbs/pteridophytes, 12 graminoids, eight bryophytes and seven dwarf shrub species. The most common and abundant species recorded in the stands are species with a continuous distribution in Fennoscandia. Two species peculiar to northernmost forests are *Allium schoenophrasum* subsp. *sibiricum* having northern circumboreal distribution and *Veratrum album* subsp. *virescens*, which is restricted to the northernmost parts of Norway. Alpine species (plants with their main distribution above the forest limit) were very rare, only few occurrences of *Phleum alpinum, Saussurea alpina, Salix glauca, Sellaginella selaginoides, Viola biflora, Veratrum album, Betula nana, Bistorta vivipara, and Bartsia alpina.* The separation of alpine plants was based on the list of alpine species reported in Danielsen (1971).

Species abundance and total cover (%) data are reported in Supplement S1. The total number of vascular plant species in the plots varied between 5 and 16 (Mean: 10 ± 3) and the number of alpine plants varied between 0 and 5 (1 ± 1). The first division (eigenvalue = 0.479) of TWINSPAN analysis separated plots into two categories i.e. plots exclusively dominated by herbs/pteridophytes (n = 7) from plots dominated by herbs/pteridophytes and dwarf shrubs (n = 21). In the second division (eigenvalue = 0.293), the larger group (n = 21) was further subdivided into two: the first group (n = 12) is dominated by dwarf shrub species such as *Empetrum nigrum* and *Vaccinium myrtillus*; and the second group of plots were rich in bryophytes such as *Polytrichum commune*. The three major floristic communities obtained from TWINSPAN analysis are (Supplement S2): 1. *Empetrum-Cornus-Vaccinium* type (ECV), 2. *Polytrichum-Cornus* type (PC) and highly luxuriant 3. *Cirsium-Viola* type (CV). Number of vascular plant species in ECV, PC and CV type were 28, 39 and 41, respectively.

Distribution, age and morphology of birch trees

Most of sampled birch stands are close to the CRL and at low altitudes (Fig. 2). The distribution of studied dominant field layer communities in birch stands do not point to a clear transition with increasing altitude and distance to CRL (Fig. 2).

Tree age, tree height and DBH by plot are shown in Table 1. The age of the trees varied between 11 and 77 yr (37 ± 14 yr) and the diameter at breast height varied between 1 and 19.5 cm. The stands included monocormic (Mean tree height = 6.3 m, Mean DBH = 15.3 cm), polycormic (Mean tree height = 6.7 m, Mean DBH = 13 cm) and dense shrubs (Mean tree height = 1.9 m, Mean DBH = 2.4 cm) growth forms. The tree height and DBH were strongly correlated ($r = 0.845$, $p < 0.001$) whereas age of the trees showed a weaker correlation with the DBH ($r = 0.563$, $p = 0.002$) and tree height ($r = 0.653$, $p < 0.001$).

Soil properties

The ranges of soil properties were as follows: pH (3.9–6.1), Ca (596–8232 mg kg^{-1}), Mg (270–1771 mg kg^{-1}), P (11–210 mg kg^{-1}), K (112–914 mg kg^{-1}), OM (8–47%), BD (0.2–0.6 Mg m^{-3}) and SM (26–74%). The eigenvalues and explained variation of the PCA axes 1 and 2 were 0.369/36.87 and 0.269/63.77 respectively. The first principal

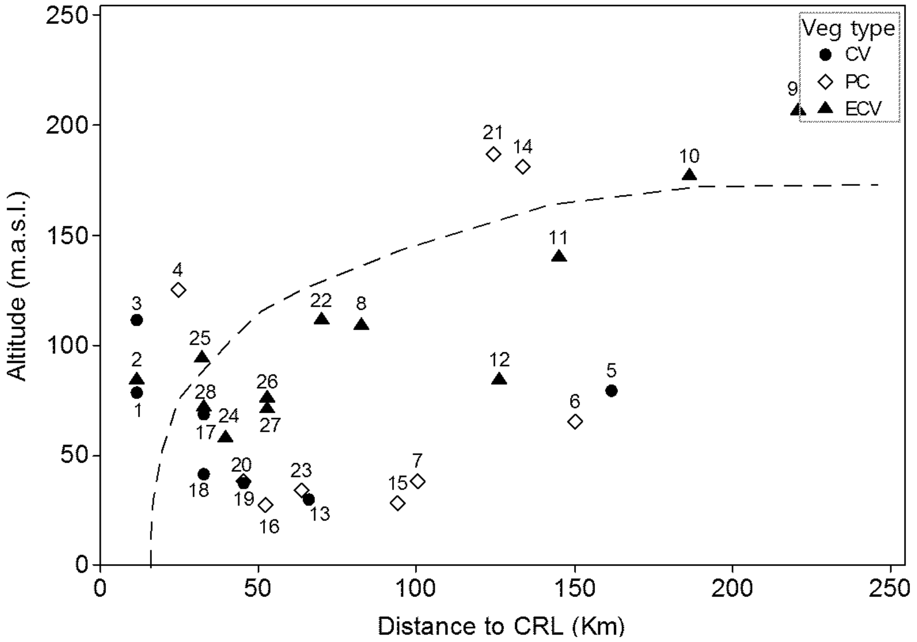

Fig. 2. Scatter diagram of altitude vs. distance to CRL. The dotted line in the graph separates the high altitude plots from low altitude plots. The plots are categorized based on dominant vegetation in the plot: CV = *Cirsium-Viola* type, PC = *Polytrichum-Cornus* type and ECV = *Empetrum-Cornus-Vaccinium* type.

component axis (Fig. 3) was positively correlated with K, P, Mg and soil moisture. Plots on the extreme left of PCA axis 1 have nutrient-rich wet soils. The second PCA axis shows positive correlation with soil bulk density and organic matter, and negative correlation with pH and Ca. The average soil properties for each plot are given in Supplement S3. Most of the plots within each vegetation type are confined to different parts of the PCA diagram. The *Cirsium-Viola* type plots (lower left) had high pH and low organic matter. The *Polytrichum-Cornus* type plots are concentrated in the middle part of the diagram with intermediate values for soil properties, while the *Empetrum-Cornus-Vaccinium* type plots (upper right) had low pH and high organic matter.

A one-way ANOVA analysis, showed decrease in pH levels (df = 2, $F = 3.96$, $p = 0.036$) with increasing distance from sea in forest and scattered tree plots. Comparison of forest/scattered tree ($n = 23$) and shrubby ($n = 5$) plots, using the Kruskal-Wallis multi-comparison test showed significant results only for K concentration (df = 1, $p = 0.02$).

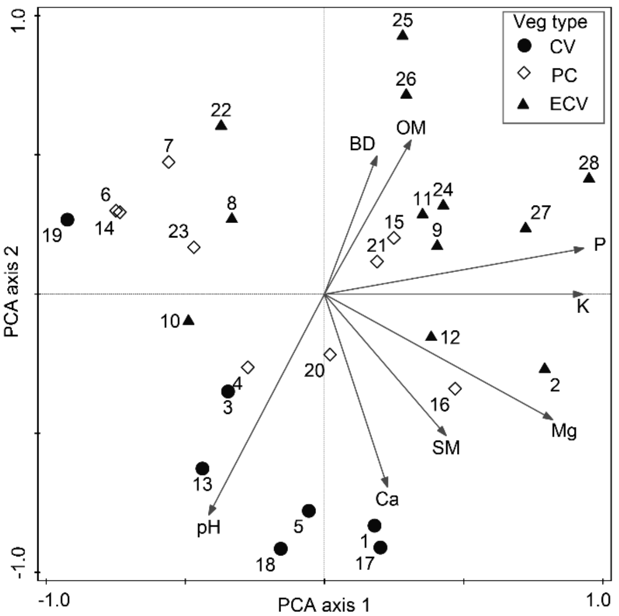

Fig. 3. PCA diagram of relative plot positions based on soil properties. Total variation is 196. BD = bulk density (Mg m^{-3}), OM = organic matter (%), Ca = calcium (mg kg^{-1}), K = potassium (mg kg^{-1}), P = phosphorus (mg kg^{-1}), Mg = magnesium (mg kg^{-1}), pH and SM = soil moisture content (%). The plots are categorized based on dominant vegetation in the plot: CV = *Cirsium-Viola* type, PC = *Polytrichum-Cornus* type and ECV = *Empetrum-Cornus-Vaccinium* type.

Air and soil temperature conditions

The annual average air temperature 2.5 ± 0.7 °C. The growing season length ranged from 107–132 days with an average air temperature of 9.5 ± 0.5 °C. The air temperature heat sum ranged from 1122 to 1392 dd and the frost sum ranged from −835 to −265 dd. The average July and

January air temperatures were 12.0 ± 0.9 °C and −6.0 ± 2.3 °C. The lowest average January air temperature was −15 °C at plot number 1.

All temperature variables calculated were compared by Kruskal-Wallis multi-comparison tests to check for differences in temperature conditions between forests (n = 12), scattered tree (n = 11) and shrubby (n = 5) plots. Since, no significant differences were found between the medians of the aforementioned three categories; we have not mentioned results in the article. Based on average temperature conditions (Supplement S4), we observe no differences in the average temperature conditions in forests, scattered tree and shrubs, hence we will now discuss the temperature conditions across entire birch forest and treeline ecotone (including shrubs).

The average annual soil temperature 3.9 ± 0.4 °C, which is higher than the average air temperature. The average growing season soil temperature was 9.4 ± 0.6 °C and growing season length was 105–147 days. The growing season length calculated based on soil temperature was low, around 107 ± 2 days for two plots. This may be due to the delay in melting of frozen soil present at these areas. Heat sums ranged from 915–1513 dd. The soil remained frozen (i.e. < 0 °C) for 174 ± 42 days with average soil frost values of −217.4 ± 60.6 dd. Snowmelt occurred on day of the year 148 ± 11, i.e. in May. The onset of the growing season took place on day of the year 155 ± 10, i.e. in June with the average thaw days being 7 ± 6 days. Average July and January soil temperatures were 11.1 ± 1.0 and 0.7 ± 0.2, respectively.

Average air (r = −0.680, p < 0.001) and soil (r = -0.609, p = 0.001) temperatures are negatively correlated with distance to shore, but not with altitude or distance to coastal reference line. Weak correlations were evident between air temperature and slope (r = 0.394, p = 0.035) as well as soil temperature and slope (r = 0.448, p = 0.017). Air and soil temperatures were highest on southerly and southeasterly aspects; air temperatures were lowest on westerly aspects and soil temperatures were lowest on northerly and westerly aspects.

Vegetation communities and environmental gradients

A CCA analysis (with interactive-forward selection) was conducted using vegetation data with environmental data (includes altitude, distance to shore and CRL, soil properties, air and soil temperature variables) gave a total variation of 3.07 with the explanatory variables accounting for 37.5% of variation. The eigenvalues and explained variation of axes 1 and 2 were 0.515 / 16.77 and 0.194 / 23.11, respectively. The forward selection results showed pH to be the most significant factor, explaining 15.6% (p = 0.002) of the floristic variation, followed by average July air temperature, explaining 6.4% (p = 0.002) and thaw days, explaining 4.9% (p = 0.024).

A DCA diagram (Fig. 4) shows the distribution of plots belonging to the three vegetation groups derived from TWINSPAN analysis and significant environmental

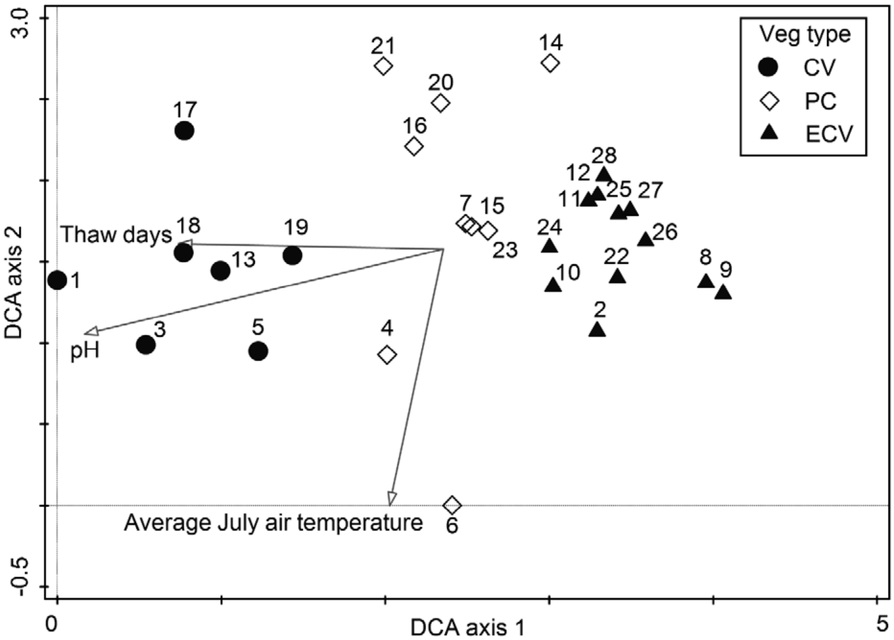

Fig. 4. DCA diagram of relative plot positions based on the vegetation groups (classified by TWINSPAN) and significant environmental variables obtained from CCA-Interactive forward selection analysis. The plots are categorized based on dominant vegetation in the plot: CV = *Cirsium-Viola* type, PC = *Polytrichum-Cornus* type and ECV = *Empetrum-Cornus-Vaccinium* type.

variables obtained from CCA with interactive-forward selection. The three vegetation types are fairly well separated along the two main DCA axes. The gradient length and eigenvalues for DCA axes 1 and 2 were 4.06/0.611 and 2.72/0.236 respectively. The main gradient axis (DCA axis 1) separated relatively wet, eutrophic, vegetation dominated by tall-herbs such as *Cirsium heterophyllum, Viola biflora, Geum rivale, Filipendula ulmaria* and *Trollius europaeus* (i.e. CV type) from relatively dry heath vegetation dominated by *Vaccinium myrtillus* and *Empetrum nigrum* (i.e. ECV type). The gradient in the vegetation was explained by pH and thaw days on axis 1; both the variables were negatively correlated with axis 1.

On the other hand, DCA axis 2 separates moist graminoid vegetation dominated by *Calamagrostis purpurea, Carex panacea, Agrostis capillaris* and *Deschampsia cespitosa* from herbaceous species such as *Bistorta vivipara* and *Veratrum album.* The second axis is negatively correlated with average July air temperatures.

Discussion

Distribution of birch forests

In Fennoscandia, mountain birch is considered a subspecies of *Betula pubescens* Ehrh. that ranges from southern Greenland to the central Kola Peninsula (Väre 2001; Wielgolaski & Nilsen 2001; Jónsson 2004; Karlsson et al. 2004; Aune et al. 2011). We have not distinguished between different *B. pubescens* subspecies in this study. Probably both subsp. *pubescens* (*B. odorata* Bechst.) and subsp. *czerepanovii* ((N.I Orlova) Hämet-Ahti, (formerly subsp. *tortuosa* (Ledeb.) Nyman) are common, however according to Lid & Lid (2005) it is not possible to separate between these two in most parts of the country. The birch stands studied are distributed in the coastal areas of Finnmark and are limited by either latitude or altitude. The mountain heights in Finnmark are low, and the highest forest stands were found at 207 m a.s.l. This is consistent with previous studies showing that the forest limit lies below 200 m a.s.l. in the northernmost parts of Norway (Aas 1964; Moen 1999). Greenland birch forests extend to their latitudinal limits, where the treeline is located at 150 m a.s.l. for forests and 250 m a.s.l. for shrubs, while in northern Iceland the treeline is between 200–550 m (Böcher 1979; Hecht et al. 2007; Wöll 2008). The northernmost forest stand in this study was found a few kilometers south of Honningsvåg, close to 71° N (Plot No. 13, Fig. 1). Most forest stands in the northernmost localities were found growing in sheltered sites protected from strong wind. Terrain was often steep, with more than 15° slope. The trees or shrubs were often polycormic with the trunks pressed downward, probably a result of snow creep. The size and frequency of birch forests decreased strongly northwards. Similar patterns are described from Iceland, Greenland and in the Murmansk Region where narrow patches of birch forests occupy plains and low mountains and form forest tundra boundaries (Böcher 1979; Koroleva 2001; Wöll 2008). This distribution pattern wherein the forests are found occupying only small low lying patches, strongly indicates lack of potential favorable growth sites in certain areas that restrict the latitudinal distribution of the forests.

In the current study, stands with tall (6 m) and old (around 50–70 yr) trees were found 71° N, and the forest limit can therefore not have advanced northwards since last few years. Stands analyzed (with an average age of 37 yr) in this study lie further north than the forest limit proposed by Hofgaard et al. (2013). According to results of the present study and Ahti et al. (1968), there has hardly been any recent northward advance of birch forests during the last century.

Birch morphology and tree age

We encountered birch trees spanning a wide morphological range from upright mono-stemmed trees 2–9 m, to crippled dense stands with multi-stemmed stunted individuals 1.5–2 m and multi-stemmed trees up to 10 m. Monocormic and polycormic forms are both common. According to Bylund & Nordell (2001), polycormic trees have larger stems and are taller than monocormic trees. In the current study, we found similar heights and stem diameters among the two different forms. The weaker correlations between age, tree height and DBH can be explained by the presence of shrubby forms, which remain suppressed at 2 m with small stem diameters.

Few of the trees sampled were relatively old up to nearly 77 yr. This is a high age compared to other trees studies in northernmost Europe (Kullman 1979; Sonesson & Hogesteger 1983; Jónsson 2004). Tree age in the current study is lower than that reported in Aune et al. (2011) who found an average tree age at treelines to be 70.8 ± 28.1 yr with average tree height of 3.0 ± 0.6 m in coastal areas of Kola Peninsula. According to Wehberg et al. (2005), by the age of 90–100 yr, the decay of trunks is accelerated.

Vegetation types and comparison with other studies

There was little variation in the number of vascular plant species between the stands and number of alpine plant species was surprisingly low in all plots. Studies of birch forests close to their distribution limits are generally assumed to include a high number of alpine plants (Nordhagen 1943; Moen 1999).

In this study, there were two floristic gradients observed. Firstly, dry heath to moist meadow vegetation and, secondly, vegetation growing in nutrient-poor to nutrient-rich conditions. Field layer vegetation comparable to the first type are found in birch forests of Murmansk Region which is dominated by *Empetrum-Cornus*, and shows transition from heath to meadow vegetation (Koroleva 2001). In current study, a decrease in species richness was observed from *Cirsium-Viola* type to *Polytrichum-Cornus* and *Empetrum-Cornus-Vaccinium* type; and are associated with soil pH and thaw days (Fig. 4). There is a clear distinction between each community along these three gradients.

Birch forests in northern Fennoscandia were studied by Hämet-Ahti (1963), but the extreme northern areas were not included. In that study, similar types to those reported here were termed as *Empetrum* type, *Cornus-Myrtillus* type, meadow - heath forest and meadow forest. A study of field layer in birch forest limits in Iceland separates three vegetation groups based on dominant species i.e. highly fertile herbaceous type, medium fertile *Vaccinium* spp. type and low fertility *Empetrum* type (Hecht et al. 2007). In the Fischer Peninsula close to Norwegian-Russian border on the Barents Sea coast, Kalela (1939) reported the following forest types according to dominant species: *E. nigrum*-heath type, *E. nigrum-V. myrtillus* heath type, *V. myrtillus* heath type and *V. myrtillus-Dryopteris linnaeana* heath type. The amount of *B. pubescens* in these types was variable.

Temperature conditions

The average annual air temperature, growing season temperature and temperature during warmest month (i.e. July in case of Norway) in the present study was higher than at birch limits in the Murmansk area, Abisko, Greenland, Iceland or southern Norway (2.4 °C) (Böcher 1979; Berglund et al. 1996; Hecht et al. 2007; Wöll 2008; Aune et al. 2011; unpublished data of G. Bandekar et al.). Despite the contrasts in average temperature conditions, the growing season lengths in this study are in agreement with other areas of birch forests with an average growing season length 105–134 days (Veijola 1998; Blinova & Chmielewski 2015; unpublished data of G. Bandekar et al.). According to Körner & Hoch (2006), the distribution of trees at high elevation is limited by low soil temperatures. Soil temperatures increased rapidly after snowmelt in the present study (thaw days = 7.4 ± 6 days). This indicates a rapid start of growing season after snowmelt in the northernmost forests. The average soil temperatures during the warmest month for this study is higher than the warmest month temperatures (6.7–10 °C) in other forest limits (Körner 1998; Körner 2003; Hecht et al. 2007; Bandekar et al. unpubl.(a)). The heat sums reported for northernmost birch forests are very high i.e. 1202 ± 153 dd compared to those report in southern forest limits (762 ± 132 dd) and in Scotland (700 dd) (Kenworthy & Forbes 1973; unpublished data of G. Bandekar et al.). The growing season length decreased with increasing distance from CRL, This observation agrees with results presented in Karlsen et al. (2008). In Kola Peninsula and Pasvik, the growing season lengths based on phenological data are very low i.e. 69–78 days as compared to Northern Norway (Shutova et al. 2006). Based on the above discussions we conclude that temperature conditions in northernmost forests during the study period are warmer than other birch forest at high latitudes, although long-term temperature data needs to be collected to confirm this.

Variation in soil properties

The plots dominated by *Empetrum-Cornus-Vaccinium* type have slightly acidic soil that was rich in K, P and organic matter. Similar soil conditions are reported in Bråthen et al. (2010 and references therein), wherein *Empetrum* dominated soils are associated with high humus and low pH conditions. In contrast, soils in *Cirsium-Viola* type plots were rich in Ca and were alkaline. The few plots belonging to the *Polytrichum-Cornus* type had nutrient-poor soils. Soil pH was highest in the low altitude coastal areas; as distance from the coast and altitude increased, the pH decreased. The lowest pH value (3.9) was recorded at the plot that was situated the farthest away from the sea (11.3 km) and at the highest elevation (207 m a.s.l.). The pH values reported in this study are in agreement with results of Grime et al. (1988) and Orlova et al. (2013), where authors found occurrences of birch at a pH of 3–6 in the Sheffield region and Khibiny Mountains (Russia) respectively. The range of soil properties reported from northernmost birch forests in Fennoscandia and Khibiny Mountains were K (270–1270 mg kg^{-1}), Ca (540–4448 mg kg^{-1}), Mg (400–1640 mg kg^{-1}) and P (99–1085 mg kg^{-1}) (Wielgolaski 2001; Orlova et al. 2013). The results from this study are similar to the results of Wielgolaski (2001), for extractable Mg concentration but K and P concentration were slightly lower and Ca values were higher. Overall, the K concentration was higher in shrub plots (635 ± 175 mg kg^{-1}) than in forest and scattered tree plots although the latter were highly variable (112–914 mg kg^{-1}).

Ecological conditions in forests, scattered tree and shrubs

Temperature conditions and soil properties (with the exception lower K concentration in forest plots) were similar in forest, scattered tree and shrub plots. Shrubs mostly cover large open areas at low altitudes, closer to CRL whereas forests were mostly dominant in sheltered areas protected from wind. This suggests that factors such as high wind velocity, rather than temperature or soil properties, might have determined growth form.

Factors limiting birch forests

The overall temperature conditions in the present study were warmer than in other northern limit birch forests. The northernmost limit of *B. pubescens* in this study does not coincide with the 10 °C isotherm for limiting treelines as suggested by Körner (1998) and references therein. In another study (unpublished data of G. Bandekar et al.), we have found that temperature conditions in coastal heaths north of northernmost forest and above the treeline in Norway are favorable for birch growth. This finding suggests these forests are not temperature limited but there might be some other environmental factors responsible for its limitation. It is possible that a dense field layer consisting of *Empetrum-Vaccinium-Betula* heaths beyond northernmost birch limit prevents establishment of birch seedlings (Miles & Kinnaird 1979; Atkinson 1992; Bråthen et al. 2010; unpublished data of G. Bandekar et al.). Other researchers have also proposed that coastal birch stands were more extensive up to the beginning of the last century owing to the presence of warmer than present regional climate (Hämet-Ahti 1963; Ahti et al. 1968; Tuhkanen 1984; Allen et al. 2007; Huntley et al. 2013). However, most forests have been destroyed by increased human activities, and woodlands were replaced by treeless dwarf-shrubs. Hämet-Ahti and Ahti (1969) have suggested that Fennoscandian birch forests are neither subarctic nor arctic, and are limited by the presence of the Barents Sea to the north. The effects of topography and strong winds prevalent along the coastal and high altitude regions in Finnmark might also contribute to the current distribution of birch (Heikkinen et al. 2002; Bryn et al. 2013). It may be noted that a similar effect of cold north-easterly winds on the northernmost limits of birch forests limits their distribution to sheltered areas (in Iceland and Greenland) as is discussed in Grime et al. (1988) and references therein. Hence, more environmental variables (e.g. wind exposure) and long-term datasets should be included on these northernmost forests to further strengthen the knowledge about occurrences of these birch forests

Finally, we conclude that the ground vegetation in current study was subdivided to three groups dominated by *Empetrum-Cornus-Vaccinium* type, *Polytrichum-Cornus* type and *Cirsium-Viola* type with pH, average July air temperatures and thaw days explaining gradients in floristic variation. The studied birch forests have similar field layer communities but do not have similar temperature conditions when compared with other such transitional zones. The majority of investigated birch trees had minimum ages of 11–77 yr, indicating there has not been a recent northward migration of birch. There were no differences in the temperature and soil properties in forest, scattered tree and shrub stands (with an exception of differences in K concentration). We found elevated levels of Ca in current study.

Lastly, we can say that sites beyond the current limit of birch growth are too steep, too exposed or rocky, with the ultimate limit being the Barents Sea itself. This suggests that empiric northernmost treelines are not truly bioclimatic and should not be used to separate between the arctic and the boreal. However, more extensive studies will be needed to confirm this claim.

Author contributions

G.B. and A.O. have both equally contributed towards planning the project, sampling of data, performing statistical analysis and writing of the manuscript.

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Supplement S1. Species abundance data.
Supplement S2. Shortened table of TWINSPAN classification of the field layer communities.
Supplement S3. Soil chemical properties.
Supplement S4. Average air and soil temperature variables.
Supplement S5. Photos of sampling sites.

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Paper III

Gauri Bandekar, Live Semb Vestgarden, Andrew Jenkins, Arvid Odland. Bioclimatic gradients and soil properties of coastal heaths from North Norway to Spitsbergen (Svalbard). (Submitted to Polar Biology: Under review)

Bioclimatic gradients and soil properties of coastal heaths from North Norway to Spitsbergen (Svalbard)

Gauri Bandekar, Live Semb Vestgarden, Andrew Jenkins, Arvid Odland

Abstract

In the far high north of the Norwegian mainland in the county of Finnmark, boreal forest is replaced by heaths. This northernmost treeline has been equated with the boundary between the boreal and Arctic biomes (heaths north of this treeline are referred as Arctic). To deepen the knowledge about these heaths and to justify if heaths north of treeline belong to Arctic; data on vegetation, temperature and soil properties were collected from coastal heaths in Finnmark both south- and north of the northernmost treeline, and below and above the altitudinal treeline. In addition, we collected data from unequivocally Arctic areas such as Bear Island (only temperature data) and Adventsdalen, to quantify latitudinal and altitudinal gradients in heath vegetation from north Norway to Adventsdalen. As expected there was a clear trend in climatic variables along the axis Finnmark - Bear Island - Adventsdalen. Vegetation analysis using TWINSPAN classification, identified five vegetation communities, two on Adventsdalen and three in Finnmark and established a clear vegetation difference between the two areas which could be explained by maximum average air temperature, average annual air temperature and soil frost sum. In contrast, heath communities north and south of the treeline in Finnmark were not distinguishable in terms floristic composition, air temperature, soil temperature or soil properties. Neither was there any clear distinction between high and low-altitude plots. Furthermore, temperature measurements were not consistent with the presence of permafrost, a hallmark of Arctic heaths. We conclude that the previously-used division of heaths in Finnmark into boreal, alpine and Arctic biomes is not justified.

Keywords: alpine, Arctic, air temperature, soil properties, soil temperature

1 Introduction

In most circumpolar regions, there is a gradual, orderly and easily recognized progression from boreal forest to heaths with increasing latitude and altitude. The boundary between the boreal and Arctic biomes is defined principally by the position of the Arctic treeline (Elvebakk et al. 1999). Based on vegetation and summer temperatures, the Arctic has been categorized into five subzones, A to E (Walker 2005). Comprehensive studies conducted in Alaska, Canada and Northern Russia describe bioclimatic variations from subzone E to A and show decreasing air temperatures, changes in soil pH, and altered precipitation patterns (Walker 2003; Walker et al. 2012). The Norwegian Arctic Islands i.e. Bear Island and Adventsdalen on Svalbard are included in subzone C.

The northernmost part of the Norwegian mainland is the county of Finnmark, here latitudinal and altitudinal limits of the boreal biome exists and beyond these limits, treeless coastal heaths dominate. The northernmost parts of the Norwegian mainland north of the Arctic treeline have been assigned to the Subzone E also called as southern Arctic zone (Elvebakk et al. 1999; Moen 1999; Walker et al. 2005). Heaths are common immediate south of this Arctic treeline occupying large areas along lowlands (boreal heaths) and above the treeline (alpine heaths). The limited ecological knowledge on these coastal heaths have discouraged suitable delineation and comparisons of the heaths in a wider context.

In Finnmark, conditions conspire to make definition of the boreal/Arctic boundary difficult. The first is the North Atlantic Thermohaline Circulation, which draws warm waters from the region of the Gulf of Mexico up along the west coast of Europe and around the northern coast of Norway into the Barents Sea. This allows boreal forest to extend far beyond its normal latitudinal limits. Secondly, the observed limits of boreal forest lie close to the northern coast of mainland Norway; between there and the unequivocally Arctic Svalbard archipelago there is only sea and a few scattered islands. This means that the progression of Arctic subzones cannot be observed. Lastly, the northern coast of Finnmark is mountainous and windswept, such that exposure and altitude further complicate the bioclimatic situation.

Vegetational variation of heaths in North Norway, Bear Island and Spitsbergen has been described previously (CAFF 1994; Edvardsen et al. 1988; Elvebakk 1999; Haapasaari 1988; Oksanen and Virtanen 1995; Virtanen and Eurola 1997; Virtanen et al. 1997; Walker 2005; Yurtsev 1994). Studies have been performed along gradients of latitude, altitude, oceanity, air temperature, precipitation, effect of the North Atlantic current (west to east gradient) and ground conditions such as permafrost and bedrock (Billings 1973; Bråthen 2016; Crawford 2008; Karlsen et al. 2008; Oksanen and Virtanen 1995; Oksanen 1997).

Relationship between coastal heath communities belonging to either boreal, alpine or Arctic areas could be demonstrated in terms of different temperature variables. Temperature directly or indirectly affects photosynthesis, nutrient absorption, productivity, and can limit plant growth at high altitudes and latitudes (Chapin 1983; Klanderud et al. 2015; Körner 2003). Temperature variables such as growing season length, growing season temperature, heat sum, summer warmth index, temperatures during the warmest month, winter frost and precipitation are pivotal to this delimitation (Chernov and Matveyeva 1997; Oksanen and Virtanen 1995; Robeson 2002; Skaugen and Tveito 2004; Virtanen et al. 2016; Young 1971). Both July air temperatures and summer warmth index been used extensively in circumpolar vegetation studies (Walker 2005), while according to Karlsen et al. (2005), temperature sum is one of the best parameters to explain plant growth conditions. According to Eurola (1974), soil temperatures, are highly important for the separation of the alpine and Arctic biomes. Unfortunately, mainly air temperatures have been included in previous studies, and there is sparse data on soil temperature conditions (Graae et al. 2012; Körner 2003; Skaugen and Tveito 2004). Vegetation cover, albedo and soil frost influences the relationship between air and soil temperature, thus making prediction of soil temperature from air temperature difficult (Graae et al. 2012; Odland 2011; Odland et al. 2017). Hence, it is important to include both air and soil temperatures in bioclimatic studies. Other soil parameters such as soil nutrients (usually scarce in Arctic habitats), pH and moisture also play an important role (Billings and Mooney 1968; Walker 2000).

In this study, we have collected data on vegetation, air- and soil temperatures, and soil properties, in order to quantify latitudinal and altitudinal gradients in heath vegetation from northernmost Norway, Bear Island, and Adventsdalen (Spitsbergen). These findings will supplement to existing knowledge on coastal heaths on mainland Norway, and to investigate whether their division into Arctic, boreal and alpine biomes is justified.

2 Materials and methods

2.1 Study areas

Studies were conducted in Finnmark County (70 - 71 °N, 21 - 29 °E), Bear Island (74 °N, 18 - 19 °E) and Adventsdalen (78 °N, 15 - 16 °E) in Spitsbergen (Svalbard), ca. 10 km east of Longyearbyen (Fig 1). Altogether, 37 plots were established at low (< 200 m a.s.l.) and high (> 200 m a.s.l.) elevations; along latitudinal gradient representing several bioclimatic zones.

In Finnmark, landscape is rugged (although elevation is modest) and the coastline is deeply indented. Much of the coastal region of Finnmark is open to the winds of the Barents Sea with maritime climate, although the rugged topography also affords sheltered areas. The bedrock in Finnmark comprises of sandstone, shale, metamorphic and igneous rocks (Bedrock map of Norway, 1: 1 million, NGU 1984). The soil type is shallow leptosol or podzol (Jones et al. 2005). Eleven sites were selected on heaths north of the treeline (i.e. in subzone E or Arctic) in the vicinities of the towns of Honningsvåg, Nordkapp, Mehamn, Gamvik and Berlevåg, choosing the most northerly sites available. The southern boundary of these heaths lie approximately between 70 - 71 °N, and is dominated by *Betula pubescens* Ehrh. (Refer Bandekar and Odland (2017) for definition of forest limit and treeline)(cf. Fig 1). Twelve sites were selected on heaths south of the treeline i.e. boreal and alpine heaths in the vicinity of the towns of Sørøya, Hammerfest, Gamvik, Båtsfjord and Berlevåg. The sample plots were located from 21 to 337 m a.s.l., with slopes ranging from 0 - 15 degrees.

Bear Island is halfway between mainland Norway and the Svalbard archipelago. The island is ca. 178 km^2 in area. The sampling on Bear Island was conducted along the north coast near the meteorological station, which has a maritime climate (Engelskjøn 1986). The northern part of the island has low average elevations and bedrock here comprises of dolomite, limestone, sandstone and shale. Soils with peat deposits are common on Bear Island. Five plots were established on relatively flat, well-drained terrain at altitudes ranging from 6 to 52 m a.s.l.. Bear Island is isolated, with a steep coastline surrounded by rough seas. As we were unable to obtain access, neither soil sampling nor vegetation analysis could be performed. The staff of the meteorological station planted soil temperature data loggers and provided photographs of the vegetation at the sites. A vegetation consisting of dwarf shrubs (especially *Salix herbacea*), vascular plants, graminoids and bryophytes could be seen; detailed vegetational analysis was not possible.

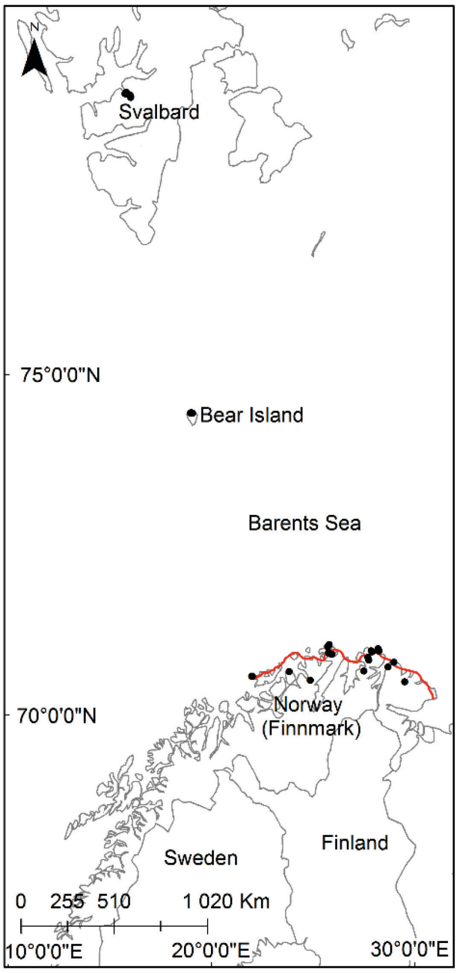

Fig 1 Map of study area. Black points indicate study areas. Red line in figure shows the northernmost distribution limit of birch forests in Finnmark.

Adventsdalen branches off the inner, south-eastern end of the Isfjord, which is the largest fjord on Spitsbergen and broad enough to bring maritime conditions and the effects of the North Atlantic current as far inland as Adventsdalen. Adventsdalen is also less prone to fog than surrounding area, with the result that conditions are somewhat warmer than at Isfjord Radio Weather Station (Engelskjøn 1986; Johansen and Tømmervik 2014). The bedrock comprises largely of sedimentary rocks such as sandstone and shale. There is soil cover on most of the ice-free parts of island, the dominant soil type being cryosol (Jones et al. 2009). Nine plots were established, at elevations ranging from sea level to 482 m a.s.l., with and slope varying from 0 to 25 degrees.

The study plots in Adventsdalen and Bear Island are located within the continuous permafrost zone, whereas the plots in Finnmark are located out of the permafrost zone (Brown et al. 1998, revised February 2001.). Wild and domesticated grazers such as reindeers, birds and other herbivores are common throughout study area on Spitsbergen and Finnmark (cf. Virtanen et al. 1997 and references therein). On the other hand, Bear Island is free from mammalian grazers; however, there are some herbivores like Diptera spp., mites, sawflies and the island is foraged annually by migrating birds (Owen and Gullestad 1984; Virtanen et al. 1997).

Precipitation data was collected from nearby stations without interpolating for topography, given as monthly normals (1961-1999) from www.eklima.no. Majority of precipitation was received from September to January in all the studied areas. The amount of precipitation received decreases with latitude; for instance coastal heaths in Finnmark receive 650 mm yr^{-1}, Bear Island 371 mm yr^{-1} and Spitsbergen 210 mm yr^{-1}. Annual air temperature data from coastal areas of Finnmark, Bear Island and Adventsdalen during the study period were 1.5 °C, 3.3 °C, 4.2 °C higher than normal temperature (1961-99) respectively. Similarly, high temperature conditions were observed for July temperatures during the study period. Air temperatures in Finnmark, Bear Island and Adventsdalen were 2.0 °C, 2.2 °C and 1.5 °C higher than the normal average July air (1961-99) temperatures respectively.

2.2 Vegetation data collection and analysis

At each selected site, a 2 x 2 m quadrat was placed randomly within an area of homogeneous heath vegetation. Vascular plants were identified according to Lid and Lid (1994); and cryptogams were identified according to Frisvoll et al. (1995) and Holien and Tønsberg (2006). Abundances were estimated visually and expressed as percentage cover. Vegetation data analysis was performed with TWINSPAN program (Hill and Šmilauer 2005) which classifies samples and species hierarchically and produces a two way table of their occurrence. Taxa were assigned to pseudospecies on the basis of identity and cut levels (0, 5, 10, 20, 40 and 60). Taxa with less than 2 occurrences were excluded. Species occurrences and abundance (SOA) within the selected communities identified were expressed as SOA-values (Odland et al. 1990).

Canonical correspondence analysis (CCA) with interactive forward selection was conducted using all air- and soil temperature variables and soil properties to determine which variables explained the floristic gradients. All environmental variables were Log$_{10}$ transformed and standardized for CCA analysis. Detrended correspondence analysis (DCA) analysis was run to obtain the main floristic gradients. In this analysis, species data were square-root transformed; the most important environmental variables derived from the CCA analysis were included as supplementary variables.

2.3 Temperature data collection and analysis

At the center of each quadrat, a TRIX8 temperature data-logger (LogTag recorders limited, Auckland, New Zealand) was buried in the topsoil at a depth of 10 cm. Soil temperatures were recorded twice daily at 01:00 and 13:00; the average of these two values was the daily average temperature estimate. These data were then used to derive other soil temperature variables (Table 1). Air temperature data provided by Norwegian Meteorological Institute was obtained from 1 km^2 resolution gridded dataset (Mohr 2008; Skaugen and Tveito 2004). From this data air temperatures at 01:00 and 13:00 at a height of 2 m above the surface were obtained and used to calculate average daily air temperature for each site. Estimated air temperature variables are presented in Table 1. In order to make study comparable, temperature (air and soil) variables from all four coastal heath zones, such as start of growing season, and growing season length were calculated by using a common threshold value of 5 °C. For variables such as start of growing season, the data is given as day of the year (DOY). Since the study was conducted during August 2013 to August 2014, the first DOY has been taken as 1.1.2014 and the last DOY is taken as 31.12.2013 to form a continuous dataset. This method of temperature data analysis does not affect interpretation of results.

Regression analysis was used to investigate the relationship between (1) latitude and air temperature and (2) latitude and soil temperature. The analyses were performed separately for low altitude (< 200 m) and high altitude (> 200 m) plots. The relationship between altitude and temperature was similarly investigated for Finnmark and Spitsbergen separately. Mann-Whitney tests were used to determine if there were differences in temperature variables between heath plots south and north of the treeline or at low and high altitudes in Finnmark.

Table 1 Overview of soil and air temperature variables, with abbreviations and measurement units used in the context of this study. In each plot, the following variables are estimated. (Note: the variables Avg, Avg(July), Avg(Jan) and GSL were calculated for air and soil temperatures and will be followed by (A) and (S) respectively in further analysis for e.g. Avg(A) for average annual air temperatures).

Abbr.	Definition
Avg	Average annual temperature (°C).
Max	Maximum temperature (°C).
Min	Minimum temperature (°C).
Avg(Jul)	Average July temperature (°C).
GSST	Average soil temperature during the growing season (°C).
GSAT	Average air temperature during the growing season (°C).
STHS/ATHS	Heat sum for soil (STHS) and air (ATHS) temperature is the sum of all daily average soil and air temperatures ≥ 5 °C respectively, measured throughout the study period (Degree days (dd)).
STFS/ATFS	Frost sum for soil (STFS) and air (ATFS) temperature is the sum of all daily average soil and air temperatures ≤ 0 °C respectively, measured throughout the study period. (Degree days (dd)).
SWI	Summer warmth index (SWI) is the sum of mean monthly temperatures greater than > 0 °C (Walker 2005; Young 1971).
SGS	Start of growing season (SGS) is measured as DOY when soil temperature rose to 5 °C for 5 consecutive days.
GSL	Growing season length (GSL) is measured as the number of days between SGS and the DOY when temperature (air and soil temperature) in autumn was last recorded to be 5 °C.
ThD	Thaw days (ThD) is measured as number of days between snowmelt (i.e. when ground temperature was ≥ 1 °C) and start of growing season (SGS).
SF	Soil Frozen period (SF) is the number of days when soil temperature was ≤ 0 °C (Days).

2.4 Soil sampling and analysis

Soil samples were collected at the end of the measurement period in August 2014. Soil was sampled from the four corners of the vegetation plots to a depth of 5 cm in the topsoil using a 7 cm diameter steel cylinder. Soil samples from the four corners were homogenized, air-dried and passed through 2 mm sieve. Soil moisture was estimated by ASTM D 2216 (Standard test method for laboratory determination of water (Moisture) content of soil). Soil samples were analyzed for plant-available Phosphorus (P), Calcium (Ca), Magnesium (Mg) and Potassium (K), by the ammonium lactate method (Egnér et al. 1960) using a Perkin Elmer HGA 900 (Graphite furnace) and AIM 3000 series Flame atomic absorption spectroscope. Organic matter content was estimated by the loss-on-ignition method (Dean 1974). Bulk density was estimated using the method of Page-Dumroese and Jurgensen (1999).

Two-way ANOVA (analysis of variance) was applied to determine the individual and interaction effects of latitude and altitude on each of the soil properties. Altitude was divided into two levels (< 200 m a.s.l. (low)), and > 200 m a.s.l. (high)) and latitude into three levels (70 °N, 71 °N and 78 °N). Furthermore, one-way ANOVA was used to test differences in the mean values of each soil property for heaths in Finnmark north and south of the treeline and at high and low altitude. A post-hoc Tukey test to confirm which of the groups were significantly different from one another. Analyses were performed in Minitab (Minitab-17 2010), R software (R-software 2014) or Canoco 5 (ter Braak and Šmilauer 2012).

3 Results

3.1 Differences in temperature variables

The air- and soil temperature data are shown in Table 2. In Finnmark, average annual soil temperature was 2.6 ± 0.5 °C, n = 12 for plots south of treeline and 2.8 ± 0.3 °C, n = 11 for plots north of treeline; on Bear Island it was 1.2 ± 0.6 °C, n = 5 and on Adventsdalen it was -2.5 ± 1.5 °C, n = 9. Average July soil temperature decreased northward from south of treeline (11.1 ± 1.0 °C, n = 12); to north of treeline (10.6 ±1.4 °C, n = 11) in Finnmark, through Bear Island (8.1 ± 1.1 °C, n = 5) and Adventsdalen (6.7 ± 0.9 °C, n = 9). The number of days taken to thaw the soil (Thaw Days) was lowest at Bear Island (12 ± 3.4 days, n = 5).

Table 2 Average temperature (air and soil) variables and soil properties from the different study areas. The averages are reported for both high and low elevation plots in separate columns with standard deviation values (±SD) and n = sample size. Abbreviations and terminologies used here for temperature variables along with their units of measurement are explained in Table 1. Soil properties include; pH, P = phosphorus (mg/100g), Ca = calcium (mg/100g), Mg = magnesium (mg/100g), K = potassium (mg/100g), OM = organic matter (%), SM = soil moisture (%) and BD = bulk density (g/cm^3).

Variable	Finnmark (Mainland Norway)		Finnmark (Mainland Norway)		Bear Island	Adventsdalen	
	South of treeline heaths		North of treeline heaths				
Elevation	Low, *n*=3	High, *n*=9	Low, *n*=6	High, *n*=5	Low, *n*=5	Low, *n*=6	High, *n*=3
Avg(S)	2.9±0.1	2.4±0.6	2.8±0.4	2.9±0.3	1.2±0.6	-1.7±0.9	-4.3±0.7
Max(S)	14.9±4.1	15.3±2.4	13.4±2.4	14±1.6	10±1.3	9.9±2.1	10.9±0.8
Min(S)	-5.2±3.4	-4.9±4.4	-5.7±3.3	-1.4±1.2	-7.0±3.4	-10.5±3.3	-15.4±3.2
STHS	1043±66	973±71	1083±182	939.7±95	694±100	397±123	267±76
STFS	-134±88	-230±221	-189±120	-37±30	-396±237	-1140±333	-1952±298
SF	99±26	111±70	128±46	61±39	181±38	232±5	255±4
ThD	16±2	16±11	23±13	13±10	12±3	22±7	20±6
SGS	155±1	171±12	162±13	170±10	164±10	176±6	185±9
Avg(JulS)	10.4±1.1	11.3±0.8	10.4±1.5	10.9±1.2	8.1±1.1	6.9±0.9	6.2±0.8
GSL(S)	128±1	109±13	120±13	110±9	104±11	61±13	49±10
GSST	8.5±0.4	9.2±0.4	9±0.7	8.8±0.4	7±0.7	6.5±0.6	6±0.4
SWI(S)	39.3±1.6	36.2±2.3	39.5±4.8	35.5±3.1	26.5±2.7	18.6±3	13.6±1.5
Avg(A)	3.3±0.7	2.0±0.9	2.6±0.2	2.9±0.4	0.2±0.1	-2.3±0.1	-4.7±0.2
Max(A)	19.9±0.3	18.2±1.2	17.6±1	17.2±0.9	10.2±0.1	10.6±0.1	8.2±0.2
Min(A)	-9.8±1.7	-12.1±2.2	-10.3±0.4	-10±0.3	-11.4±0.1	-18±0.1	-20.4±0.2
ATHS	1348±97	1089±156	1164±29	1121±104	449±15	489±17	191±31
ATFS	-362±112	-551±196	-412±51	-291±24	-600±16	-1493±22	-2055±44
Avg(JulA)	12.8±1.1	11±1.3	10.6±0.5	10.2±0.7	6.2±0.1	7.1±0.1	4.7±0.2
GSL(A)	141±7	129±6	129±0	130±2	85±0	83±1	46±3
GSAT	9.9±0.3	8.8±0.8	9.1±0.2	8.8±0.6	6.2±0.1	6.5±0.1	4.7±0
SWI(A)	48±3.6	39±5.5	41.7±0.9	41±3.7	21.5±0.4	21.4±0.4	11.9±0.7
pH	4.3±0.1	4.6±0.5	4.6±0.4	5.2±0.3		5.5±0.4	5.5±0.3
P	7.2±0.5	3.3±2.1	6±3.2	2.7±0.5		3.5±1.5	2±0.1
Ca	142.7±30.2	114.1±128.7	179.1±130.1	146.4±73.9		244.2±154.4	133.7±25.5
Mg	133.2±14.4	51.4±52.3	108.5±66.9	84.7±38.4		43.1±14.9	36.8±5.3
K	46.2±3.2	20.8±16.9	37.3±18.7	18.9±5.4		11.6±3.7	12.4±2.6
OM	80.5±8.5	27.1±26.2	56.6±33.8	28.4±12.4		13±5	7±2.6
SM	67.4±1.3	38.6±14.3	53.6±19.9	44.2±10.8		34.3±7.1	15.5±5.1
BD	0.2±0	0.7±0.3	0.5±0.4	0.6±0.2		0.7±0.2	1±0

Regression analysis demonstrated a strong relationship between the average annual air and soil temperatures along the gradient from Finnmark to Adventsdalen at both high elevation (Avg(S) = 0.38 + 0.90*Avg(A); *rs*= 0.88) and at low elevation plots (Avg(S) = 0.53 + 0.83*Avg(A), rs = 0.84). There was a significant correlation between latitude and all temperature variables except thaw days; r^2 values were higher for high elevation plots (Fig 2, Online Resource 1). It is evident from Fig 2 and Online Resource 1 that there is a decrease in temperatures both with increasing altitude and latitude (with exception of thaw days).

The growing season length was similar in Finnmark, it was 131 days based on air temperature and 115 days based on soil temperature; heath plots south and north of treeline did not differ, nor did high and low altitude plots. The same applies to growing season temperature, growing season length, heat sum and average July temperature (Table 2).

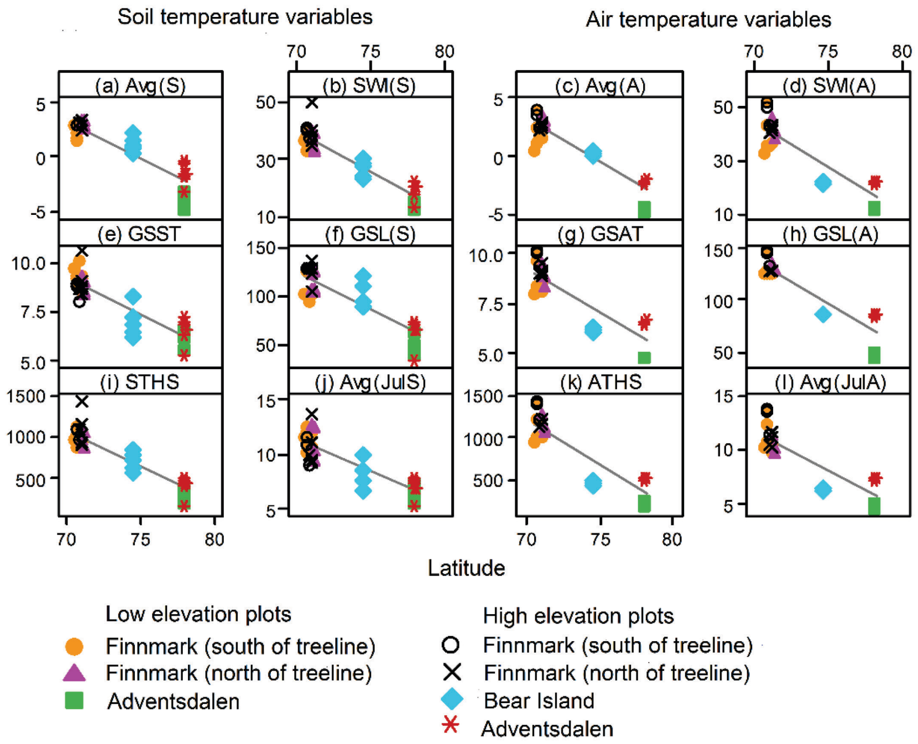

Fig 2 Scatter plot of temperature variables vs latitude for all study plots. (a) Avg(S) = average annual soil temperature (°C), (b) SWI(S) = summer warmth index, (c) Avg(A) = average annual air temperature (°C), (d) SWI (A) = summer warmth index, (e) GSST = growing season soil temperature (°C), (f) GSL(S) = growing season length (days), (g) GSAT = growing season air temperature (°C), (h) GSL(A) = growing season length (days) (i) STHS = heat sum (dd) (j) Avg (JulS) = Average July temperature (°C), (k) ATHS = Heat sum (dd) and (l) Avg (JulA) = Average July temperature (°C).

The effect of altitude on temperature variables differed between Finnmark and Adventsdalen. Regression analysis (Online Resource 2) showed correlations only for SGS, GSL (S) and GSAT in Finnmark, while on Adventsdalen, strong correlations were seen for Avg(S), STFS, SF, ATHS, ATFS, GSAT and GSL (Online Resource 2).

3.2 Variation in soil properties

Soil property data is shown in Table 2. Alkalinity increased with latitude. Plant available soil nutrients (with exception of Ca), OM and SM were higher in Finnmark as compared to Adventsdalen (Table 2). A two - way ANOVA was used to investigate individual and interactive effects of latitude and altitude on the soil properties. Latitude significantly affected pH ($F(2,25) = 19.4$, $p < 0.0001$), K ($F(2,25) = 4.3$, $p = 0.025$), SM ($F(2,25) = 8.0$, $p = 0.002$), BD ($F(2,25) = 4.2$, $p = 0.026$) and OM ($F(2,25) = 5.97$, $p = 0.008$). Altitude significantly affected P ($F(2,25) = 11.3$, $p = 0.003$), Mg ($F(2,25) = 4.89$, $p = 0.036$), K ($F(2,25) = 6.4$, $p = 0.018$), SM ($F(2,25) = 10.9$, $p = 0.003$), BD ($F(2,25) = 7.07$, $p = 0.013$) and OM ($F(2,25) = 8.27$, $p = 0.008$). No significant interaction effects of latitude and altitude were found.

Results of Mann-Whitney test indicated that medians of soil property values were similar for plots north and south of the treeline in Finnmark at both high and low altitudes (Mann-Whitney test, see Online Resource 3).

3.3 Vegetation communities and associated environmental variables

Altogether, 72 plant taxa, including 56 vascular species, were recorded. Vascular plant species richness did not vary greatly with latitude; the number of species for Finnmark heaths south of treeline, north of treeline and Adventsdalen being 29, 25 and 26 respectively.

The results of TWINSPAN analysis are shown in Online Resource 4. The first TWINSPAN division (eigenvalue = 0.796) separated Finnmark plots from Adventsdalen i.e. suggesting a markedly strong difference in vegetation with latitude. The second division (eigenvalue = 0.508) separated snowbed plots from dwarf shrub - dominated plots in Finnmark. The third division (eigenvalue = 0.775), separated vegetation communities from low and high elevation plots in Adventsdalen. In the subsequent division, *Empetrum* heaths in Finnmark were separated in to two groups based on the abundance of *Betula nana, Vaccinum vitis-idaea, Ptilidium ciliare* and *Arctous alpinus*. The five vegetation communities obtained from TWINSPAN analysis were: (1) *Salix herbacea - Carex bigelowii* (SC) (snowbed); (2) *Empetrum nigrum - S. herbacea* (ES); (3) *E. nigrum - B. nana - Ptilidium ciliare* (EBP); (4) *Dryas octopetala - Cassiope tetragona - Poa arctica* (DCP) and (5) *Alopecurus magellanicus - Sanionia uncinata* (AS).

Canonical correspondence analysis (CCA) with interactive forward selection and Bonferroni correction was conducted to estimate which of the temperature and soil properties best explained the vegetation differences. The eigenvalues and explained fitted variation on axes 1, 2 and 3 were 0.79 / 44.1, 0.35 / 63.55 and 0.30 / 80.57 respectively. Maximum air temperature explained most variation (17.2 %, p = 0.002), followed by soil temperature frost sum (7.3 %, p = 0.002), air temperature growing season length (6.5 %, p = 0.002), soil moisture (5.4 %, p = 0.002) and air temperature frost sum (4.3 %, p = 0.006).

DCA analysis was used to explore floristic gradients between the study plots. The vegetation clusters from TWINSPAN analysis and the temperature variables and soil properties selected through CCA were included as supplementary variables (Fig 3). Eigenvalues / gradient lengths for axes 1, 2 and 3 were 0.85 / 5.45, 0.31 / 3.44 and 0.23 / 2.01 respectively. DCA axis 1 clearly separates Finnmark and Adventsdalen. Most of the floristic gradient of DCA 1 was explained by temperature and soil properties. DCA axis 2 display a gradient from low to high elevations. In Adventsdalen, there was a distinct separation of the low elevation *Dryas octopetala - Cassiope tetragona - Poa arctica* heaths, distributed on calcareous substrates (Fig 3, lower part of DCA axis 2) from high elevation exposed ridge heaths. The low and high elevation heaths in north Norway were poorly separated, indicating small floristic and temperature differences.

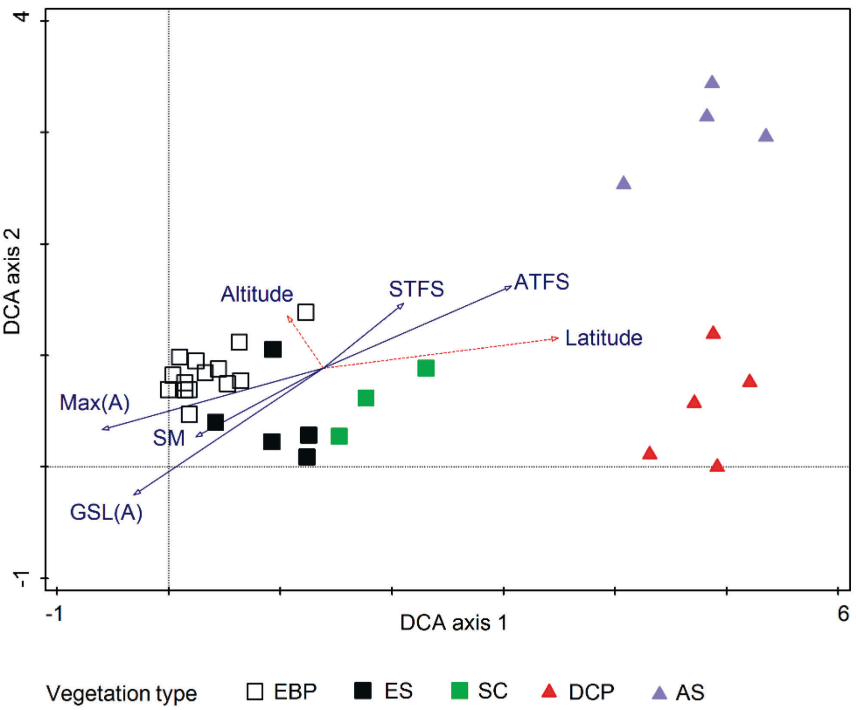

Fig 3 DCA diagram showing clustering of vegetation communities based on TWINSPAN analysis and the main environmental variables (temperature variables and soil properties) obtained from CCA - Interactive forward selection. Altitude and latitude have been added as supplementary data. The vegetation types EBP = *Empetrum nigrum* - *Betula nana* - *Ptilidium ciliare*, ES = *Empetrum nigrum* - *Salix herbacea*, SC = *Salix herbacea* - *Carex bigelowii*, AS = *Alopecurus magellanicus* - *Sanionia uncinata* and DCP = *Dryas octopetala* - *Cassiope tetragona* - *Poa arctica*. The total variation was 4.39. Max(A) = Maximum air temperature (°C), STFS = soil temperature frost sum (dd), GSL(A) = growing season length (based on air temperature)(days), SM = soil moisture (%) and ATFS = air temperature frost sum(dd).

4 Discussion

The present study indicates, that separation of heath vegetation in northernmost Finnmark into three different bioclimatic zones (alpine, boreal and Arctic) is rather questionable. We will discuss the vegetation communities, temperature conditions and soil properties within these heaths on mainland Norway; and how they relate to heaths in Bear Island and Adventsdalen.

4.1 Vegetation differences

The studied coastal heaths were located in heterogeneous topography, spanning from 70 - 79 °N at elevations ranging from sea level to 482 m a.s.l. prevalent with maritime climatic condition. Change in vegetation occurs naturally as a consequence of variation in topography and environmental conditions. The TWINSPAN classification separated the study plots into five communities, out of which three were found on mainland Norway and two in Adventsdalen. Three communities dominant on mainland Norway included *E. nigrum* - *B. nana* - *P. ciliare, E. nigrum* - *S. herbacea* and *S. herbacea* - *C. bigelowii* were commonly distributed in south- and north of treeline plots on mainland

Norway. The three communities in northernmost Finnmark were floristically strongly related and separated by less than 2 SD units on the DCA axis 2 (Fig 3) while the plots in Adventsdalen showed large differences, especially along the altitude gradient. Maximum air temperature, growing season air temperature and amount of soil frost are the three main variables explaining the vegetation variation from Finnmark to Adventsdalen. Temperature data also show small differences between the plots in northernmost Finnmark (Table 2). Studies (Karlsen et al. 2005; Young 1971) suggests vegetation based method can be used for mapping local climatic conditions and vice versa. Since, the vegetation south and north of treeline is similar, it can be presumed to have similar climatic conditions. Several studies (e.g. (Elvebakk et al. 1999; Walker et al. 2005)) have omitted coastal heaths south of subzone E (i.e. south of treeline). They have previously been referred as either boreal or alpine biomes (Moen 1999). (CAFF 1994) have included the forested areas south of coastal heaths in north Norway under Arctic - alpine biomes. According to Oksanen and Virtanen (1995), the differences in Arctic and alpine vegetation can be reflected through the winter temperatures and precipitation. From Mann-Whitney results and Table 2, we see the differences in winter temperature conditions are very small further supporting our claim.

The *D. octopetala - C. tetragona - P. arctica* community separated in Adventsdalen show similarities with descriptions given by Elvebakk et al. (1999). *C. tetragona* is dominant in the C zone and occurs circumpolarly. The vegetation communities occurring in Adventsdalen are distinctly different from those found on mainland Norway (Online Resource 4) and include mainly calciphile species. This is in accordance with Virtanen and Eurola (1997) who maintain that on Spitsbergen, the whole range of vegetation communities consists of species which can be regarded as calciphilous. The high elevation plots in Adventsdalen is separated from the lowland plots by ca. 2.5 SD units (Fig 3), which is mainly associated with differences in temperature variables (Table 2).

The communities consisting of exclusively acidophilous species, which dominate in north Norway, are uncommon on Spitsbergen. This is probably due to low precipitation, permafrost, and base rich bedrock which directly or indirectly affect soil (Virtanen and Eurola 1997). Major vegetation differences between north Norway and Adventsdalen should be expected since Adventsdalen is situated within the Arctic C subzone.

In north Norway, the SC and ES communities were found at high elevations only, both south- and north of the treeline. The majority of the investigated plots (the EBP community) dominated by *E. nigrum, B. nana* and *P. ciliare*, were found at both high and low elevation plots in Finnmark (Online Resource 4). One of the probable explanation for occurrence of similar vegetation communities at low and high elevation could be due to similarities in start of growing season length and growing season temperature.

4.2 Variation in air and soil temperature

4.2.1 Air and soil temperatures in Finnmark

Mann-Whitney test comparing the medians of south- and north of treeline heath plots (at low- and high elevation) showed that there were no significant differences between the groups (Online Resource 3) indicating that heaths plots were not different from one another. The regression results for Finnmark show that start of growing season, growing season length based on soil temperatures and growing season air temperature did not vary substantially with altitude. This can be explained by low mountain elevations along the coastal areas in Finnmark (ca. 300). The summer warmth index values in Finnmark (> 35) are higher than the values reported from Arctic areas in Eurasia and North America (Walker et al. 2012). According to Skaugen and Tveito (2004) the start of growing season was 31/5 to 14/8 (1961-90) for Finnmark, which fits well with the start of growing season for current study (i.e. June) based on air temperature. The limit of forests in northernmost Norway has an average air and soil temperature heat sum of 1231 ± 90 dd, $n = 28$ and 1202 ± 153 dd, $n = 28$ beyond which the forest ceases to occur (Bandekar and Odland 2017). In this study, average July temperatures were higher than 10.2 °C, both measured in the air and in the soil, and growing season length were longer than 110 days. These variables lie within the tolerated range for birch forests (Holtmeier 2003), and indicates that birch forests could have been growing in most of the study sites (both alpine and Arctic) based on evaluation of these variables. However, the main problem for birch would probably be exposure to wind, rocky and undulating topography and lack of land due to presence of Barents Sea in north

4.2.2 Air and soil temperatures in Adventsdalen

In lowlands, growing season length in Adventsdalen is less than 61 days and 83 days based on soil and air temperatures respectively. Average annual temperatures were lower than -2 °C. Most temperature variables show significant decreasing trends with altitude. In Adventsdalen, the average annual temperature conditions, soil frost sum, air temperature heat sum, air temperature frost sum, growing season air temperature and growing season length decreased strongly with increasing altitude (Online Resource 2).

In Arctic areas, Walker (2010) described five elevational belts, each extending 333 m, with a temperature difference equivalent to 2 °C. In the Adventsdalen study area, two altitudinal zones (c and b) could be separated according to (Walker 2010). The regression results in Online Resource 2 shows that the decrease in soil temperature (Avg(S)) is 2 °C with an altitudinal increase of 333 m.

4.2.3 Gradients from Finnmark to Adventsdalen

Increasing latitude causes shifts in temperature conditions; our results suggest strong changes are evident mostly at high elevations rather than low elevations along latitudinal gradient (Online Resource 1). Conditions in Bear Island, located between mainland Norway and the Svalbard Archipelago show intermediate values (Fig 2, Table 2). It should, however be remembered that there are no data from high altitudes on the Bear Island. Most significant are the increases in frost-related variables increase toward the Svalbard, and the warmth-related variables increase toward Finnmark. The only variable that show no significant latitudinal trend was length of the thaw period (ThD) and start of growing season (at high elevation). This indicates that temperature increases in the study sites in Adventsdalen were not significantly different from the study sites in Finnmark. Thawing of the upper soil layer on the relatively well-drained, minerogenic and dry soils in the Dryas heaths took a relatively short time. Similar thawing duration has also been found in Dryas heaths at high elevation in south Norway (Reinhardt and Odland 2012).

The average July air temperatures from our study in subzone E, Bear Island and Adventsdalen are in range of previously measured temperatures in Walker et al. (2005) and references therein. The air temperature heat sums in current study are similar to those presented in Karlsen et al. (2005) and Engelskjøn (1986) for Finnmark and Bear Island respectively. The summer warmth index values reported for heaths north of treeline, Bear Island and Adventsdalen in the current study are higher than the values reported in Eurasia and North America (Walker et al. 2012).

Generally, the Arctic is characterized by presence of permafrost, which is mainly a product of the low air temperatures. Permafrost, or permanently frozen ground, is soils or sediments that remain at or below 0 °C for at least two consecutive years (Harris et al. 2009). The active layer or the permafrost undergoes freeze and thaw cycles annually (Harris et al. 1988). According to Westermann et al. (2010), temperatures in the upper layer can increase rapidly in the warm season. According to King (1986) and Isaksen et al. (2008), and the distribution limit of permafrost corresponds to where mean annual air temperatures are lower than -1 to -2 °C. Average annual air temperatures in the Finnmark study areas were higher than 2 °C, and had relatively low values of air and soil temperature frost sums compared to Bear Island and Adventsdalen (Table 2). The temperature variables from Finnmark therefore comply with the fact that there is no permafrost in coastal areas of Finnmark (Isaksen et al. 2008). According to study of (Mazhitova 2008), the author suggested that in Fennoscandia there are practically no mineral soils with seasonal freezing layer reaching the permafrost table. This suggests that coastal areas in Finnmark are free from permafrost.

4.3 Soil properties

The soils in the boreal, low Arctic and sub-Arctic are characterized by the presence of O horizon (Jones et al. 2009). As mentioned earlier, the permafrost cover is continuous over Arctic areas and it decreases/becomes discontinuous as we move south (Brown et al. 1998, revised February 2001.). The Arctic soils mostly remain frozen from 25 - 90 cm making it impossible for trees to grow. In summers, however we can see the top active layers of permafrost thawing in Arctic leaving the ground soggy (in flat terrain), while the alpine soils are better drained. This can particularly explain high soil moisture values at high latitudes and altitudes (Table 2). Walker (2000) showed that it is important to include the combined effects of climate, parent material and topography when studying vegetation responses. This is mainly due to the fact that low temperatures and presence of permafrost cover reduces the rate of weathering; eventually leading to lower mineral input to the soil (Chapin 1983). This was confirmed from ANOVA results, which showed significant ($\alpha = 0.05$) results for decrease in potassium, soil moisture and organic matter with latitude. The decrease in soil moisture could be associated with low annual precipitation recorded at high latitudes occurring because northern areas usually lie north of polar front (Oksanen and Virtanen 1995). According to (Walker 2000), pH is the most important soil property affecting vegetation. The soil alkalinity is seen increasing with latitude and can be explained with increasing calcium content of the soil (Table 2). The overall calcium content of the soil at low elevation in Adventsdalen plots was very high, this can partly explain the dominance of calciphilous vegetation (Online Resource 4). Virtanen and Eurola (1997) reported similar observations. According to Walker et al. (2012), pH conditions in subzone C were higher in North America (7.8) than in Eurasia (4.5). The soil organic matter is another important parameter indicating soil quality

(Schoenholtz et al. 2000) and was three times higher in Finnmark than in Adventsdalen plots (Table 2). The results comply well with the Bockheim et al. (1996), who reported that the organic carbon content was reduced from nearly 50 kg m^{-2} near treeline to negligible amounts in extreme north.

Decrease in potassium, magnesium, phosphorus, soil moisture, bulk density and organic matter content with increasing altitude could have occurred due to high frost sum values and large number of days with frozen soil at high altitudes. Arctic heaths of mainland Norway are an exception to this as they had higher frost sums at low elevations.

Mann-Whitney results were not significant for differences in means of coastal heaths south- and north of treeline from mainland Norway. This indicates that the soil chemical properties are similar in both the vegetation zones on mainland Norway (Online Resource 3).

4.4 Do coastal heaths of northernmost Norway belong to Arctic?

Where and how to separate the boreal and Arctic biomes have been discussed for decades, however, investigations have led to unsettled discussion on whether the treeless coastal heaths of northernmost Norway are Arctic or not (Ahti et al. 1968; Elvebakk 1999; Eurola 1974; Hustich 1979; Sjörs 1963). The coastal heaths of the northernmost Norway are an enigma in many ways owing to the numerous criteria developed across world used to define the Arctic. Problems associated with the separation between the Arctic and boreal biomes have particularly been difficult in areas strongly influenced by an oceanic climate (Elvebakk 1999). The coastal heaths of northernmost Norway extend towards east to Kola Peninsula (Aleksandrova 1980; Koroleva 1994), and similar heaths have also been described from Iceland and Greenland (Böcher 1979). Out of the numerous criteria developed to define the Arctic biome; vegetation (Ahti et al. 1968; Aleksandrova 1980; Elvebakk et al. 1999), summer temperature (Walker et al. 2005; Young 1971), permafrost (Crawford 2008) and position north of treeline (Elvebakk et al. 1999; Walker et al. 2005) have mostly been emphasized. Environmental data associated with the boreal/Arctic transition has, however rarely been studied, except for air temperatures.

Walker et al. (2005) used mainly the treeline to define the Arctic tundra region. It has been emphasized that the current polar treeline position in Norway used to delineate Arctic is a consequence of anthropogenic activities occurred over past century leading to shrinking of formerly widespread boreal zone (Ahti et al. 1968; Elvebakk 1999). In exposed, oceanic areas, however use of occurrence of trees or forest as the only criterion for delimiting Arctic might be an unsatisfactory approach. In a previous study (Bandekar and Odland 2017), air and soil temperatures associated with the northernmost occurrences of birch forests were investigated; and the results indicate that this forest limit should not be classified as a climatic forest limit. Main reasons being the limit of *B. pubescens* does not coincide with the 10 °C isotherm, and is not considered to be limited by temperature conditions (Bandekar and Odland 2017). Thus making it an unreliable criteria to define transition between boreal and Arctic biome.

Earlier literature reveals that ecologists using vegetation criterion have excluded heaths north of the treeline in Norway and Kola Peninsula from the Arctic zone due to dominance of large number of southern (boreal) species in this zone (Ahti et al. 1968; Aleksandrova 1980; Tuhkanen 1984; Yurtsev 1994). Areas not defined by a temperature-limited forest limit have been described as “pseudo tundra” or “pseudo-Arctic” (Hustich 1960). Hustich (1960) refers to pseudo-Arctic vegetation in Scandinavia, Iceland and Greenland, implying that this vegetation has the physiognomic appearance of tundra but it should be included in the boreal zone. (Ahti et al. 1968; Böcher 1979; Eurola 1974; Haapasaari 1988) maintained that nowhere in Fennoscandia is there truly regional Arctic vegetation at sea level, and that the oceanic sea-level heaths largely belong to the mainly wooded northern boreal zone.

In Walker et al. (2005) combinations of summer temperature variables and vegetation characteristics have been used to delimit altitudinal vegetation zones. If summer temperature is to be used as the sole variable to separate vegetation zones and biomes, then heaths south - and north of treeline should not be treated as separate zones as they have fairly similar growing season temperature, growing season length and heat sums based on both air and soil temperature. In the current study, the summer warmth index based on soil temperatures is similar in heaths south - and north of treeline, but different when we compare the summer warmth index calculated by air temperatures. This indicates that separation of different vegetation zones based on summer warmth index alone can also be questionable.

Our main conclusion based on analysis of vegetation, temperatures and soil chemical properties suggests that heaths south and north of treeline in Finnmark shows no significant differences, and consequently it would not be ecologically justifiable to separate them into different biomes. However, more vegetation data, ecological data and research is needed to support our claim.

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