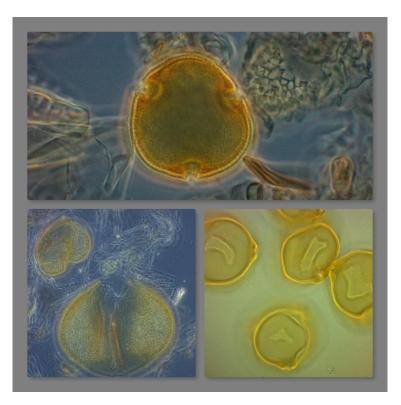
Post-glacial (Holocene) tree-line and climate dynamics at Høvringen, eastern Norway, inferred from pollen, mega- and macrofossils



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Front cover photo: Pollen grains of Tilia cordata, Pinus sylvestris and Betula pubescens, by Kristina F. Svare

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Abstract

Data from palaeoecological investigations provide useful information about changes in tree-line and climate dynamics as well as impacts of abrupt climate change in the past. This is beneficial for providing a long-term perspective about ecological responses to climate change. Here, I investigate post-glacial development and fluctuations of tree-lines, forest lines and climate in both a local and a regional perspective. Reconstructions are based on peat-sequences from two study sites situated at different elevations in the Høvringen area near Rondane, eastern Norway. The study includes two sites, Stripåtmyrin (990 m a.s.l.) and Heimfjellsmyren (1097 m a.s.l.), both located close to ecological ecotones between alpine forests and tree-lines of Betula pubescens and Pinus sylvestris. Peat sequences did not extend beyond ca. 9600 cal. yrs BP, therefore pollen records could not be used to fully infer the entire Holocene vegetation and climate. Additionally, too few megafossils were obtained to date the establishment of treebirch and pine. Nevertheless, pollen, stomata, macrofossils (e.g. leaves, needles and seeds) and megafossils (bigger remains of pine and birch) give evidence of tree-birch and pine forests established before 9600 cal. yrs BP in the study area. This reflects an early Holocene (9600-8200 cal. yrs BP) mean July temperature of at least ll°C, roughly l°C higher than present. Regionally, the mean July temperatures reached 12-14°C according to pollen of Corylus, Quercus and Ulmus. The Holocene Thermal Maximum (HTM) might have occurred in the early Holocene according to the high pollen influx values and the occurrence of Hippophaë rhamnoides at Stripåtmyrin. During the mid-Holocene (ca. 8200-4000 cal. yrs BP) the temperature was at least 10°C during a period of slightly drier and cooler conditions, perhaps showing traces of the 8200-event ("Finse event"). Few changes were detected throughout the late Holocene. My results were further compared to similar studies assessing the vegetationand climate history along an east-west transect in the mountains of eastern Norway (e.g. Paus, 2010; Paus & Haugland, 2017).

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1. INTRODUCTION

Climate change caused by anthropogenic greenhouse gas emissions has been a major focus of research over the last decades. From the mid-20th century until the end of the 21st century, emissions of greenhouse gases are expected to cause an increase in the global mean temperature at least 0.3-1.7 °C (IPCC, 2014). Alpine plant species are especially sensitive to temperature rise as they often occur at their ecotonal boundaries or distributional limits mainly determined by temperature (Pauli *et al.*, 1996; Bergman *et al.*, 2005). An understanding of past fluctuations in climate can give useful insight into present climate change. Addressing responses of past plant communities to climatic fluctuations will be beneficial in terms of e.g. understanding and managing alpine ecological issues in the present and future. Additionally, an understanding of the past is necessary for distinguishing anthropogenic influences from natural cycles.

Changes in abundance and occurrence of combined biological proxies can provide valuable information on the past. To investigate past changes in vegetation and climate, palaeoecological approaches are hence widely used. Vegetational variations can be studied by looking at both pollen percentage- and influx-values of different taxon along a time sequence (Gunnarsdóttir, 1996). Additionally, proxies such as macrofossils (smaller remains of e.g. bark and seeds) and megafossils (larger remains such as trunks and branches) preserved in lakes and mires can give information on past tree- and forest lines (Gunnarsdóttir, 1996; Paus & Haugland, 2017). To reconstruct Holocene tree-lines using megafossils, many specimens from very small areas (10-15 km²) must be obtained (Paus & Haugland, 2017). As only four specimens were dated from the Høvringen area and nine from the adjacent Raphamn area (Table 4, Figure 11), a reliable reconstruction could not be made based on these. The position of tree-lines is also highly affected by climatic fluctuations such as summer temperature and growing-season length (Kullman & Kjällgren, 2006) and can thus be used as a proxy for vegetation and temperature changes in the past (Kullman, 1995).

Previous palaeoecological investigations have attempted to elucidate the past climate and vegetation patterns and development in the mountains of south-east Norway (e.g. Barnett *et al.*, 2001; Paus, 2010; Paus *et al.*, 2011; Paus & Haugland, 2017). Kvisvik *et al.* (2015) shows that Skriufonnen, the only glacier in Rondane, started retreating ca. 10 000 years before present (BP). Yet the post-glacial vegetation- and climate history in the Rondane area through the Holocene (the last 11 700 years) has not been reconstructed. In Rødalen (ca. 60 km north-east of the Høvringen area) tree-birch established ca. 10 300 cal. yrs BP, 150 years earlier than pine

(Paus, 2010). In the Dovre area (ca. 30 km north of the Høvringen area) pine established no later than ca. 9700 cal. yrs BP, slightly after tree-birch (ca. 10 000 cal. yrs BP) (Paus *et al.*, 2011). This trend of tree-birch establishment before pine is rather synchronous in alpine study sites in mid-Scandinavia (e.g. Bergman *et al.*, 2005; Bjune, 2005; Velle *et al.*, 2005a; Paus & Haugland, 2017). Further, megafossils give evidence of establishment of pine in the Swedish Scandes already during the early Holocene (Kullman, 1996;2001;2002;2008; Kullman & Kjällgren, 2006). More information can still be revealed regarding the climate and vegetation development in this area since the last ice age.

Two sites located close to present-day ecological ecotones between alpine forests and open tree communities (section 2.1) were chosen for sampling of peat. These were the mires Stripåtmyrin (990 m a.s.l.) and Heimfjellsmyren (1097 m a.s.l.), situated in the Høvringen area near Rondane, eastern Norway. Mires of small size were chosen for sampling as they represent autochthonous deposits and therefore exhibit local vegetation (Birks, 1993). Using a multiproxy approach, the aims are to reconstruct changes in local tree-line and climate dynamics in the Høvringen area through the Holocene, and to time the establishment of tree-birch and pine. It also aims to time the disputed Holocene Thermal Maximum (HTM) (Risebrobakken et al., 2011) and the short cold anomaly ("Finse event") which occurred approximately 8200 cal. yrs BP (Nesje & Dahl, 2001; Seppä et al., 2007; Paus et al., 2019). The HTM presumably occurred somewhere between 11 500-4000 cal. yrs BP in the Scandinavian mountains (cf. e.g. Hammarlund et al., 2004; Bjune et al., 2005; Seppä et al., 2009; Kullman & Kjällgren, 2006; Velle et al., 2010; Paus et al., 2019). Using microfossil analysis (pollen, charcoal and stomata), rarefaction analysis and dating of macro- and megafossils, past plant communities are inferred. The indicator species approach is used to infer the climate history in the study area. Although phenotypic variation could have led to different ecological tolerances and should thus be considered, presumptions are that the taxa have the same ecological tolerances to present environments as they had to previous (Birks, 1993; Birks, 2008). The presence of indicator species may therefore reflect Holocene minimum values of July mean temperatures.

Further, the study area lies between areas of previous palaeoecological investigations conducted along an east-west transect in the mountains of south-east Norway (Paus, 2010; Paus *et al.*, 2011; Paus & Haugland, 2017). The results from those studies are here being compared with the Høvringen findings, in terms of timing of deglaciation and the development of vegetation and climate.

2. Study area

2.1 GEOGRAPHY, TOPOGRAPHY AND GLACIO-ISOSTATIC UPLIFT

The Høvringen study area is situated in the municipality of Sel in Oppland county, eastern Norway. The area is located close to the Rondane national park and was earlier considered one of Norway's largest hamlets for summer farming, with more than 30 farms. The Rondane national park was the first national park to be established in Norway (1962) and is now one of Europe's few remaining refugees for wild reindeer. The area is thus moderately disturbed by grazing and hunting. The topography in the area ranges from 2178 m a.s.l. (Storronden) in Rondane national park to ca 890 m a.s.l. at Høvringen. After the deglaciation, there was an uplift of earth's surface following the melting of the Late Weichselian ice sheet (Fjeldskaar et al., 2000). The effects of this glacio-isostatic uplift were considerable in the mountainous areas of mid- and southern Norway (Fjeldskaar et al., 2000; Lyså et al., 2008). An altitudinal increase in the study area during the post-glacial must therefore be considered when investigating the past climate (section 6). The area includes the two study sites Stripåtmyrin (990 m.a.s.l.) and Heimfjellsmyren (1097 m.a.s.l.) (Figure 1) and covers a total area of approximately 20 km². The study sites are located close to a cabin field, in mountainous areas used for hiking and recreation, though in areas relatively undisturbed by hiking. Stripåtmyrin is located just above the forest line for Pinus sylvestris (mean ca. 957 m a.s.l.), but below the forest line for Betula pubescens (mean ca. 1045 m a.s.l.). Heimfjellsmyren (1097 m a.s.l.) is located just above the forest line yet below the tree-line for B. pubescens (mean ca. 1095 m a.s.l.) (Table 2). The location of these sites near present ecological ecotones is beneficial for assessing the Holocene climate oscillations (Paus et al., 2019).

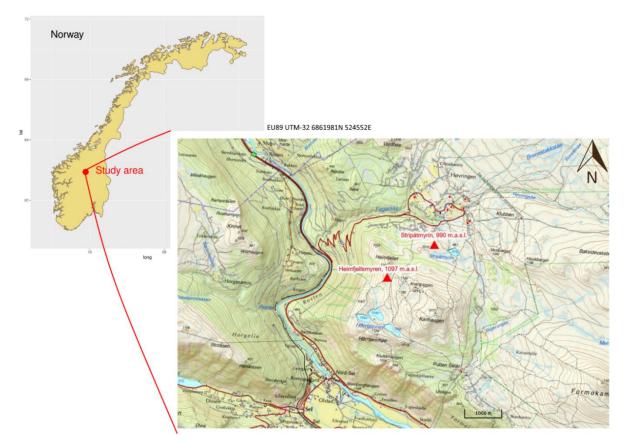


Figure 1: A map over the study area (EU89 UTM-32 NP 6861981N 524552E), where the two sites Stripåtmyrin (990 m a.s.l.) and Heimfjellsmyren (1097 m a.s.l.) are displayed by red triangles. The green line stretching north to south-east show the boundaries of the Rondane national park.

2.1.1 Stripåtmyrin (990 m a.s.l.)

Stripåtmyrin (990 m a.s.l.) (UTM 32V NP 6861160.72, 524744.94) is situated ca. 350 m south of Høvringen cabin field and faces north (Figure 1). The mire, which can be classified as poor and minerotrophic, covers a total area of ca. 0.43 km² and is essentially flat, though the surface rises slightly towards the south along a north-south transect. The coring site covered a flat area with a total of ca. 509m² (Figures 2 & 6). The mire drains towards north-east into a dammed lake (980 m a.s.l.).



Figure 2: Stripåtmyrin, with tree-birch branches to stand on, right next to the coring point.

2.1.2 Heimfjellsmyren (1097 m a.s.l.)

Heimfjellsmyren (1097 m a.s.l.) (EU89 UTM32 6860206N 523615E) is south-faced and situated in the valley between the mountains Nordre (eng. "northern") Heimhaugen (ca. 1144 m a.s.l.) and Anaripiggen (1209 m a.s.l.), 1.4 km south-west of Stripåtmyrin (Figure 1). The site, which can be classified as a nutrient-poor ombrotrophic mire, is part of a larger wetland area covering a total of approximately 0.23 km², stretching from Heimhaugen in north to Vesletjønn (1049 m a.s.l.) in south. The specific site for coring covered a relatively flat area of approximately 260 m² (Figures 3 & 9).



Figure 3: Heimfjellsmyren, where 110 mm diameter PVC tubes were beaten into the ground with help from prof. Aage Paus.

2.2 Geology & Climate

The bedrock in the Rondane area is dominated by felt-spathic sandstone (sparagmite) formed in the late pre-Cambrian or very early Cambrian (Oftedahl, 1950; Kvisvik *et al.*, 2015). Previous studies suggest an early deglaciation in adjacent areas, both in the Dovre (Paus *et al.*, 2015) and the Rondane mountains (Dahl *et al.*, 1997), dating to around 11 500 cal. yrs BP. Both study sites are situated in areas of nutrient-poor bedrock with thin discontinuous superficial deposits of moraine material (till), which might facilitate patches of richer vegetation. Heimfjellsmyren is surrounded by exposed bedrock.

The study sites are located close to each other, and they are both situated in the transect between the bioclimatic sections for continental and oceanic climate (OC) (Moen, 1999). Summer temperatures are relatively high with a long growing season (130-140 days with \geq 5 °C per year) followed by low winter temperatures (Moen, 1999). The normal annual air temperature for the period 1961-1990 was 1-0 °C (0-2 °C for 1971-2000) (Figure 4A), while the normal annual precipitation during the same period was 500-700 mm (Meteorological Institute, 2019; Moen, 1999) (Figure 4B).

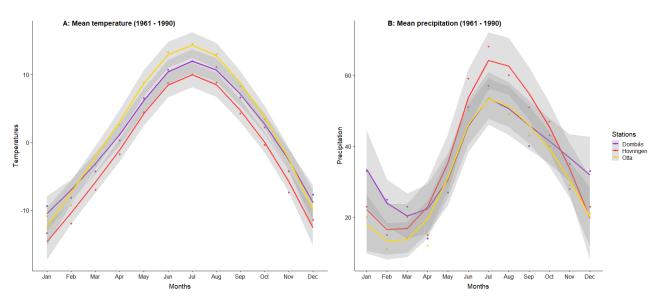


Figure 4: The figure shows the normal annual precipitation (*A*) and air temperature (*B*) for Dombås (645 m a.s.l., purple line), Høvringen (ca. 1000 m a.s.l., red line), and Otta (285 m a.s.l., yellow line) in the normal period of 1961-1990. No temperature data was available from Høvringen, so the red line in figure A shows a calculated mean of Dombås and Otta, adjusted by 0.6°C for every 100m altitudinal increase according to Laaksonen, 1976.

2.3 VEGETATION

All taxa found at both study sites are listed in Table 1.

2.3.1 Stripåtmyrin

Stripåtmyrin is situated in the northern boreal (NB) vegetation zone, also called the subalpine zone. NB is recognized by alpine tree-birch forests, thin boreal forests and large mires, often minerotrophic (Moen, 1999). The upper boundary of NB is usually set at the transition between the climatic forest limit and the low alpine zone (Moen, 1999). The site can be divided into two parts depending on the vegetation cover. The part where the coring was conducted (part 1) consisted of sparse and poor minerogenic vegetation dominated by *Eriophorum angustifolium* and *Sphagnum* spp., with a few additional species of vascular plants (Table 1). The other, adjacent part (part 2) had sparse vegetation in terms of vascular plants but was more diverse in terms of bryophytes and lichens (Table 1) with a total of six taxa in addition to *Sphagnum* spp. Due to nutrient-poor vegetation, this part of the site could also be classified as oligotrophic. The dominant vegetation in this part consisted of *Sphagnum* spp. and *Rubus chamaemorus*. The mire was flat, and small drier tufts could be found in various locations. On these tufts, some small and dying individuals of *Picea abies* could be found in part 2, and the dwarf shrub *Betula nana* and the shrub *Salix glauca* in part 1.

2.3.2 Heimfjellsmyren

Heimfjellsmyren is situated in the low alpine (LA) vegetation zone. In this region, this zone reaches from the forest limits up to at least 1400 m a.s.l. (Moen 1999) and is recognized by heaths consisting of alpine plant species such as the dwarf shrubs *Vaccinium myrtillus, Phyllodoce caerulea, Betula nana* and shrubs of *Salix* spp. (Moen, 1999). LA is the zone of highest altitude where peat accumulates and can be classified as a region for alpine mires (Moen 1999). LA is further characterized by alternating ridge, leeside and snow bed plant communities (Moen

1999), depending on topography, and wind snow cover. At Heimfjellsmyren the vegetation was sparse and nutrient-poor, classified as oligotrophic and ombrotrophic. The dominant species consisted of the vascular plant R. chamaemorus and the bryophyte Sphagnum spp., in addition to other vascular plants such as Andromeda polifolia, Trichoforum cespitosum ssp. cespitosum and lichens (i.e. Cetraria islandica and Cladonia rangiferina). The plant community



Figur 5: Sapling of Picea abies found at Heimfjellsmyren (1097 m a.s.l.), presumably dying from winter-stress.

in this site was more diverse and contained more taxa than Stripåtmyrin (Table 1). Frequencies of *E. angustifolium, E. vaginatum, Pedicularis palustris, S. glauca* and *Vaccinium vitis-idaea* varied depending on the soil moisture. Saplings of *P. abies* (Figure 5) and *P. sylvestris,* presumably dying from winter stress (section 6) were found on drier tufts. Two more nutrient-demanding species were found, these were the pteridyphyte *Equisetum variegatum* and the more lime-demanding vascular plant *Saussurea alpina*.

Table 1: List of species found at Heimfjellsmyren (1097 m a.s.l.) and Stripåtmyrin (990 m a.s.l.), both at the coring site and in the surrounding area of the latter arranged in alphabetical order after plant groups.

	Stripå	tmyrin (990 m a.s.l.)	Heimfjellsmyren (1097 m a.s.l.)	
Vascular plants:	At site:	Surrounding area:		
Andromeda polifolia	x		x	
Avenella flexuosa			x	
Betula nana	x		x	
Betula pubescens		x	x	
Calluna vulgaris			x	
Carex chordorrhiza	x		x	
Carex lasiocarpa			x	
Carex paupercula		x	x	
Carex vaginata			x	
Empetrum nigrum			x	
Eriophorum angustifolium	x		x	
Eriophorum vaginatum		x	x	
Juniperus communis			x	
Pedicularis palustris			x	
Picea abies		x	x	
Pinguicula vulgaris			x	
Pinus sylvestris		x	x	
Rubus chamaemorus		x	x	
Salix glauca	x		x	
Saussurea alpina			x	
Trichoforum cespitosum ssp. cespitosum	x		x	
Vaccinium myrtillus			x	
Vaccinium vitis-idaea			x	
Bryophytes:				
Sphagnum spp.	x	x	x	
Lichens:				
Cetraria islandica			x	
Cladonia arbuscula		x	x	
Cladonia rangiferina		x	x	
Cladonia sp.		x	x	
Cladonia stellaris		x	x	
Flavocetraria cucullata		x	x	
Flavocetraria nivalis		x	x	
Pteridophytes:				
Equisetum variegatum			x	

3. MATERIAL AND METHODS

3.1 Fieldwork

The peat coring at Stripåtmyrin (990 m a.s.l.) and Heimfjellsmyren (1097 m a.s.l.) were carried out in June and July 2017, while the search for megafossils was conducted during the summers of 2017 and 2018. The research material collected consisted of peat sequences, pollen surface samples and megafossils, and the surrounding vegetation was described at each coring site. Further, the location of present-day tree and forest lines of *B. pubescens* and *P. sylvestris* were investigated in the catchment area.

3.1.1 Stripåtmyrin

A 54 mm diameter Russian peat corer was used to test for depth and accessibility at various coring points along both a north-south and an east-west transect before the exact location was chosen based on the largest depth (Figure 6). A 110 mm diameter corer was then used to collect research material (Figures 7 & 8). Three peat samples were collected, one (ST-1) covering 307 to 207 cm depth, one (ST-2) 207 to 107 cm and one (ST-3) 107 to 30 cm. In addition to these three peat cores one surface sample (ST-5) was collected, located 0.5m from the coring point, as well as a PVC tube (110 mm diameter) sample (ST-6) covering 0-55 cm depth. An extra sample was also extracted using a 54 mm diameter Russian corer (ST-4), covering 308-286 cm depth. ST-6 was sealed using plastic lids and duct tape, while the four peat samples from the Russian corer were contained in PVC tubes that were longitudinally cut into two halves, then properly sealed using plastic wrapping and duct tape. ST-4 was to be used for ¹⁴C radiocarbon dating due to findings of silt in the bottom layer, but this core was lost from the cooler at the Department of Biological Sciences at the University of Bergen due to an unaccounted power failure and subsequent clean-up. ST-5 was not used, since the surface layers were represented by samples extracted from 2 cm depth of ST-6 (section 3.2.2). ST-6 was compressed approximately 15 cm, resulting in a 40 cm sequence covering 55 cm of peat. Due to this compression assumed to be of similar magnitude throughout the tube, every 10th cm equals ca. 7 cm. This was determined and calculated before the pollen analysis, with 7 cm = 10 cm, 14 cm = 20 cm etc. No megafossils were found at this site.

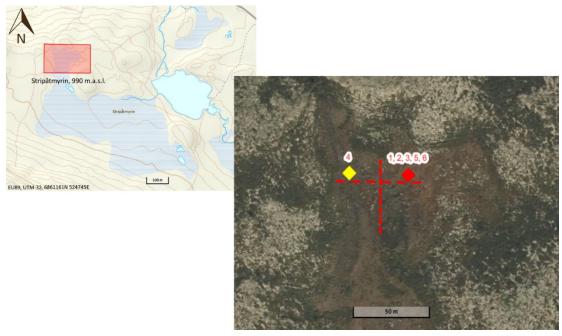


Figure 6: The figure shows the study site Stripåtmyrin (990 m a.s.l.). Red, stapled line shows the east-west and north-south transect where the test cores were conducted. Cores are assigned numbers, referring to ST-1 – ST-6 (Table 5). Coring point one is represented by a red point, while the extra sample (ST-4) is represented by a yellow point.

Figure 7 (right): Extraction of a peat sequence from Stripåmyrin with help from Rein Tveit, using a 110 mm diameter Russian corer.





Figure 8: Peat sequences extracted from Stripåtmyrin using a 110 mm diameter Russian corer. Samples were sealed using plastic wrapping and duct tape.

3.1.2 Heimfjellsmyren (1097 m a.s.l.)

The exact location for the coring site was chosen based on test cores along a north-south transect (Figure 9) using a 54 mm diameter Russian peat corer. The deepest point was chosen for peat coring, and 110 mm diameter PVC tubes were used for sampling. Collection of a peat sequence of 200-0 cm depth was attempted in an area with thick peat (BP-1), estimated to be close to the deepest part of the mire (ca. 210 cm). Here, an underground channel of a diameter of ca. 50 cm was discovered (Figure 9). An additional core tube was therefore obtained (BP-2), and 182 cm (208-26 cm depth) of peat was successfully sampled. At BP-2 the uppermost layer of moss (25 cm) were removed before sampling to descend as deep as possible using a PVC tube, collecting a core of ca. 182 cm length. Additionally, there was a compression of ca. 15 cm in the top peat layers of BP-2. For these reasons, the top layer from BP-1 was used for analysis. Both tubes were hammered into the ground using a club, then a ditch was dug around the tubes using a shovel to extract them from the mire. During coring, a total of seven megafossils determined to *B. pubescens* were found at 90, 105, 110, 135, 142 and 160 depths, respectively. Their proximate ages were determined by interpolation from radiocarbon dates.

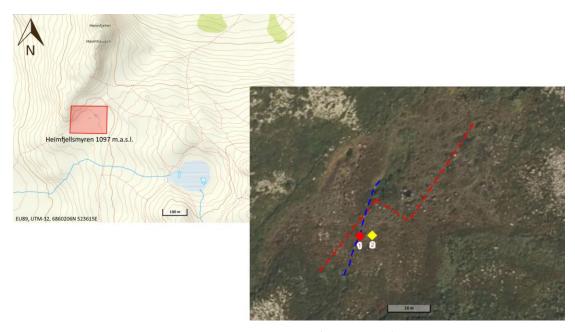


Figure 9: The figure shows the study site Heimfjellsmyren (1097 m a.s.l.). Red, stapled line shows the northsouth transect were the cores were conducted. Cores are assigned numbers, referring to BP-1 and BP-2 (Table 6). Coring point one is represented by a red point, while coring point two is represented by a yellow point. Blue stapled line shows the location of the underground channel.

3.1.3 Tree- and forest lines

To determine changes in tree- and forest lines of *B. pubescens* and *P. sylvestris* throughout the Holocene and up to the present, a mapping of present day limits had to be conducted. To accomplish this, both an east-west and a north-south transect in the Høvringen area was investigated, using local online maps (norgeskart.no) to trace vegetation and elevation. The chosen areas were inspected, using a GPS tracker with coordinate system EU89, UTM-32V NP. Results are displayed in Table 2. Individuals of ≥ 2 m height were determined as trees, while several trees standing within ≤ 30 m distance and measuring $\geq 2-3$ m height were determined as forest.

3.1.4 MEGAFOSSILS

Megafossils are relatively large plant remains, often found as trunks and branches in oxygen deprived environments such as lakes and mires. Megafossils can either represent a forest or a single tree, and conditions must be good for preservation in the search area (Gunnarsdóttir, 1996). To distinguish forest lines from tree-lines, a large amount of megafossils should therefore be obtained. To ensure similar growing conditions and land-uplift history, they should further be obtained within a small area (Paus & Haugland, 2017). Lakes and mires in proximity to the two coring locations were searched for pine megafossils during the summers of 2017 and 2018. A total of 20 megafossils (Table 3) were found in locations close to the study sites and in the surrounding areas, primarily in the surface layers of mires. Where larger trunks were found, a hand-held saw was used to detach a smaller piece for sampling. The pieces were rinsed, dried and stored in plastic zipper bags before they were transported to the University of Bergen for further species determination and preparations.

3.2 LABORATORY WORK

3.2.1 LITHOSTRATIGRAPHIC DESCRIPTION

All collected material was stored in a cold room at the Department of Biology, University of Bergen, before subsampling and sediment description. Peat samples stored in PVC tubes were cut lengthwise at Department of Earth Science, University of Bergen, to access the peat. The top layer was then rinsed using a knife to avoid contamination, before the lithostratigraphic layers were analysed according to Troels-Smith (1955) (Table 5 & 6). The same procedure for rinsing and description was followed for the peat samples collected using the Russian corer.

The analysis of lithostratigraphic layers was conducted on all cores from Stripåtmyrin simultaneously. Layers that started in one core and continued through another core was thus determined as one layer. Across-core layers therefore occurred (e.g. both ST-3 and ST-2 contains layer 4; Table 7). The lithostratigraphic layers (in addition to radiocarbon dating) were further used to correlate the PVC core with the ones obtained using a Russian corer, and for correlation between cores due to compression (section 3.1).

3.2.2 PEAT SUBSAMPLING, POLLEN PREPARATION AND MICROFOSSIL ANALYSIS

Pollen samples were extracted from approximately each tenth centimetre of the cores from both mires, with additional samples taken at a closer interval when needed. At Heimfjellsmyren minerogenic material was observed in both BP-1 and BP-2, but these lowermost layers crumbled and were lost. Due to this, the deepest sample from Heimfjellsmyren was extracted from 200 cm depth from BP-1. Sampling from BP-1 was restricted to parts of the sequence that had not been affected by the underground channel (Figure 9), resulting in samples extracted at 10-20 and 187-200 cm depths from BP-1 and 30180 cm depths from BP-2. From Stripåtmyrin, extraction of surface samples from 0 cm proved difficult, so samples from 2 cm depth represents the uppermost part.

To ensure accurate calculations of pollen concentration and influx values, four tablets of *Lycopodium clavatum* spores were added, each tablet containing 18.584 ± 370 (total ca. 74336, batch no. 177745) spores. The pollen samples were then prepared using acetolysis followed by treatment with hydrofluoric acid (HF) when minerogenic material was present (Faegri and Iversen, 1989).

Microscope slides were prepared by distributing the pollen material evenly onto the slide before covering it with a cover glass and sealing it with transparent nail polish. For analysis of microfossils a Zeiss research microscope with phase contrast-objectives (Planapo 40/1.6 Ph3, 63/1.4 Ph3 and Neofluar 100/1.3 Ph3), 8x oculars and immersion oil was used. For identification of pollen, determination keys (Moore *et al.*, 1991; Faegri & Iversen, 1989) and the modern-pollen reference collection in the Department of Biological Sciences, University of Bergen, were used. Some pollen types could only be identified to family or genus (e.g. Apiaceae, *Calluna*, Cyperaceae, Ericaceae, Poaceae, Rosaceae, *Salix*). To distinguish pollen grains of the dwarf shrub *Betula nana* from those of *B. pubescens* a combination of traits like grain size, exine thickness and protruding of apertures were used (Moore *et al.*, 1991; Paus, 2018, pers. comm.). All pollen grains of *Betula* were placed under either *Betula nana* or *B. pubescens*.

In addition to pollen analysis other microfossil proxies were used. These include stomata findings of *P. sylvestris* and fragments of charred microfossils (charcoal) (small <60 µm and big >60 µm). Plant stomata is valuable in determining local presence of vegetation and were identified to the lowest possible taxonomic level using Sweeney (2004) and Paus *et al.* (2011). Unidentifiable stomata are referred to as "Stomata Unknown". Fragments of charcoal can give information on early fire due to settlements and anthropogenic influence in the research area, as well as naturally occurring fires (Blackford, 2000; Scott, 2000). To infer Holocene minimum values of July mean temperatures, the indicator species approach was used. This is based on the presumption that the taxa have the same ecological tolerances to the present environments as they had to previous (Birks, 1993; Birks, 2008). Further, spores of the coprophilous fungi *Arnium* HdV-261 were used as an indicator of the presence of herbivores (van Geel *et al.*, 2003). The presence of stomata of *P. sylvestris* and charcoal located in the samples are displayed to the right in the pollen percentage diagrams (Figures 17-22). For a thorough investigation of the palaeoecological history, the aim was to analyse a minimum of

500 pollen grains for each sample. As most of the samples contained a high number of microfossils, this was accomplished for all but 270 and 300 cm depth at Stripåtmyrin, which gave a total count of 479 and 432 pollen grains, respectively. At these depths the deposition times were estimated to 4.46 to 4.74 yr/cm, which might result in a low concentration of microfossils in the layers. The highest sum of pollen counts at Stripåtmyrin was 2254 at 100 cm depth. Pollen counts at Heimfjellsmyren ranged from 503 at 90 cm depth to 2098 at 50 cm depth.

3.2.3 RADIOCARBON DATING OF MACRO- AND MEGAFOSSILS

Six megafossils of *P. sylvestris* were sent to AMS radiocarbon dating, of which four were collected in 2017 and two in 2018. Additionally, a total of 10 pine megafossils from palaeoecological investigations in the adjacent Raphamn area (Paus & Müller, unpublished) were also sent to AMS radiocarbon dating (Table 4). For radiocarbon dating of the peat sequences and calculations of sediment accumulation rates, five macrofossil samples (e.g. leaves, needles and seeds) were collected from the cores from Stripåtmyrin and seven were collected from Heimfjellsmyren. To obtain these, they were sifted out from the peat in the laboratory using mesh sizes 1000, 500 and 250 µm, handpicked and carefully cleaned of residue like hairs and dust before they were weighed (Birks, 2007). All samples were sent to Poznán Radiocarbon Laboratory in Poland (Table 7 & 8). All uncalibrated ages (BP) of megafossils were calibrated using Calib 7.10 (Stuiver et al., 2019). Median probabilities are further used in the age-depth modelling (section 4.3.3, Figures 13 & 14). Due to variations in concentration of the unstable atmospheric ¹⁴C through time (Beck *et al.*, 2001; Blaauw, 2010) stratigraphic layers of different age might contain the same amount of ¹⁴C radiocarbon (referred to as a "radiocarbon plateau"). Therefore, one single radiocarbon date might reflect two or more intervals of calibrated calendar years. All calibrations gave two intervals for 2σ , with a probability value for each. Since the standard deviation for the radiocarbon ages are all smaller than 50 years, the calibrated ages are rounded to the nearest year (Reimer *et al.*, 2013).

3.2.4 Loss-on-ignition (LOI)

To measure the organic content in the peat, loss-on-ignition (LOI (%)) was conducted. For the procedure the samples were weighed, dried at 105° C overnight and put in a desiccator for approximately 30 minutes. They were again weighed before they were burned at 550° C for 6 hours. The samples were then put back in a desiccator for another 30 minutes before a third weighing. The amount of organic material lost on ignition was calculated for each sample. Results from the LOI for all samples are displayed to the right in the pollen percentage diagrams for both localities (Figures 17 & 20).

3.3 STATISTICAL ANALYSES AND MODELLING

3.3.1 GRADIENT ANALYSIS BY INDIRECT ORDINATION

The underlying ecological gradients and vegetational patterns were investigated using gradient analyses. Dissimilarity indices were computed employing the Bray-Curtis index, using R for Statistical Computing v3.5.2 (R Core Team, 2019) and RStudio v1.1.463 (RStudio Team, 2016) with package vegan v2.5-4 (Oksanen *et al.*, 2019). Cluster analysis was then run on all terrestrial taxa based on the dissimilarity indices, using Constrained Incremental Sums of Squares, to assess variance in the datasets. Detrended correspondence analysis (DCA) was performed on calculated percentages of all terrestrial taxa to assess plant species responses to environmental gradients. Principal component analysis (PCA) was then run on the full datasets from both study sites, minus the taxa with a percentage sum of less than 2%, to analyse assemblage variation. For the plots, the 9 taxa with highest loadings on PC axis 1 and PC axis 2 were selected.

3.3.2 Age-depth modelling and pollen influx

A precise chronology is essential for palaeoecological investigations. To create a time scale for the events, an age-depth model was created using Clam v2.3.2 (Blaauw, 2010) with radiocarbon calibration assuming a Gaussian distribution of the radiocarbon ages (default). The northern-hemisphere terrestrial-calibration curve was used for the dating points (default). For the age-depth model, smooth-spline interpolation was used to smooth the data set. A dataset containing peat deposition time (yr/cm) was generated. Clam was chosen over other packages such as Bacon (Blaauw & Christen, 2011) due to few ¹⁴C radiocarbon dates of macrofossils from the peat.

As some pollen types (e.g. the abundant *P. sylvestris*) are easily dispersed by wind, a high abundance of these taxa in pollen diagrams could be due to an overrepresentation of tree pollen from long-distance dispersal. To investigate the extent of local pollen production, estimates of pollen influx (Pollen Accumulation Rate, PAR) are useful. This is the net number

of pollen grains accumulated per unit of sediment surface per unit time (grains cm⁻²yr⁻¹) (Birks & Birks, 1980). Pollen-influx estimates are independent of pollen percentages, and the value of each taxa is independent of each other. For calculation of pollen influx, the age-depth model from Clam and the R packages tidyverse v1.2.1 (Wickham, 2017) were used. Influx values were calculated for all terrestrial pollen and spore taxa. In the interpretation and discussion sections (sections 5 and 6), all pollen influx values are rounded to the nearest 50.

3.3.3 POLLEN SUM ESTIMATES AND POLLEN DIAGRAMS

Taxa were divided into groups for trees (TREES), herbs (HERBS), shrubs (SHRUBS), dwarf shrubs (DSHRUBS), unknown (UNKNOWN), fungal- and pteridophyte spores and algae (FPA), aquatics (WATER), mosses (MOSS), charcoal (CHC) and stomata (STOMATA). The basis for percentage calculation (ΣP) for the pollen diagrams comprises all terrestrial pollen taxa. For a taxon within e.g. FPA, the calculation basis was ΣP + FPA. This was done to avoid getting a higher percentage than 100 for any taxon. Taxa were chosen subjectively based on their significance for investigations of the tree- and forest lines. Low abundance indicator species not displayed in the diagrams are listed in Appendix B. Peaks in the pollen diagrams consisting of only one pollen spectrum are not believed to reflect a shift in vegetation and are generally left out of the interpretation. For both calculation of pollen sum estimates and construction of all pollen diagrams, R for Statistical Computing v3.5.3 (R Core Team, 2019) and RStudio vl.1.463 (RStudio Team, 2016) were used (Appendix C). Packages used for the diagrams were rioja v0.9-15.2 (Juggins, 2017) and tidyverse v1.2.1 (Wickham, 2017), including vegan v2.5-4 (Oksanen *et al.*, 2019) and dplyr v0.8.0.1 (Wickham *et al.*, 2019). On the left side of the pollen diagrams (Figures 17-22) depths sampled, maximum probability values of the calibrated ¹⁴C radiocarbon dates and pollen zone names are displayed. Due to time restrictions when operating R the values from LOI (%) and PCA are shown on the right side, in addition to stomata and charcoal findings and lithostratigraphic information. Influx diagrams (Figures 18 & 21) include the same taxa as the pollen percentage diagrams (Figures 17 & 20), except from the fresh water algae in Stripåtmyrin. Total diagrams were constructed to present the percentages of trees, herbs, shrubs and dwarf shrubs (Figures 19 & 22) using the R package tidyverse v1.2.1 (Wickham, 2017). The cluster analysis (section 4.4.1) was used to create local pollen assemblage zones in all pollen diagrams, while the broken stick model was used to evaluate the statistical significance of the local pollen assemblage zones (section 4.4.1, Appendix A). Further,

rarefaction analysis was run on all terrestrial taxa to estimate the palynological richness (PR) (called species richness in the pollen percentage diagrams). The pollen counts were standardized to a fixed number of grains (432, the lowest count from Stripåtmyrin, ($E(T_{432})$) (Birks & Line, 1992). The species richness is displayed to the right in the pollen percentage diagrams (Figures 17 & 20). For interpretation (section 5), threshold values were applied for determining presence of *P. sylvestris* (forest >1000 grains cm⁻²yr⁻¹, local presence >500 grains cm⁻²yr⁻¹) and *B. pubescens*, (forest >500 grains cm⁻²yr⁻¹, local presence >250 grains cm⁻²yr⁻¹) and local presence of *P.abies* (>50 grains cm⁻²yr⁻¹) (Hicks, 2001; Seppä & Hicks, 2006; Jensen *et al.,* 2007).

4. Results

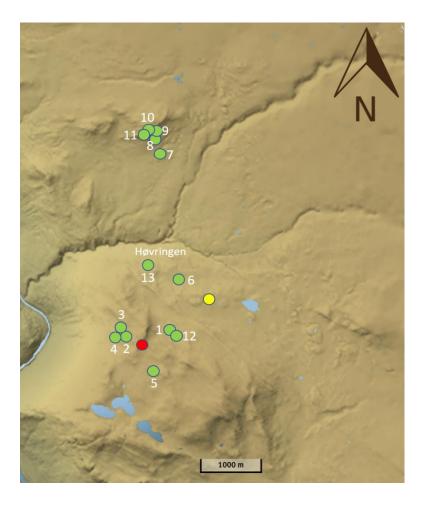
4.1 Present tree- and forest lines

Information on present day tree- and forest lines in the Høvringen area is given in Table 2, Figure 10 (present tree- and forest lines) and comparisons were made with Figures 11 & 12 (past forest lines).

Table 2: Present tree- and forest lines in the Høvringen area. Numbers refer to Figure 10 below. Number 7 was estimated after fieldwork was conducted, based on photographs and online maps (Norgeskart.no).

	Present tree- and forest lines								
No.	Туре	Inclination	Altitude (m a.s.l.)	Coordinates (EU-89	Comments				
				UTM: 32V NP)					
1	P. sylvestris, tree line	North-northwest	970	6861213N 524181E	Several trees				
2	B. pubescens, forest line	North-northwest	1050	6860588N 524097E					
3	B. pubescens, tree line	West-southwest	1082	6860495N 523441E	Height: 3.5-4 m				
4	B. pubescens, forest line	Southwest	1055	6860598N 523312E					
5	P. sylvestris, tree line	West	1063	6860553N 523360E	Height: 3.4-4 m				
6	B. pubescens, tree line	South	1124	6860007N 523930E	Height: 3.5-4 m.				
					Single tree in Salix-				
					shrubs by stream				
7	P. sylvestris, forest line	Northwest	950	6861410N 524192E	Estimation				
8	P. sylvestris, forest line	South	990	6863579N 523550E					
9	B. pubescens, forest line	South	1030	6863675N 523539E					
10	P. sylvestris, tree line	South	1055	6863715N 523485E					
11	B. pubescens, tree line	South	1080	6863768N 523460E					
12	P. sylvestris, tree line	North	1025	6860666N 524200E					
13	P. sylvestris, forest line	North	930	6861462N 523689E					

Figure 10: Present tree- and forest lines in the Høvringen area. Numbers refer to details presented in Table 2. Red dot shows the location of Heimfjellsmyren (1097 m a.s.l.), while the yellow dot shows the location of Stripåtmyrin (990 m a.s.l.). Source: Norgeskart.no.



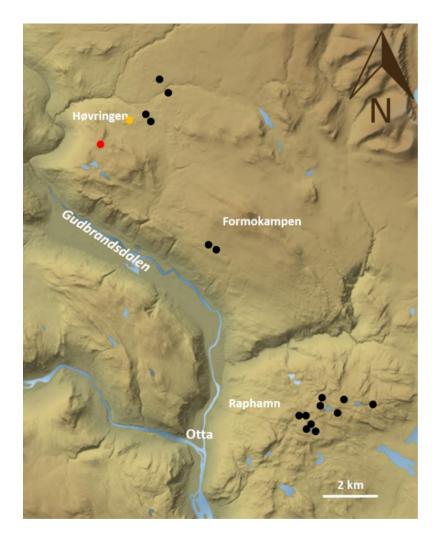
$4.2\ \text{Megafossils}$ and $\text{AMS}\ \text{Radiocarbon}\ \text{dates}$

A total of 20 megafossils were found in the Høvringen area during the summers of 2017 and 2018. Most finding were determined to either *J. communis* or *P. sylvestris*, while six were undetermined. The pine fossils found at the highest elevations of 970, 977, 1021 and 1034 m a.s.l. were sent to AMS radiocarbon dating. Number 14, 18 and 20 (Table 3) were extracted from mires, while number 16 was found in the shallow area of a dammed lake. More detailed results are displayed in Table 3.

Table 3: The table displays all megafossils found in the Høvringen area during summers of 2017 and 2018, both those undated and dated. Measurements, altitude and coordinates are given in separate columns. Number 2, 3 and 19 were believed to be J. communis but could not be properly determined. Numbers 14, 16, 18 and 20 were radiocarbon dated and assigned names Ho-2, Ho-4, Ho-3 and Ho-4, respectively (Table 4).

	Megafossils								
No.	Species	Altitude (m a.s.l.)	Coordinates (EU-89	Measurements	Comments				
			UTM: 32V NP)						
1	P. sylvestris	1080	6860528N 523440E	1m length, 7cm diameter	-				
2	J. communis ?	1072	6858975N 523665E	30cm length, 5cm diameter	Root				
3	J. communis ?	1069	6858867N 524011E	50x40 length/bredth, 15cm diameter	Root				
4	Undetermined	1071	6858158N 526478E	50cm length, 15cm diameter	Log				
5	P. sylvestris	920	6861424N 523799E	120cm length, 10cm diameter	Log				
6	P. sylvestris	920	6861424N 523799E	30cm length, 150cm diameter	Log				
7	P. sylvestris	920	6861424N 523799E	25cm length, 190cm diameter	Log				
8	P. sylvestris	920	6861424N 523799E	110cm length, 7cm diameter	Log				
9	P. sylvestris	920	6861424N 523799E	200cm length, 31cm diameter	Log				
10	P. sylvestris	920	6861424N 523799E	80cm length, 7cm diameter	Log				
11	Undetermined	970	6861256N 525265E	60cm length, 40cm diameter	Root				
12	Undetermined	970	6861256N 525265E	NA	Log				
13	Undetermined	966	6861403N 525358E	65cm length, 9cm diameter	Log				
14	P. sylvestris	970	6861403N 525358E	325cm length, 30cm diameter	Log, dated (Ho-2)				
15	Undetermined	970	6861347N 525390E	NA	Root				
16	P. sylvestris	977	6861106N 525423E	70cm length, 10cm diameter	Log, dated (Ho-4)				
17	Undetermined	980	6861031N 525446E	70cm length, 11cm diameter	Log				
18	P. sylvestris	1034	6862671N 525772E	115cm length, 9cm diameter	Log, dated (Ho-3)				
19	J. communis ?	1027	6862671N 525772E	45cm length, 3cm diameter	Branch				
20	P. sylvestris	1021	6862425N 525977E	160cm length, 20cm diameter	Log, dated (Ho-1)				

Figure 11: Megafossils (dated) found in the Høvringen area during summers of 2017 and 2018, represented with black dots. Red dot shows the location of Heimfjellsmyren (1097 m a.s.l.) while the yellow dot shows the location of Stripåtmyrin (990 m a.s.l.). Source: Norgeskart.no.



The results of the AMS radiocarbon dating are given in Table 4. All dates are given in both uncalibrated ¹⁴C radiocarbon dates and in calibrated calendar years BP.

Table 4: The table shows AMS radiocarbon dates of megafossils found during the summers of 2017 (Ho-1 - Ho-4) and 2018 (Hf-1 - Hf-2) in addition to megafossils from the Raphamn area (Paus & Müller, unpublished) (Ra-0 - Ra-9). Dates are given in both uncalibrated ¹⁴C years and calibrated calendar years BP, with median probabilities given in the right column. Both present day elevations and elevations adjusted for glacio-isostatic uplift are listed. (Lyså et al., 2008).

Sample name	Elevation (m a.s.l.) Not-adjusted/Adjusted	Lab.code	Coordinates (EU-89 UTM: 32V NP)	Uncalibrated ¹⁴ C age (BP)	Calibrated	l age (BP)	Median probability
					Date (20)	Probability	
Ra-0	1075/1015	Poz-56490	6849546N 533244E	7680 ± 50	8390 - 8561	1.000	8473
Ra-1	1068/998	Poz-96046	6850752N 533287E	8090 ± 50	8777 - 8835 9221 - 9240 8856 - 9137 9177 - 9202	0.012 0.076 0.897 0.016	9023
Ra-2	1075/1028	Poz-96047	6850592N 533296E	6150 ± 40	6943 - 7164	1.000	7060
Ra-3	1092/1022	Poz-96049	6850772N 535244E	8270 ± 50	9039 - 9045 9089 - 9432	0.006 0.994	9264
Ra 4	1075/1020	Poz-96050	6850870N 533965E	7800 ± 50	8442 - 8705	1.000	8577
Ra 5	1061/1021	Poz-96051	6849590N 532793E	6050 ± 40	6787 - 7003	1.000	6902
Ra-6	1060/1056	Poz-96052	6849607N 532880E	1105 ± 30	938 - 948 951 - 1066	0.018 0.982	1010
Ra-7	1057/997	Poz-106602	6849616N 533066E	7900 ± 50	8593 - 8811 8825 - 8871 8878 - 8978	0.735 0.093 0.172	8726
Ra-8	1051/1008	Poz-106604	6850037N 532946E	6920 ± 40	7674 - 7838	1.000	7748
Ra-9	1047/997	Poz-106484	6850005N 532897E	7580 ± 35	8345 - 8425	1.000	8391
Ho-1	1021/991	Poz-96040	6862425N 525977E	4890 ± 40	5584 - 5716	1.000	5626
Ho-2	970/935	Poz-102186	6861403N 525358E	5860 ± 40	6562 - 6594 6596 - 6756	0.063 0.912	6682
Ho-3	1034/997	Poz-106600	6862671N 525772E	5290 ± 40	5943 - 5972 5985 - 6187	0.064 0.936	6078
Ho-4	977/912	Poz-106481	6861106N 525423E	8250 ± 50	9033 - 9053 9081 - 9407	0.023 0.977	9227
Hf-1	1054/1021	Poz-106546	6856569N 528125E	5535 ± 35	6286 - 6399	1.000	6335
Hf-2	1054/1014	Poz-106480	6856569N 528125E	6285 ± 35	7159 - 7278 7284 - 7286	0.998 0.002	7216

Megafossil dates

All dated pine megafossils from both localities are displayed in Figure 12, in addition to north and south faced present day forest lines (Table 2).

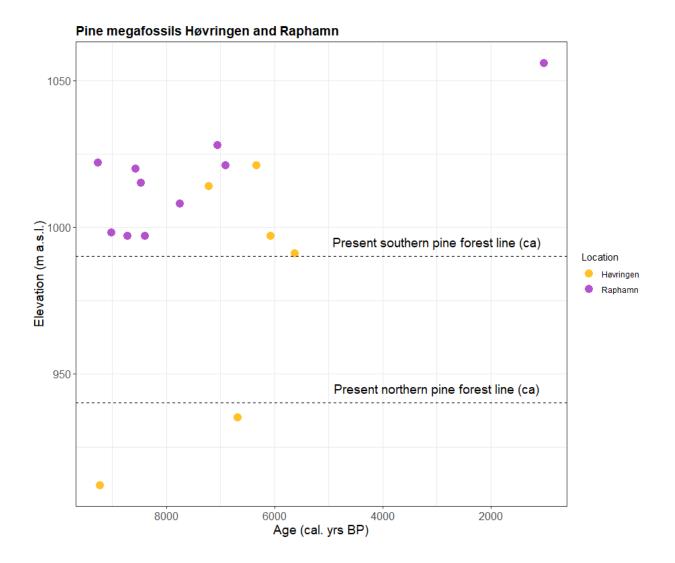


Figure 12: The figure shows all (16) dated pine megafossils from Høvringen (yellow) and Raphamn (purple), southwest of Rondane, adjusted for land uplift. The black dotted lines show an estimation of the north- and south faced present-day forest lines for pine in the area, based on the three recordings from summers of 2017 and 2018 (Table 2).

4.3 Peat sequence and dates

4.3.1 Stratigraphy

Detailed descriptions (Troels-Smith, 1955) of the lithostratigraphic layers in the pollenanalytical peat sequences are given in Table 5 & 6. These descriptions include comments on the compositional and physical properties of the lithostratigraphic layers. Short descriptions are also noted on the right-hand side in the pollen diagrams (Figures 17 & 20).

4.3.1.1 Stripåtmyrin

Descriptions of the lithostratigraphic layers in Stripåtmyrin are given in Table 5. Core names refer to section 3.1.1.

Table 5: The table shows details of lithostratigraphic data from Stripåtmyrin (990 m a.s.l.), includingsediment components and physical properties. Core names (ST-1 – ST-6) refer to core names.

	Lithostratigraphic layers, Stripåtmyrin									
Core	Layer	Depth (cm)	Sediment components	Physical properties	Description					
	1	0 - 30	Ld ² 1, Dh2, Tb1	elas. 2, nig. 2	Ca. 1 m from coring site. Slightly mudlike, homogenous <i>Limus detritus</i> . <i>Sphagnum</i> peat. Mostly herbaceous fragments; <i>Detritus</i> <i>herbosus</i> .					
ST-6 PVC tube - 110 mm	2	30 - 55	Ld ² 2, Dh1, Tb1	elas. 2, nig. 2	Ca. 1 m from coring site. Some <i>Sphagnum</i> peat. Occurrence of fragments of plant material. Most <i>L. detritus;</i> mud-like, homogenous, non-plastic depostis. Mildly decomposed. The sediments between 33 - 40 cm are slightly coarser, with bigger fragments. 15 cm compression, during coring. Total coverage therefore ca 40 cm.					
ST-3 Russian corer - 110 mm	3	30 - 70	Ld ² 2, Dh1, Tb1	elas. 2, nig. 2	Some <i>Sphagnum</i> peat. Occurrence of fragments of plant material. Most <i>L. detritus,</i> moderatly decomposed. Overlapping with ST-6, layer 2.					
ST-3 Russian corer - 110 mm/ ST-2 Russian corer - 110 mm	4	70 - 128	Ld ² 3, Dh1, Tb+	elas. 1, nig.2	Traces of <i>Sphagnum</i> peat. Most <i>L. detritus</i> . A slightly higher occurrence of plant fragments in the sediments than in layer 3. Slighty less elastic than most other layers. Medium dark color. Overlap between ST-3 and ST-2.					
ST-2 Russian	5.1	128 - 173	Ld ² 2, Dh1, Tb1	elas. 2, nig. 2	Some <i>Sphagnum</i> peat. Occurrence of fragments of plant material. 5.1 and 5.2 are both sub-layers of layer 5. Slightly decomposed <i>L. detritus</i> .					
corer - 110 mm/ ST-1 Russian corer - 110 mm	5.2	173 - 274	Ld ² 2, Dh2, Tb1	elas. 2, nig. 2	Some <i>Sphagnum</i> peat. A slightly higher occurrence of fragments of herbaceous plants. Transition between ST-2 and ST-1. 5.1 and 5.2 are both sub-layers of layer 5. Also a slight increase in <i>Detritus herbosus</i> from 185 cm depth and upwards, within the sub-layer.					
ST-1 Russian corer - 110 mm	6	274 - 307	Ag+, Ld ² 3, Dh1	elas. 2, nig.2-	Traces of silt. Decomposed detritous mud-like and homogenous material. Dark grey-brown color.					

4.3.1.2 Heimfjellsmyren

Descriptions of the lithostratigraphic layers in Heimfjellsmyren are given in Table 6. Due to a certain degree of oxidation during storage, the analysis of lithostratigraphic layers were not always accomplishable in terms of determining physical properties (assigned "NA"). Core names refer to section 3.1.2.

Table 6: The table shows details of lithostratigraphic data from Heimfjellsmyren (1097 m a.s.l.), includingsediment components and physical properties. Core names (BP-1 and BP-2) refer to the two cores.

	Lithostratigraphic layers, Heimfjellsmyren								
Core	Layer	Depth (cm)	Sediment components	Physical properties	Description				
BP-1 PVC - 110 mm	1	0 - 26	NA	NA	This layer was not analysed stratigraphically, but consisted of barely decomposed to non- decomposed <i>Sphagnum</i> peat.				
	2	26 - 59	Ld³1, Dh3	elas.0, nig.3- /nig.3	Mostly detritous material with fragments (>2 mm.) of plants. Some moderatly decomposed mud-like, non- plastic deposits. Not elastic. Color gradually darker upwards, from nig.3- to nig.3.				
BP-2 PVC - 110 mm	3	59 - 160	Ld ² 1, Dh3, Dl+	elas.0, nig.2	Mostly detritous material with fragments (>2 mm.) of plants. Some moderatly decomposed mud-like, non- plastic deposits. Fragments of wood and bark. Not elastic. Moderatly dark in color. Sub-layer with birch megafossils from 90 - 113 cm (at 90 - 93, 105 and 110 - 113 cm depths). Additionally, birch megafossils were located at 135, 142 and 160 cm depths. Mildy decomposed.				
	4	160 - 188	Ld ² 1, Dh3, Dl+	elas.0, nig.2	Mostly detritous material with fragments (>2 mm.) of plants. Some moderatly decomposed mud-like, non- plastic deposits. Fragments of wood and bark. Not elastic. Moderatly dark in color.				
BP-1 PVC - 110 mm	5	188 - 200	Ld ³ 3, Dh1, Dl+, Ag+	elas.1, nig.3+	Mostly mud-like, homogeonus, non- plastic deposits. Some herbaceous plant portions and fragments of wood and bark. Traces of silt in the bottom. Quite dark color. Barely elastic.				

4.3.2 MACROFOSSILS AND AMS RADIOCARBON DATES

Results from AMS radiocarbon datings of the in total 12 macrofossil samples from Stripåtmyrin (990 m a.s.l.) and Heimfjellsmyren (1097 m a.s.l.) are given in Tables 7 and 8 below.

4.3.2.1 Stripåtmyrin

To estimate the age of the deepest part of the peat core and for correlation between cores, S-1 and S-2 were dated. S-3 was situated in a transition with slight changes in sediment components and physical properties and was dated to assess this transition. This layer also lacked silt and had a slightly higher content of *Detritus herbosus* than the surrounding layers. S-5 was dated for estimating the sedimentation rate of the upper part of the peat core. All AMS dates were used in age-depth modelling to assess the sedimentation rates in the study area through the Holocene (section 4.3.3).

Table 7: The table shows results from the radiocarbon dating of macrofossils from Stripåtmyrin (EU89 UTM32 6861094N 524560E). Dates are given in both uncalibrated radiocarbon years and calibrated calendar years, with median probabilities given in bold.

	Macrofossil dates, Stripåtmyrin (990 m a.s.l.)									
Sample name ⁽¹⁾	Depth (cm) ⁽²⁾	Lab.code	Uncalibrated ¹⁴ C age (BP)	Calibrated	Calibrated age (BP)		Material dated ⁽³⁾			
				Date (2σ)	Probability					
S-1 (ST-1)	305-307	Poz-96158	8640 ± 50	9527 - 9704 9722 - 9730	0.993 0.007	9600	Seeds of tree birch, pine needles and bark (24mg) - (Layer 6)			
S-2 (ST-1)	277-279	Poz-96159	8350 ± 50	9149 - 9167 9248 - 9485	0.013 0.987	9370	Fragments of tree birch (x8), pine needles (x4), bark (x1), catkin fragments of tree birch (x3) (29mg) - (Layer 6).			
S-3 (ST-2)	127-129	Poz-96161	6865 ± 35	7620 - 7764 7770 - 7786	0.963 0.037	7694	Pine needles (x2), tree birch seeds, bark from Salix (16mg) - (Transition layers 5.1 - 4)			
S-4 (ST-2)	198-200	Poz-102439	8030 ± 50	8659 - 8668 8702 - 9030	0.005 0.995	8892	Leaf- and stem remains (11mg) - (Layer 5.2)			
S-5 (ST-3)	70-71	Poz-102440	4680 ± 40	5315 - 5478 5538 - 5576	0.895 0.105	5403	Leaf- and stem remains (7mg) - (Transition layers 4 - 3)			

⁽¹⁾ Parentheses refer to coring sites, see Table 5.

⁽²⁾ Depths are ordered after sample names by date of extraction from the core.

⁽³⁾ Layer numbers refer to lithostratigraphic layers given in Table 5.

4.3.2.2 Heimfjellsmyren

For correlation of cores and to determine the age of the bottom layers, the lowermost parts of both BP-1 and BP-2 (H-1, H-2 and H-4) were dated. H-3 and H-7 were dated to estimate the age of the uppermost part. To assess the sub-layer containing a high amount of birch megafossils (Table 6), H-6 was dated. H-5 was dated due to its position in the transition between layers 3 and 4, where there was a change in amount of birch megafossils found during coring. The bottom layers in BP-1 and BP-2 reach slightly different ages yet the same depths, making correlation of cores rather difficult. As the asynchrony reflects an unreliable age-depth relationship in the bottom layers of BP-2, only H-1 from BP-1 was used in age-depth modelling (section 4.3.3) to assess the sedimentation rates during the early Holocene.

Table 8: The table shows results from the AMS radiocarbon dating of macrofossils from Heimfjellsmyren (EU89 UTM32 6860206N 523614E). Dates are given in both uncalibrated radiocarbon years and calibrated calendar years, with median probabilities given in bold.

Sample name ⁽¹⁾	Depth (cm) ⁽²⁾	Lab.code	Uncalibrated ¹⁴ C age (BP)		Heimfjellsmyren (1097 Calibrated age (BP)		Material dated ⁽³⁾
				Date (2σ)	Probability		
H-1 (BP-1)	197.5-200	Poz-96156	8650 ± 50	9530 - 9709 9716 - 9735	0.981 0.019	9607	Fragments of bark and wood (42mg) - (Layer 5)
H-2 (BP-2)	186-188	Poz-96157	8620 ± 50	9520 - 9697	1.000	9584	Wood fragments, leaves and bark (57mg) - Transition layers 5 - 4)
H-3 (BP-2)	57-59	Poz-96245	4475 ± 35	4976 - 5016 5032 - 5290	0.087 0.913	5165	Fragments of bark and wood (17mg) - (Transition layers 3 - 2)
H-4 (BP-2)	191-193	Poz-102272	8630 ± 50	9524 - 9701	1.000	9592	Leaf- and stem remains (46mg) - (Layer 5)
H-5 (BP-2)	159-161	Poz-102438	8100 ± 50	8782 - 8832 8862 - 8919 8954 - 8962 8968 - 9144	0.046 0.039 0.003 0.848	9040	Leaf- and stem remains (17mg) - (Transition layers 4 - 3)
H-6 (BP-2)	107-108.5	Poz-102209	6950 ± 40	7685 - 7860 7903 - 7919	0.970 0.030	7778	Leaf- and stem remains (99mg) - (Layer 3)
H-7 (BP-2)	29-31	Poz-102217	2215 ± 30	2150 - 2321	1.000	2230	Leaf- and stem remains (52mg) - (Layer 2)

⁽¹⁾ Parentheses refer to coring sites, see Table 6.

⁽²⁾ Depths are ordered after sample names by date of extraction from the core.

⁽³⁾ Layer numbers refer to lithostratigraphic layers given in Table 6.

4.3.3 Age-depth modelling and peat accumulation rates

For both localities the AMS dates in calibrated ages BP are displayed in smooth-spline depth-age plots modelling the accumulation rates through time (Figures 13 & 14). The dates are given in 2 SD intervals in both plots, and confidence intervals are calculated at 95% (default). Calculation of peat accumulation rates (yr/cm) are based on AMS radiocarbon dated macrofossils obtained from the peat sequence (section 4.3.2).

4.3.3.1 Stripåtmyrin

The relationship between the calibrated ages (BP) and the depths in Stripåtmyrin (990 m a.s.l.) is displayed in Figure 13. The plot suggests a high accumulation rate in the lowermost layers (section 5), with a decrease towards the surface layers.

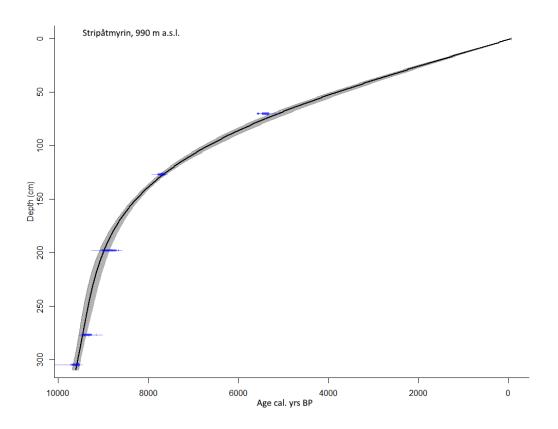


Figure 13:

The figure shows an age-depth model for Stripåtmyrin (990 m a.s.l.), made using Clam v2.3.1. Blue marks show the dated macrofossils (cal. yrs BP), while the grey area defines the 95% confidence envelope.

4.3.3.2 Heimfjellsmyren

The relationship between the calibrated ages (BP) and the depths in Heimfjellsmyren (1097 m a.s.l.) is given in Figure 14. Data suggest high accumulation rates in the deepest layers of the mire, followed by a gradual decrease towards the upper depths.

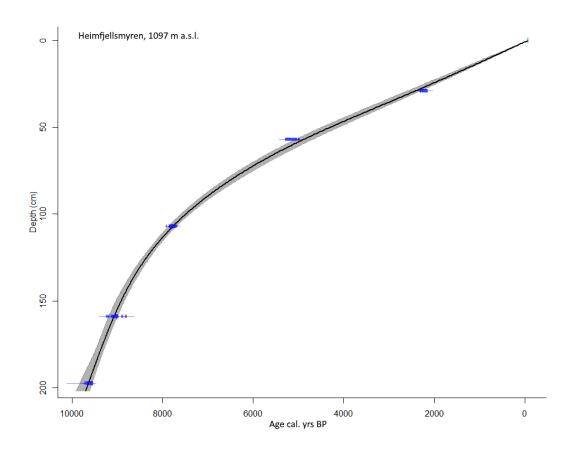


Figure 14:

The figure shows an age-depth model for Heimfjellsmyren (1097 m a.s.l.), made using Clam v2.3.1. Blue marks show the dated macrofossils (cal. yrs BP), while the grey area defines the 95% confidence envelope.

4.4 Statistical analyses

4.4.1 Cluster analysis

According to the broken stick model (Appendix A) the pollen assemblage zones based on the cluster analysis did not prove significant due to highly homogenous datasets with little variance. Four local pollen assemblage zones were therefore chosen mostly for interpretation of the pollen diagrams (Figures 17-22), although still based on the cluster analysis. The largest zones were manually divided into sub-zones for better interpretation.

4.4.2 PRINCIPAL COMPONENT ANALYSIS

A Detrended Correspondence Analysis (DCA) shows that the gradient length of the first axis from both Stripåtmyrin (1.2756) and Heimfjellsmyren (1.5169) are less than 2 SD units. The plant species response to environmental gradients thus suggest linear, homogenous datasets (Jongman *et al.*, 1987) and a Principal Component Analysis (PCA) was run. Results from the PCA are displayed in Figures 15 and 16.

4.4.2.1 Stripåtmyrin

Based on the species distribution within Figure 15, PC axis 1 (horizontal axis) might reflect a gradient in terms of moisture, increasing with axis values. Though sparse taxa on the lefthand side of the plot, taxa to the right (Alnus, B. pubescens, Cyperaceae and Poaceae) indicate higher moisture than *P. sylvestris*, situated to the far left. *Corylus* slightly light open and a moderatly dry environment, while P. abies, Sorbus and R. chamaemorus reflect somewhat moister yet slightly light-open conditions. The vector lengths of *B. pubescens* and *P. sylvestris* suggest that PC axis 1 is highly positively correlated to the abundance of *B. pubescens* and strongly negatively correlated to the abundance of *P. sylvestris*. Additionally, PC axis 2 (vertical axis) is highly positively correlated to the abundance of B. nana. PC axis 2 might reflect a gradient in vegetation density with an increase towards lower axis values. While the arctic-alpine dwarf shrub B. nana requires an open environment, low competition and high amounts of light, species such as *P. sylvestris* and *B. pubescens* are better adapted to a forested, higher density environment. The upper right quadrant shows high representations of A. incana and Cyperaceae in the low and middle part of the pollen sequence. These commonly grow in moist to wet and open environments. Although Cyperaceae may vary in terms of ecological requirements, *Alnus* can commonly be found in soils of both average and poor fertility. The

lower right quadrant is characterized by the rapid colonizers and pioneers Poaceae and *B. pubescens. P. sylvestris,* which is situated in the bottom left quadrant, is commonly found in drier, more forested and competitive environments. Most samples are also assembled in this quadrant, reflecting a forested environment through most of the sequence.

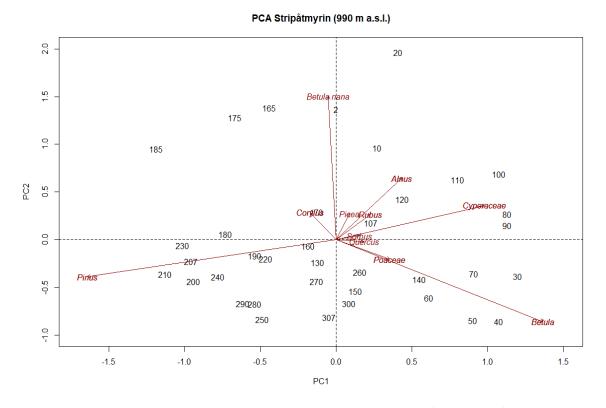
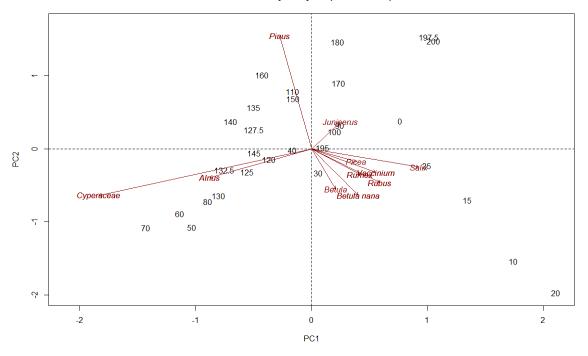


Figure 15: Results of PCA performed on the dataset from Stripåtmyrin (990 m a.s.l.). The plot shows the distribution of species and sites (depths) along two gradient axes.

4.4.2.2 HEIMFJELLSMYREN

The species distribution along the axes of Figure 16 suggests a moisture gradient along PC axis 1, where degree of moisture increases with falling axis values. PC axis 1 seems to be the one dominant gradient in the dataset. PC axis 2 presumably reflects a gradient in vegetation density, where density slightly increases with increasing axis values. The plot displays an arch effect, which could suggest a unimodal distribution along the gradients. Yet, as there is little turnover in the datasets this is unlikely, and both gradients are necessary for interpretation. The lower right quadrant is characterized by an assemblage of light-demanding pioneer taxa,

including *B. pubescens, B. nana, R. chamaemorus, Vaccinium*-type, *Rumex* and *Salix*, reflecting open conditions in the uppermost layers. *P. abies* also indicate a more open environment. The moisture demanding taxa *Alnus* and Cyperaceae is situated in the bottom left quadrant, reflecting a moist and rather light-open environment mid-sequence. PC axis 1 seems to be positively correlated to the abundace of Cyperaceae, while PC axis 2 has a positive correlation with the abundance of *P. sylvestris*. The upper left quadrant only includes *P. sylvestris* and suggests a forested, somewhat dry environment during the early- to mid Holocene. *Juniperus communis* suggests good drainage. The genereal pattern shows increasing moisture mid- to late Holocene.



PCA Heimfjellsmyren (1097 m a.s.l.)

Figure 16: Results of PCA performed on the dataset from Heimfjellsmyren (1097 m a.s.l.). The plot shows the distribution of species and sites (depths) along two gradient axes.

5 POLLEN DIAGRAMS – RESULTS AND INTERPRETATION

Pollen diagrams with selected pollen types are displayed in Figures 17-22. Total diagrams (Figures 19 & 22) display pollen percentages for trees, shrubs, dwarf shrubs and herbs. The interpretation is based on pollen percentage- and influx values, radiocarbon dating of macro- and megafossils, LOI, PCA, PR, stomata- and charcoal findings. However, the total influx values (27 200 grains $yr^{-2}cm^{-1}$) in the deepest layers (below 260 cm depth) from Stripåtmyrin are very high. Stripåtmyrin was a lake in the early Holocene. Lakes are prone to receiving in-washed material resulting in vastly exaggerated influx values (Hicks & Hyvärinen, 1999). So, pollen brought by running water during the initial lake-phase (which ceased when peat started to develop) could be the cause for the high influx values. Further, there is very slow peat accumulation in the initial accumulation phase. This could imply that the extrapolated accumulation rates below the lowermost dated sample may result in unreliable age-depth models (section 4.3.3) and result in too high influx estimates. Hence, it makes it uncertain to what degree the fixed threshold influx values (Seppä & Hicks, 2006; Jensen et al., 2007) can be used in this early phase determining local plant communities at this site. Therefore, for interpreting the dynamics in the depths below 260 cm at Stripåtmyrin I mainly focus on the above-mentioned proxies, except pollen influx values. The influx values recorded in the deepest layers at Heimfjellsmyren are also high for many taxa including tree-birch and pine, but mostly coincide with high pollen percentages, and are hence assumed reliable. Further, the high influx values could also be caused by a slow peat accumulation. Taxa not displayed in the pollen diagrams (Figures 17-22) are found in Appendix B.

5.1 Stripåtmyrin

Figure 17 (right): Pollen percentage diagram for Stripåtmyrin (990 m a.s.l.), with a selection of pollen taxa represented. Maximum probability values of the calibrated ages, depths and pollen zone names are displayed to the left. LOI, PC axis 1 (PCA1), PC axis 2 (PCA2), Species richness $(E(T_{432}))$, stomata, charcoal and lithostratigraphic properties are displayed to the right. Shaded areas show a 10x exaggeration of the scale. Dotted lines show the local pollen assemblage zones.

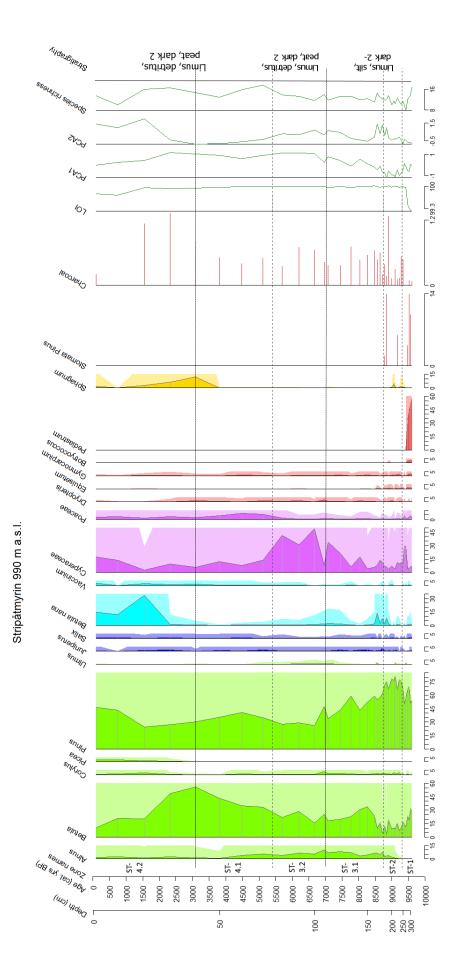
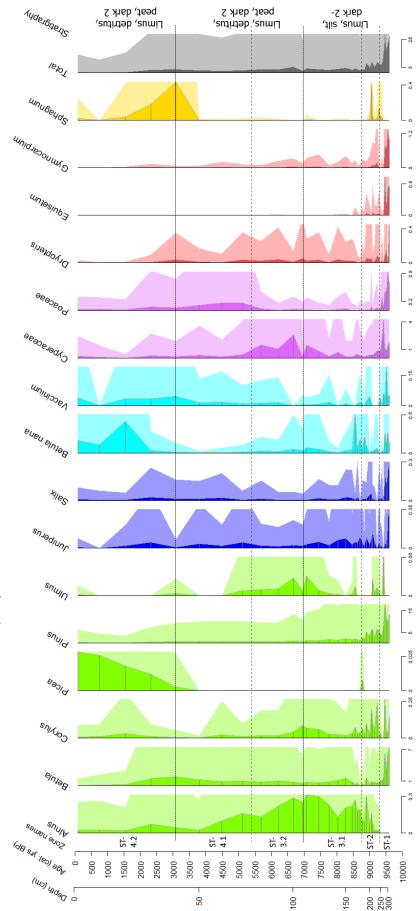


Figure 18 (right): Pollen influx diagram for Stripåtmyrin (990 m a.s.l.), with a selection of pollen taxa represented. Maximum probability values of the calibrated ages, depths and pollen zone names are *displayed to the left. Total* influx and lithostratigraphic properties are displayed to the right. Shaded areas show a 10x exaggeration of the scale. Dotted lines show the local pollen assemblage zones. All taxa (x-axis) are given in 10³ pollen grains cm⁻²year⁻¹.



Stripåtmyrin 990 m a.s.l.

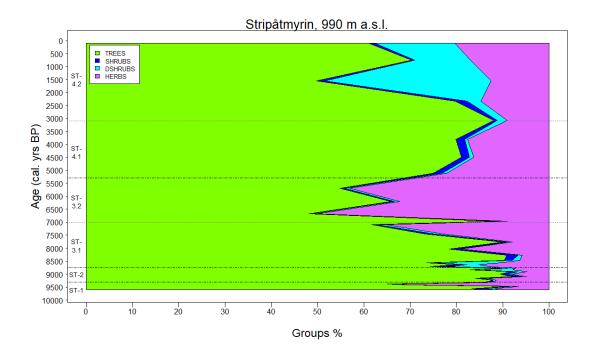


Figure 19: Total diagram from Stripåtmyrin (990 m a.s.l.) displays the various percentages of the main plant groups (TREES, SHRUBS, DWARF SHRUBS and HERBS). Dot-dash lines show the local pollen assemblage zones, while dotted (grey) lines show the sub-zones. Local pollen assemblage zone names are displayed on the left side.

ST-1: CA. 9600-9300 CAL. YRS BP (BOTRYOCOCCUS – PEDIASTRUM ZONE, 307-250 CM DEPTH)

From ca. 9600 cal. yrs BP, Stripåtmyrin was an open lake as shown by pollen from the aquatic plants *Potamogeton*-type, *Sparganium*, *Hippuris* and *Menyanthes trifoliata* accompanied by the freshwater algae *Pediastrum* and *Botryococcus*. High pollen percentages of tree-birch (32%) and pine (70%), pine stomata (at 300, 290 and 280 cm, with 10, 14 and 4 counts, respectively) and macrofossils (Table 7) give evidence of local tree-birch and pine forests. The layers contain fragments of charcoal, both small (<60 μm) and big (>60 μm), which further suggests local trees. Pollen of *Juniperus communis, Rumex* sect. *Acetosa* and dwarf shrubs indicate patches of light-open areas, the former also indicating well-drained soils. Additionally, pollen of *Populus* which was central in the pioneer forests and the reforestation after the last ice age (Mangerud *et al.*, 2018) suggest rather dry conditions. *Salix* shrubs grew on moister patches (Birks & Birks, 2008). Conditions are generally rather dry (PC axis 1) and forested (PC axis 2). The light demanding pioneer *Hippophae rhamnoides* has poor pollen dispersal. Low pollen percentage values therefore suggest local presence (ca. 0.4%; Barnett *et al.*, 2001; Paus, 2010) which together with high PR and silty layers (Table 5) indicate traces of

eroded glacial deposits and pioneer conditions. The high LOI show that a successional stage towards developed soils has started, underlined by pollen of the nitrogen and nutrient demanding tall-herbs Apiaceae and *Filipendula* (Lid & Lid, 2005). About 9400 cal. yrs BP there was a rapid transition from lake to mire, as indicated by a disappearance of freshwater algae and a rise in pollen of Cyperaceae and spores of pteridophytes (*Gymnocarpium dryopteris*-type reaching 3%) and *Sphagnum*. The occurrence of *Quercus* and *Artemisia*-type pollen in the peat is presumably due to wind dispersal (Birks, 2008; Iversen, 1954; Paus, 2010), and give evidence of favourable conditions, fertile soils and dry conditions regionally.

ST-2: CA. 9300-8750 CAL. YRS BP (*Alnus – Juniperus* zone, 250-180 CM depth)

Alnus, presumably the less warmth-demanding A. incana which is believed to have migrated into the study area from east (Tallantire, 1974; Giesecke, 2005b; Paus, 2010) reach the threshold values in pollen influx/pollen accumulation rates indicating local presence (>100 grains cm⁻²yr⁻¹; Vorren *et al.*, 1996; Moe, 1998) ca. 9000 cal. yrs BP. High influx values suggests that both pine (>1000 grains cm⁻²yr⁻¹; Hicks, 2001) and tree-birch pollen are part of the local forests (>500 grains cm⁻²yr⁻¹; Hicks, 2001). *Picea abies* pollen sparsely appear ca. 8780 cal. years. Pollen from Filipendula suggests it grew in nitrogen rich, moister areas. Fungal spores of Arnium HdV-261 are continuous until ca. 9060 cal. yrs BP and indicate the presence of herbivores and an open forest landscape (section 3.2.2). J. communis and light demanding dwarf shrubs have overall high influx/percentage values and presumably grew in open areas. No dated pine megafossils were older than from ca. 9230 cal. yrs BP. However, macrofossils (Table 7) and pine stomata give evidence of local presence of both tree-birch and pine at least 9600 cal. yrs BP. There were no finds of pine stomata younger than from ca. 8780 cal. yrs BP. The high values (≤400 spores cm⁻²yr⁻¹) of *Sphagnum* recorded from ca. 9300 cal. yrs BP coincides with a stable appearance of pteridophytes. This, in addition to the rise in A. incana, suggests a transition to moister, perhaps cooler local conditions around 9000 cal. yrs BP.

ST-3.1: CA. 8750-7000 CAL. YRS BP (Alnus – Cyperaceae zone, 180-107 CM depth)

A. incana is present locally (>100 grains cm⁻²yr⁻¹) throughout the zone, mixed with forests of tree-birch and pine. Although *Sphagnum* spores are briefly present, *Sphagnum* peat is prevalent in the lithostratigraphic layers (Table 5). Pollen of nitrophilous herbs (*Filipendula*, Asteraceae sect. *Cichorium*) give evidence of a tall-herb woodland in forest-openings

(Artsdatabanken, 2018; Fremstad, 1997). Pteridophytes (*Dryopteris-* and *G. dryopteris-*type, *Selaginella selaginoides*) and *Melampyrum* grew in moist patches. The shrubs *J. communis* and *Salix* have moderately high and continuous pollen curves (influx and percentage). A modest rise in spores of pteridophytes and pollen of Cyperaceae in addition to macrofossils of *Salix* (Table 7) give further evidence of a continued transition towards moister (PC axis 1) and more open (PC axis 2) conditions locally. PR is moderate and steady and LOI values are still very high. Peat accumulation rates increase from 13 to 40 yr/cm towards the lower depths.

ST-3.2: CA. 7000-5300 CAL. YRS BP (JUNIPERUS – CYPERACEAE ZONE, 107-70 CM DEPTH)

A. incana pollen influx has a steady decrease towards the upper zone boundary. The decline in pollen influx values of trees and the slight increase in pollen of light-demanding species (*Juniperus*, Poaceae and *Vaccinium*-type) suggest lower temperatures about 7000-6000 cal. yrs BP. Despite a thinning of local forests influx values indicate scattered presence of pine locally (Seppä & Hicks, 2006). Dated megafossils of pine also give evidence of local presence (Table 4) around 7000-6000 cal. yrs BP. The rise in Cyperaceae pollen (reaching 2550 grains cm⁻²yr⁻¹), spores of *Dryopteris*-type and *Sphagnum* indicate increasing moisture. Nutrient demanding herbs such as *Filipendula*, *Melampyrum* and Asteraceae sect. *Cichorium* grew in tall-herb communities in richer patches. Species richness has a slight increase towards the upper zone boundary.

ST-4.1: CA. 5300-3100 CAL. YRS BP (BETULA – POACEAE – SPHAGNUM ZONE, 70-40 CM DEPTH)

A. incana pollen disappears locally ca. 4400 cal. yrs BP. Pine pollen values barely exceed the threshold for local forests. Local birch-forests are present (reaching 56% and 1800 grains cm⁻²yr⁻¹ca. 3085 cal. yrs BP), increasing slightly towards the upper zone boundary. Pollen of the drought-tolerant *J. communis* (\leq 50 grains cm⁻²yr⁻¹) and Poaceae indicate more light-open conditions. Along with the subsequent drop in Cyperaceae pollen and *Dryopteris*-type spores this suggests a brief period with drier conditions until ca. 4000 cal. yrs BP. After this point, conditions again become moist as indicated by the rapid increase in spores of *Sphagnum* (\leq 450 spores cm⁻²yr⁻¹) and *Dryopteris*-type and pollen of *A. incana*. Pollen of *Calluna* give evidence of acidification. Further, the simultaneous appearance of pollen of the low nutrient indicator *Rubus chamaeomorus* (Fremstad, 1997) give evidence of a paludification (Giesecke, 2005b). This is underlined by an increase in PR and humidity (PC axis 1) and a drop in vegetation density (PC axis 2). Peat accumulation rate range from 65.6 yr/cm to 74 yr/cm, with a steady increase towards the surface layers. A decline in pollen of warmth-demanding broadleaved trees suggest a regional soil deterioration and/or cooler climate.

ST-4.2: CA. 3100-105 CAL. YRS BP (PICEA – BETULA NANA – VACCINIUM ZONE, 40-2 CM DEPTH)

According to pollen influx values, the local pine forests disappear ca. 3085 cal. yrs BP followed by a scattered presence until ca. 1550 cal. yrs BP when it disappears locally. Still, a dated megafossil from ca. 1010 cal. yrs BP give evidence of local presence nearby (Raphamn; Table 4). A prominent decrease in *Sphagnum* ca. 1500 cal. yrs BP together with a slightly decreasing LOI give evidence of soil deterioration and higher moisture, hence leading to a thinning of local forests. The peak in *B. nana* pollen around 1500 cal. yrs BP (500 grains cm⁻²yr⁻¹) reflects a local arctic-alpine heath (Seppä & Hicks, 2006) and hence indicates a cooler environment. Tree-birch pollen subside towards the present, disappearing locally ca. 1400 cal. yrs BP (interpolated). There is a slight increase in Cyperaceae pollen influx towards the upper zone boundary. Additionally, the increase in PR and PC axis 2 give evidence of more open conditions. Peat accumulation rates slow down towards the present. Regionally, pollen of the more shade tolerant *Picea abies* appears (<50 grains cm⁻²yr⁻¹; Hicks, 2001), expanding towards 50 grains cm⁻²yr⁻¹ ca. 130 cal. yrs BP.

5.2 Heimfjellsmyren

Figure 20 (right): Pollen percentage diagram for Heimfjellsmyren (1097 m a.s.l.), with a selection of pollen taxa represented. Maximum probability values of the calibrated ages, depths and pollen zone names are displayed to the left. LOI, PC axis 1 (PCA1), PC axis 2 (PCA2), Species richness ($E(T_{432})$), stomata, charcoal and lithostratigraphic properties are displayed to the right. Shaded areas show a 10x exaggeration of the scale. Dotted lines show the local pollen assemblage zones.

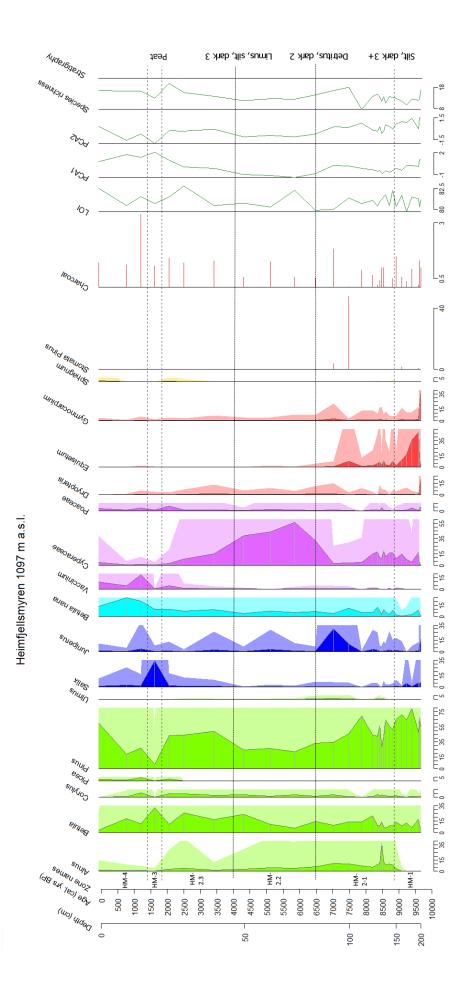
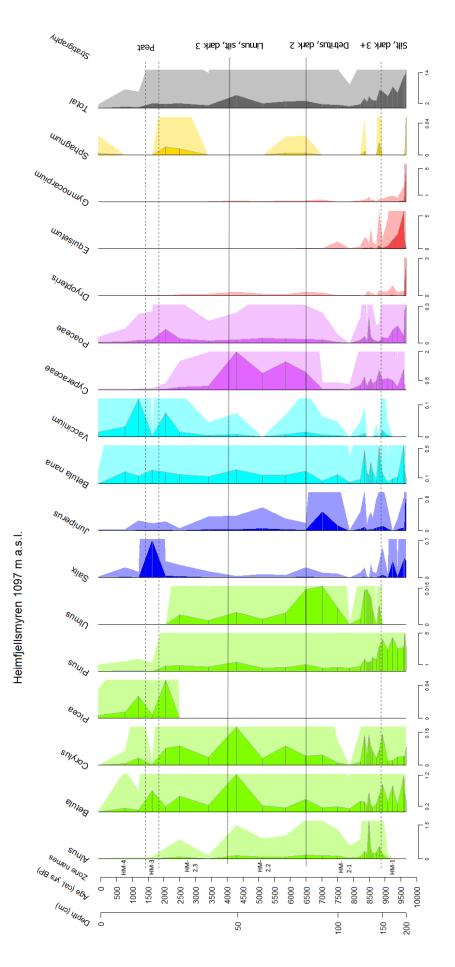


Figure 21 (right): Pollen influx diagram for Heimfjellsmyren (1097 m a.s.l.), with a selection of pollen taxa represented. Maximum probability values of the calibrated ages, depths and pollen zone names are displayed to the left. Total influx and lithostratigraphic properties are displayed to the right. Shaded areas show a 10x exaggeration of the scale. Dotted lines show the local pollen assemblage zones. All taxa (x-axis) are given in 10³ pollen grains cm⁻ ²year⁻¹.



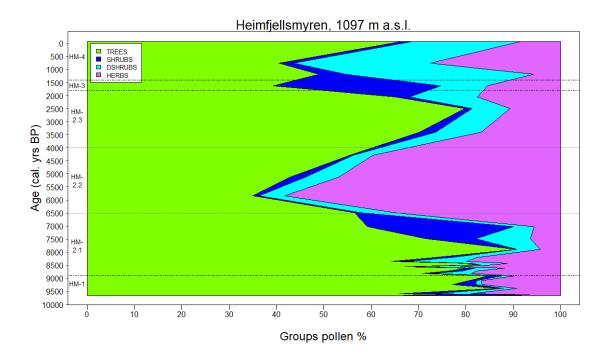


Figure 22: Total diagram from Heimfjellsmyren (1097 m a s.l.), showing the percentages of the main plant groups (TREES, SHRUBS, DWARF SHRUBS and HERBS). Dot-dash lines show the local pollen assemblage zones, while dotted (grey) lines show the sub-zones. Local pollen assemblage zone names are displayed on the left side.

HM-1: CA. 9640-8900 CAL. YRS BP (POACEAE – *Pteridophyte – Salix* zone, 200-160 cm depth)

The pollen data suggest that local pine dominated forests (reaching 5000 grains cm⁻²yr⁻¹) with elements of tree-birch (\geq 500 grains cm⁻²yr⁻¹ in most spectra) were established from ca. 9620 cal. yrs BP. The local presence of pine is underlined by pine stomata about 9610 and 9080 cal. yrs BP. Probably, *Salix* and *B. nana* (reaching 550 grains cm⁻²yr⁻¹) grew in forest openings and pteridophytes, *Melampyrum* and *Sphagnum* grew in moister areas. Herbs such as Apiaceae, Asteraceae sect. *Cichorium, Filipendula* grew where the soil contained more nitrogen and some moisture, in open forest landscapes. *Potentilla*-type pollen also indicate an open-forest environment (Birks, 1993). Poaceae reaches its highest influx values with 300 grains cm⁻²yr⁻¹ (ca. 9635 cal. yrs BP). *Dryopteris*-type and *G. dryopteris*-type reach their maximum spore influx values, with 3050 and 5700 spores cm⁻²yr⁻¹ respectively, before they level out at low values. *Equisetum* also peaks ca. 9600 cal. yrs BP, with 5800 spores cm⁻²yr⁻¹. Although the pteridophyte spores, Cyperaceae pollen and *Sphagnum* spores give evidence of moist conditions at the coring site, soils were generally dry (PC axis 1) with rather high vegetation density (PC axis 2). Small fragments of charcoal is recorded in all depths. Species richness is modest. LOI values range from 80% to 82%, while peat accumulation rates increase slightly yet steadily towards the upper zone boundary. *Thalictrum alpinum* is prone to wind-dispersal (Steven & Waller, 2004) and hence suggests base-rich soils, early snow-beds and open forests regionally ca. 9080 cal. yrs BP (Lid & Lid, 2005). Pollen of *Corylus* and *Quercus* give evidence of favourable conditions in the lowlands.

HM-2.1: CA. 8900-6500 CAL. YRS BP (*Alnus – Juniperus* zone, 160-80 CM depth)

According to influx values local tree-birch forests disappeared ca. 8500 cal. yrs BP (<500 grains cm⁻²yr⁻¹). Yet, birch-megafossils (Table 6) suggest further presence of local trees. After ca. 8150 cal. yrs BP, pollen influx values indicate that local pine-forests disappear. High amount (48) of pine stomata found ca. 7555 cal. yrs BP could suggest local scattered trees. However, these could origin from the same individual. A. incana reaches maximum pollen influx values with 1700 grains cm⁻²yr⁻¹ and is locally present from ca. 8750, coinciding with pollen of the drought-intolerant R. chamaemorus and Sphagnum spores. This suggest a brief period with higher moisture and perhaps lower temperatures. Pollen of B. nana reaches its maximum influx values, with 450 grains cm⁻²yr⁻¹ ca. 8275 cal. yrs BP. Equisetum spores has high pollen influx values, decreasing towards the upper zone boundary. The slight increase in Vaccinium-type pollen suggest a more acidic environment, pointing to a degradation of the local soils. However, scattered occurrences of pollen of Apiaceae and Filipendula give evidence of more nitrogen-rich patches. Around 8200 cal. yrs BP there is a decline in A. incana. Pollen of the drought-tolerant J. communis peaks with 450 grains cm⁻²yr⁻¹ ca. 7180 cal. yrs BP. The warmth-demanding broadleaves Corylus and Ulmus decline ca. 8200-7100 cal. yrs BP. The rather synchronous decline in regional broadleaved trees and local A. incana could perhaps suggest a brief period with cool and dry conditions regionally. LOI range from 79.9% to 82.3%. The peat accumulation rate is stable, ranging from 18.2 yr/cm to 58.6 yr/cm, increasing towards the upper zone boundary.

HM-2.2: CA. 6500-4000 CAL. YRS BP (BETULA – CYPERACEAE ZONE, 80-50 CM DEPTH)

The rapid increase in Cyperaceae pollen (reaching 2000 grains cm⁻²yr⁻¹) accompanied by a continued fall in pollen of *A. incana* (disappearing locally ca. 6000 cal. yrs BP), tree-birch

and *J. communis* ca. 6500 cal. yrs BP coincides with similar recordings in south-western Sweden (Digerfeldt & Håkansson, 1993). This shift may be due to soil degradation accelerated by climate deterioration and increased soil leaching (Digerfeldt & Håkansson, 1993). This is further suggested by a regional drop in *Ulmus* around 6500-5000 cal. yrs BP. In general HM-2.2 reflects moist conditions (PC axis 1) with moderate vegetation density (PC axis 2). However, the following increase in broadleaved trees (e.g. *Corylus* and *Quercus*) suggest a new transition to favourable conditions regionally. Small fragments (<60 μ m) of charcoal is recorded in all depths. Species richness is steady, and LOI range from 80.3% to 82.3%. The peat accumulation rates increase from 67.6 yr/cm to 86.4 yr/cm.

HM-2.3: CA. 4000-1800 CAL. YRS BP (VACCINIUM – SPHAGNUM ZONE, 50-25 CM DEPTH)

According to pollen influx values, scattered birch-trees grew in dry areas surrounding the mire (500-200 grains cm⁻²yr⁻¹). Pollen of the less nutrient demanding *R. chamaemorus, Rumex-* and *Solidago*-type suggest further soil deterioration. Yet, the more base- and nutrient demanding Apiaceae, *Filipendula* and *Thalictrum alpinum* reflect occasional patches of richer soils. Pollen of *P. abies* appears abruptly with almost 50 grains cm⁻² yr⁻¹ ca. 1890 cal. yrs BP (just below the limit for local presence of 50 grains cm⁻²yr⁻¹; Hicks, 2001) and indicates spruce establishing regionally. Accompanied by pollen of *Salix*, Poaceae, the acidophile *Vaccinium*type and *Sphagnum*-spores this give evidence of further leaching and degradation of soils and paludification (Giesecke, 2005b). The general trend in HM-2.3 shows a brief period with drier conditions (PC axis 1), moderate vegetation density (PC axis 2) and high species richness. The decline in regional taxa (*Corylus, Qeurcus* and *Ulmus*) towards the upper zone boundary further suggest a shift towards less favourable conditions in the lowlands. Small fragments of charcoal are recorded in all depths. LOI range from 80.4% to 82.8%. Peat accumulation rates fall from 90.7 yr/cm to 88 yr/cm. In contrast to the previous zones, the accumulation rates suggest a slightly faster accumulation towards the surface layers.

HM-3+HM-4: CA. 1800 CAL. YRS BP-PRESENT (*VACCINIUM - SPHAGNUM* ZONE, 20-0 CM DEPTH)

All trees decline towards present (0 cm depth, influx tot. 200 grains cm⁻²yr⁻¹). The rise in pollen of *B. nana* (reaching 200 grains cm⁻²yr⁻¹) suggests arctic-alpine heath (Seppä & Hicks, 2006) and cool conditions. *Vaccinium*-type pollen reaches its maximum influx value ca. 1050 cal. ys BP. Establishment of *Sphagnum* peat, *Rubus chamaemorus*, shrubs and dwarf shrubs give evidence of moist, open and poor-nutrient conditions with a further paludification towards the surface. This coincides with an increase in LOI and PC axis 2 and a decrease in PC axis 1. Regionally, *P. abies* reaches its maximum pollen influx value at ca. 1050 cal. yrs BP, with 30 grains cm⁻²year⁻¹. Small fragments of charcoal are recorded in all depths. Species richness has a slight increase towards the surface. Values from LOI range from 80.4% to 82.5%. Peat accumulation rate decreases from 85.1 yr/cm to 83.5 yr/cm at the surface.

The total percentage diagrams (Figures 19 & 22) suggest a slightly earlier deforestation than the influx values. Trees are replaced by a pollen maximum in non-arboreal pollen (NAP) a little after 7000 cal. yrs BP at Stripåtmyrin and 6000 cal. yrs BP at Heimfjellsmyren. Simonsen (1980), suggests that a maximum in NAP could suggest a forest-line phase.

6 DISCUSSION

Tree-line specimens require favourable microhabitats and local topography and are often situated far away from environments with preservation potential such as bogs or lakes (Paus & Haugland, 2017). Alpine bogs and mires only form in the low-alpine zone or below, hence restricting the possibilities of recovering megafossils in the areas of my study (Paus & Haugland, 2017). Due to the few megafossil finds a very firm reconstruction could not be made, yet my study adds new points of megafossil and pollen-data. More and perhaps older tree-remains could perhaps be obtained from lakes in the surrounding area.

6.1 HOLOCENE TREE- AND FOREST LINE DYNAMICS

Local forests of pine had established at least 9600 cal. yrs BP at both study sites based on the influx estimates. According to the pollen influx, tree-birch forests were established at least from 9600 cal. yrs BP at Stripåtmyrin (990 m a.s.l.), and ca. 9500 cal. yrs BP at Heimfjellsmyren (1097 m a.s.l.). Tree-birch megafossils indicate local presence at least 9080 cal. yrs BP at Heimfjellsmyren (ca. 1030 m a.s.l., adjusted for glacio-isostatic uplift; cf. Lyså *et al.*, 2008) (Table 6). Yet megafossils, especially smaller fragments, might be prone to movement and thus not found in their primary deposition. Pine-forests seem to have disappeared from the area around Heimfjellsmyren ca. 8150 cal. yrs BP according to the pollen records. Pine stomata give evidence of pine trees growing locally at the site until at least 7180 cal. yrs BP (Figure 20). The deforestation seen in the influx estimates was followed by a scattered local presence until ca. 1400 cal. yrs BP.

In the Røros mountains pine-pollen give evidence of an expansion around 10 000-9200 cal. yrs BP, while megafossils show local presence ll 200-13 800 cal. yrs BP in the Swedish Scandes (Kullman & Kjällgren, 2006; Kullman, 2002; 2008). In addition to pine stomata findings from Dovre (Paus et al., 2011), this suggests a rapid spread from favourable mountain peaks (nunataks) during the late-glacial/early Holocene. In Jotunheimen, ca. 60 km south-west of Rondane, pine is believed to have established ca. 9785 cal. yrs BP (Barnett et al., 2001), while pine megafossils from a nearby area date to ca. 9600 cal. yrs BP (Paus & Haugland, 2017). This delay could be due to a later deglaciation in the Jotunheimen area (Barnett et al., 2001, Gunnarsdottir, 1996). Nevertheless, present forest lines in Jotunheimen (Scandinavias highest mountain range) reach the highest altitudes in Scandinavia. This is presumably caused by the Massenerhebung effect (Odland, 2015; Paus & Haugland, 2017), which increases the temperature and causes a rise of vegetation belts in large mountain massifs (Paus & Haugland, 2017). It would therefore be reasonable to assume that this effect also was effective in the early Holocene, causing lower forest lines in the Høvringen area compared to Jotunheimen. In the Dovre area (1253-1316 m a.s.l.) ca. 30 km north of the Høvringen area, pine established no later than 10 200 cal. yrs BP according to pollen records, while birch forests established a little earlier (ca. 10 700 cal. yrs BP) (Paus et al., 2015; 2019). Similar trends for establishment of tree-birchand pine have been recorded for other alpine study sites in mid-Scandinavia (Bergman et al., 2005; Bjune, 2005; Paus & Haugland, 2017). In Rødalen, Tynset, situated ca. 60 km north-east of the Høvringen area, tree-birch established ca. 10 300 cal. yrs BP at 1100 m a.s.l., ca. 150 years earlier than the local pine rise (Paus, 2010). Pine then dominated between 9900 and 8500 cal. yrs BP, followed by tree-birch forest until 1300 cal. yrs BP (Paus, 2010). Since my peat sequences did not extend beyond the tree-birch and pine establishment, this trend in pine establishing a little after tree-birch could not be stated.

In the Høvringen area, finds of pine stomata (Figure 17) and macrofossils (Table 7) give evidence of local establishment of pine at Stripåtmyrin from ca. 9600 until at least ca. 7700 cal. yrs BP. Influx values suggest the presence of local pine-forests until ca. 3000 cal. yrs BP. A thinning presumably occurred when conditions became cooler and/or moister, followed by expansion of *Sphagnum*-mires and paludification, with scattered occurrence of local trees until

present day. Further indications of early presence of local pine in the Høvringen area is given by megafossils dated to ca. 9230-1010 cal. yrs BP (Table 4).

According to pollen influx records, tree-birch forests disappeared from Heimfjellsmyren ca. 8520 cal. yrs BP, followed by scattered presence of local trees until ca. 1400 cal. yrs BP. This is earlier than the recorded thinning of birch-forests in the Dovre area ca. 7000 cal. yrs BP (Paus *et al.*, 2011) and coincides more with the retreat around 8500-8000 cal. yrs BP in west-central Sweden (Bergman *et al.*, 2005). At Stripåtmyrin the pollen influx records give evidence of tree-birch forests until ca. 2300 cal. yrs BP, after which the influx values suggest these forests disappeared locally.

In brief, when comparing the two study sites the pollen influx values suggest that local pine forests disappeared from the area around Heimfjellsmyren ca. 8150 cal. yrs BP, ca. 5000 years before it disappeared from the area surrounding Stripåtmyrin. As already mentioned, the pollen influx values further suggest that tree-birch forests disappeared from Heimfjellsmyren ca. 8520 cal. yrs BP and from Stripåtmyrin ca. 2300 cal. yrs BP. Following, the pollen influx records indicate that birch-trees disappeared locally after ca. 1400 cal. yrs BP from the Heimfjellsmyren area and after ca. 700 cal. yrs BP from the Stripåtmyrin area. This is not in accordance with present day vegetation. Heimfjellsmyren is at present situated beneath the tree-line for treebirch, while Stripåtmyrin is situated beneath the forest line for tree-birch (section 2.1). According to Hicks (2006), no pollen does not necessarily mean no trees. Discrepancies could hence be due to scattered trees, trees not producing pollen due to either unfavourable temperatures, young age or mechanical damage caused by e.g. moth larvae. Further, these deviations could be caused by inaccuracies during the extrapolation of age-depth estimates and following influx calculations.

The delay in establishment and the earlier decline of pine at Heimfjellsmyren could be due to the altitudinal difference (ca. 107m) between the study sites, reflecting ca. 0.6°C colder conditions at Heimfjellsmyren (cf. Laaksonen, 1976).

The south-faced early Holocene pine forest line was situated at least 1030 m a.s.l. (adjusted for glacio-isostatic uplift, cf. Heimfjellsmyren (at present 1097 m a.s.l.)), which is ca. 40 m higher than today (Table 2). The early Holocene pine forest lines following a southwest-northeast transect in the Scandes Mountains reached 210-170 m higher than today (Paus & Haugland, 2017). It is hence reasonable to believe that the Holocene pine forest-line was situated at least 1160 m a.s.l. in the Høvringen area, when adjusted for glacio-isostatic uplift.

The pine tree-line extended above 1020 m a.s.l. during the early Holocene (Table 4) and presumably higher than the present tree-line (1055 m a.s.l.) due to higher temperatures (see section 6.6). The birch tree-line in the eastern part of Jotunheimen presumably increased with ca. 40-100 meters during the early Holocene (Bjune, 2005). As the Massenerhebung effect (Odland, 2015; Paus & Haugland, 2017) was strongest in Jotunheimen, this increase was presumably larger here than in the Høvringen area. Too few megafossils were found and dated to reconstruct the early Holocene tree- and forest lines reliably (cf. Paus & Haugland, 2017). Further, a peat stratigraphy covering a longer period is needed to assess the entire Holocene tree-line history.

6.2 HOLOCENE PINE-MAXIMUM

In the Høvringen area, the pine maximum seems to have occurred between 9600 and 8900 cal. yrs BP according to the pollen percentages and influx values. This is synchronous with records from west-central Sweden, suggesting a pine maximum ca. 9200-8500 cal. yrs BP (Bergman et al., 2005). Bjune (2005) found that the pine tree-line ascended to the highest altitudes about 9300-8600 cal. yrs BP in Jotunheimen, while Gunnarsdóttir (1996) suggests a pine maximum (also in Jotunheimen) to have occurred 9700-7600 cal. yrs BP. Investigations in the Rødalen area suggest a pine dominance ca. 9900-8500 cal. yrs BP (Paus, 2010), while in Ottadalen (400-905 m a.s.l.), situated ca. 25 km north-west of the Høvringen area, an increase in pine was recorded ca. 9700-9500 cal. yrs BP (Fossheim, 2007). Further, megafossils give evidence of local pine growing at least 1022 m a.s.l. ca. 9260 cal. yrs BP in the Raphamn area (Table 4). In the nearby area of Dovre, no megafossils extend 1105-1110 m a.s.l. (Paus, 2010; Paus et al., 2019). Further, climate reconstructions in the Rødalen area indicate that pine-forests did not extend higher than ca. 170-200m (adjusted for glacio-isostatic uplift) above the present forest lines during the pine maximum (Paus & Haugland, 2017). This would suggest when adjusting for land-uplift that local pine trees were growing at least 1225-1230 m a.s.l. in the Høvringen area during the early Holocene (Table 2). Conversely, in the Jotunheimen area (ca. 60 km north-east of Høvringen) influx values suggest pine-forests growing close to 1260-1300 m a.s.l. ca. 9700-6000 cal. yrs BP (Velle et al., 2010). For further information on the Holocene pine-maximum in the Høvringen are, an extensive search for megafossils must be conducted.

6.3 HUMAN IMPACT

The Høvringen area has a history of coal- and ore mining dating to the Roman Iron Age (ca. 1900 BP) (Larsen, 2004), which could explain the rather high amounts of charcoal in the peat (Figures 17 & 20). Yet, as levels of charcoal in the Høvringen area are rather uniform and the analysis show no further evidence of human activities (e.g. grazing indicators, pollen from cereals, prominent decline in tree-pollen), the charcoal finds are presumably caused by naturally occurring fires. Further, the small size (<60 µm) of most fragments could be due to long-distance transport (Blackford, 2000). A decline in tree-lines can be caused by a combination of human impact and changes in climate (Bjune, 2005). The coal- and ore mining was presumably extensive during the 13th century (Larsen, 2004), and could result in a lowering of tree-lines due to the subsequent deforestation. But, although my pollen-records show a drop in local tree-pollen around 1400 cal. yrs BP the resolution in my samples is too low to fully determine the decline in trees in the Høvringen area. It could be due to the presence of domesticated animals and summer farming, but the pollen data from the two sites show no indications of this. Yet, early anthropogenic activities such as hunting and trapping of wild reindeer are known from Grimsdalen (ca. 26 km north-east of Høvringen) and Rondane (Jordhøy et al., 2005; Stene & Hassel, 2015) as early as the Late Bronze Age (ca. 3000-2500 BP). Traps for catching wild reindeer have been located merely ca. 2 km south-southeast of Heimfjellsmyren (Barth, 1996). Grimsdalen has also facilitated summer farming the last 2000 years (Risbøl et al., 2011). Human impact (grazing animals and summer farming) is evident in Jotunheimen the last 2000 years and in the Dovre area about 2500 cal. yrs BP (Bjune, 2005). Still, the drop in pollen-records around 1400 cal. yrs BP is followed by a gradual increase in dwarf shrubs during the late Holocene, suggesting climatic deterioration and a gradual shift towards more open conditions due to changes in climate.

6.4 The rise and expansion of *Alnus incana*

According to the pollen records *A. incana* was present locally (>100 grains cm⁻²yr¹; Vorren *et al.*, 1996; Moe, 1998) at the lowest altitudinal site Stripåtmyrin from ca. 9000 cal. yrs BP. This is ca. 200 years before it was present at Heimfjellsmyren from ca. 8800 cal. yrs BP, only disappearing locally ca. 8200-7560 cal. yrs BP; section 6.6.2). The difference could be due to variance in local factors such as moisture, development of soils, topography or sloping of the terrain. Also, summer temperature is an important factor for alder pollen production, which is

prone to be lower at higher altitudes (Moe, 1998). However, the calibrated dates are given in intervals of a 380-470 years (Table 7 & 8) and hence reflects a major uncertainty dating the *Alnus*-rise.

The *A. incana* rise in the Høvringen area is later than a recorded rise ca. 9500-9200 in other parts of the Scandes mountains (e.g. Tallantire, 1974; Gunnarsdöttir, 1996; Giesecke, 2005a; Segerström & von Stendingk, 2003). In the Dovre mountains a rise in *A. incana* was correlated to the warming following a 9300 cold-event (Paus *et al.*, 2019). During the expansion of *A. incana* the forest composition changed to a more mixed forest, with an alder-, tree-birch and pine-canopy and some more nitrogen-demanding herbs growing in the understory (e.g. *Filipendula* and Apiaceae). Further, symbiotic relations might have formed between *A. incana* and soil actinomycetes (*Frankia* strains), increasing the content of soil-nitrogen (Bosco *et al.*, 1992; Ridgway *et al.*, 2004) hence improving conditions for more nutrient demanding taxa (section 6.6.1). There was a gradual decrease in *A. incana* towards the surface layers, only represented by scattered long-distance transport after ca. 4400 cal. yrs BP at Stripåtmyrin and ca. 6000 cal. yrs BP at Heimfjellsmyren. Today, individuals of *A. incana* grow in the lowlands.

6.5 THE EXPANSION OF PICEA ABIES

Heikkilä *et al.* (2009) give evidence of spruce growing in the eastern Baltic regions already in the Younger Dryas. It may then have migrated to Fennoscandia during the early Holocene. Fossil DNA give evidence of spruce growing in Trøndelag, (central Norway) 10000 cal. yrs BP (Parducci *et al.*, 2012). Spruce megafossils (Kullman, 1996;2001;2002) and expansions (Segerström & von Sedingk, 2003; Paus & Haugland, 2017) have further been recorded in nearby areas already in the late glacial and early Holocene. In the Dovre area, spruce expansion has been recorded to ca. 2500-1300 cal. yrs BP (Paus, 2010), while local presence was recorded ca. 4300 cal. yrs BP in northern Norway (Bjune, 2004). Further, establishment of spruce has been recorded at ca. 1200 cal. yrs BP in the inland areas of Vestfold (Bjune *et al.*, 2009). Pollen of spruce, *Picea abies,* first occur ca. 8780 cal. yrs BP at Stripåtmyrin, but only with two pollen grains in one spectrum. Despite the modest amount, this could indicate presence not very far from the study site. The continuous pollen influx and percentage curves start 3080 cal. yrs BP at Stripåtmyrin and 1890 cal. yrs BP at Heimfjellsmyren. Although spruce produces larger pollen grains with a higher fall speed than grains of pine (Giesecke & Bennett, 2004; Bjune *et al.*, 2009), they can still be prone to limited long distance wind dispersal (Hicks, 2001; Giesecke, 2005b). The values do not reach the threshold value for local presence (>50 grains cm⁻²yr⁻¹; Hicks, 2001) at either site throughout the peat sequences, and hence presumably reflect longdistance transport. The highest influx value of 50 grains cm⁻²yr⁻¹ recorded at Heimfjellsmyren ca. 1890 cal. yrs BP is just below the limit for local presence, and far below the limit for local forests (100 grains cm⁻²yr⁻¹; Hicks, 2001). Yet, it has been argued that even very low pollen percentage values of 1-5% can reflect local occurrence (e.g. Hicks, 1994; Giesecke & Bennett, 2004; Heikkilä et al., 2009; Latałowa & van der Knaap, 2006) due to its poor pollen production (Hicks, 1994). Further, individuals of spruce grow in the Høvringen area at present, yet with formation by vegetative growth presumably due to temperatures being too low for pollenproduction. Small spruce saplings, presumably dying from winter-stress, have also been found at both mires (Figure 5) up to ca. 100m above the present-day forest line for pine. These probably sprout due to the present global warming but die when they reach above the protective snow cover (Paus & Haugland, 2017). Additionally, in dense stands of spruce it may take up to 70 years before they set seeds (Giesecke, 2005a). Juvenile trees which do not produce pollen but shed needles and bud scales might hence grow in the area without showing up in the pollen diagrams (Giesecke, 2005a). This coincides with the previously mentioned discrepancies between pollen records and megafossils (Froyd, 2005; Hicks, 2006; Paus & Haugland, 2017). Due to the debated threshold values (cf. Hicks, 2001; van der Knaap *et al.*, 2005), it is at least reasonable to believe that spruce grew close to the study area from about 1890 cal. yrs BP. Establishment of spruce is believed to change the soil chemistry, rise the dissolved organic carbon and increase podzol formation, which may lead to enhanced soil erosion (Korsman et al., 1994; Giesecke, 2005a). Even if a local presence of spruce could not be stated the acidification towards the present may thus have been enhanced by the regional establishment of spruce as well as pine (Giesecke, 2005a).

6.6 THE HOLOCENE CLIMATE

6.6.1 THE EARLY HOLOCENE (CA. 9600 – 8200 CAL. YRS BP)

Tree-birch needs a mean tetraterm (June-September) of 7.5°C (Helland, 1912) and a mean July isotherm of ca. 10°C to establish forests in continental areas (Iversen, 1954; Odland, 1996). Simultaneously, pine requires a tetraterm of minimum 8.4°C (Helland, 1912; Tallantire, 1974) and a mean July isotherm of ca. 11°C to establish forests (Paus, 2010). Local pine-forests 9600 cal. yrs BP at both study sites give evidence of July temperatures of at least 11°C during the early

Holocene. This is in accordance with similar records of early Holocene mean July temperatures of >10.5°C (Brooks & Birks, 2000; Paus *et al.*, 2006; Paus, 2010). Further, early Holocene July mean temperatures of at least 11°C have been suggested, even at high altitudes (Hammarlund et al., 2004; Kolstrup, 1979; Paus et al., 2006; Velle et al., 2005a (Råtasjøen); Paus 2010). *Hippophaë rhamnoides* implies a minimum mean July temperature of 11-12°C (Kolstrup, 1979) at Stripåtmyrin (990 m a.s.l.). This is roughly 1°C warmer than present temperatures (Figure 4). According to the altitudinal difference between the study sites (ca. 107m) the mean July temperature at Heimfjellsmyren was ca. 0.6°C lower than at Stripåtmyrin (adjusted with 0.6°C/100m; cf. Laaksonen, 1976). The conditions were rather dry with well-drained soils and less winter snow, implied from the expansion of pine and *J. communis*. This trend seems to concur with other climate reconstructions from the Nordic region and the Scandinavian mountains (e.g. Velle et al., 2005a; Seppä et al., 2010; Paus, 2010). According to the abundance of ferns (i.e. *Dryopteris-* and *G. dryopteris-*type) and *Equisetum*, there were moist areas in the forest-openings ca. 9600-9400 cal. yrs BP. Further, the more warmth-demanding broadleaved trees Corylus, Quercus and Ulmus require tetraterms of 12.5, 12.6 and 11.2°C, respectively (Helland, 1912). These presumably grew in the nearby lowlands and hence suggest a temperate regional climate reaching July mean temperatures of 12-14°C.

6.6.2 THE MID HOLOCENE (CA. 8200 – 4000 CAL. YRS BP)

According to Helland (1912) *A. incana* requires a tetraterm of at least 7.7°C (compared to tree-birch and pine/spruce with 7.5 and 8.4°C, respectively). Considering the mean July isotherms required for tree-birch and pine to establish forests (10 and 11°C, respectively), is seems reasonable to believe that *A. incana* requires a mean July isotherm of slightly above 10°C. This nearly coincides with Tallantire's (1974) claim that *A. incana* requires a tetraterm of 8.4-10.6°C, depending on precipitation and the total length of the vegetative season. This implies a mean July temperature slightly above 10°C between ca. 6200 and 4400 cal. yrs BP at Stripåtmyrin and the surrounding area. Around Heimfjellsmyren, the scattered occurrence of pine, sporadic birch-forests and short-lived establishment of *A. incana* (ca. 7500-6100 cal. yrs BP) imply a July mean of ca. 8.4-10.0°C between 8200 and 5300 cal. yrs BP. In the Dovre area (1100 m a.s.l.), the reconstructed temperatures for the period 8500-1300 cal. yrs BP are assumed to be more than 10°C (Paus, 2010). Heimfjellsmyren, which today is situated above the local birch-forests and slightly below the birch tree-line, presumably experienced a slight cooling

after ca. 8200 cal. yrs BP. The drop in pollen influx records of *A. incana* ca. 8200-7560 cal. yrs BP corresponds with a similar drop in the Dovre area (Paus *et al.*, 2019). This could suggest a period with drier conditions, perhaps showing traces of the cold and dry phase of the 8200-event ("Finse event") (Nesje & Dahl, 2001; Seppä *et al.*, 2007; Paus, 2010). *Ulmus*, presumably regional (section 6.6.4), also disappears from the pollen records around 8200 cal. yrs BP. Still, expect from these slight declines in *A. incana* and *Ulmus*, clear traces of the 8200-event could not be found in the study area despite being located close to present-day ecological ecotones (section 2.1). The impact of the cooling event was brief, lasting ca 370 years shown by annual varves at Dovre (cf. Paus *et al.*, 2019). Hence, according to the discrepancy between establishment and pollen production (Froyd, 2005; Paus & Haugland, 2017; Paus *et al.*, 2019), a drop in pollen would be prominent but local trees would prevail. The study area might have been unaffected by this short-lasting cooling event due to local conditions at the sites. Still, the most credible explanation is the low-sample resolution during the microfossil analysis (Seppä *et al.*, 2010; Paus *et al.*, 2019).

6.6.3 THE LATE HOLOCENE (CA. 4000 CAL. YRS BP – PRESENT)

At Stripåtmyrin local presence of pine after ca. 4000 cal. yrs BP, give evidence of mean July temperatures of ca. 10°C. Tree-birch decreased towards the present, subsequent with a rise in acidophiles (i.e. *Calluna, R. chamaeomorus* and *Vaccinium*-type). However, as tree-birch forests still occur locally at Stripåtmyrin, this shows that the July mean temperature was at least 10°C. Tree-birch and pine at Heimfjellsmyren are gradually replaced by dwarf shrubs ca. 1400 cal. yrs BP. These changes at both study sites reflect climate deterioration, paludification and degradation due to leaching of soils (Digerfeldt & Håkansson, 1993). At Heimfjellsmyren the temperature during the late Holocene can be inferred from the presence of *Calluna, J. communis* and *Selaginella selaginoides*, where *Calluna* and *S. selaginoides* require tetraterms of 7°C. It is hence reasonable to believe that the mean July temperature at Heimfjellsmyren was at least 9°C during the late Holocene. This nearly coincides with the altitudinal difference reflecting 0.6°C between the sites (section 6.6.1). Additionally, the temperature in the lowlands seems to decline slightly towards the present, with a moderate drop in long-distance pollen of broadleaved trees (i.e. *Corylus, Quercus* and *Ulmus*). A deterioration in climate from ca. 4000 cal. yrs BP is also

in tree-birch towards the present. A trend towards more moist and cool conditions towards present times seems to be regional for the Scandinavian mountains (Seppä *et al.*, 2010).

At both study sites pollen of *Ulmus* appear almost subsequent with the rise in *A. incana*. Although *Ulmus* pollen presumably reflects regional conditions due to its high temperature requirements (11.2-11.4°C tetraterm; Helland 1912; Tallantire, 1974), the rise and decline is asynchronous at the two sites (Figures 17-18 & 20-21). This could reflect an occurrence closer to the Høvringen area than first believed. Macrofossils of *Ulmus* have previously been dated to the early Holocene in Sweden (ca. 740 m a.s.l.) (Kullman, 1998). Further, the synchrony with the appearance of *A. incana* could perhaps suggest that the nitrogen-fixing effect of *Alnus – Frankia* (section 6.4) favours the more nutrient-demanding *Ulmus*. The earlier decline at the higher altitude site (ca. 2360 cal. yrs BP at Heimfjellsmyren compared to ca. 5120 at Stripåtmyrin) could nonetheless reflect a gradual climate deterioration in the lowlands.

6.6.4 THE HOLOCENE THERMAL MAXIMUM (HTM)

The timing of the Holocene Thermal Maximum (HTM) has been widely discussed. In the Scandinavian mountains, HTM can be closely associated with the pine tree-/forest lines (Kullman & Kjällgren, 2006; Paus, 2010; Paus & Haugland, 2017) as they are today (e.g. Odland 1996, Moen 1999). Yet, as little snow and wind during winter can cause winter-stress (Figure 5, section 6.5) resulting in a delay in pine-establishment (Paus, 2010; Paus & Haugland, 2017). Hence, several factors should be considered when reconstructing the past climate. Several palaeoclimatological investigations have discussed the Holocene Thermal Maximum (HTM) in the Scandinavian mountains. The earliest temperature maximum (i.e. July maximum) is recorded to the early Holocene (11 500-9500 cal. yrs BP) based on reconstructions using chironomids, pollen and radiocarbon dating of megafossils (cf. e.g. Hammarlund et al., 2004; Velle et al., 2005b; Kullman & Kjällgren, 2006; Velle et al., 2010; Paus et al., 2019). A mid-Holocene warm period were recorded to ca. 8000-5000 cal. yrs BP (with 0.8°C above the Holocene mean ca. 6500 cal. yrs BP) based on chironomids in southern Scandinavia (Velle et al., 2005b). Seppä et al. (2008) set the summer temperature maximum in the northern-European tree-line region to ca. 7500-6500 cal. yrs BP (ca. 1.5°C higher than present), similar to the Dovre area (Paus et al., 2011). Further, Bjune et al., (2005) found the HTM to last from ca. 8000 to 4000 cal. yrs BP in Western Norway, with temperatures reaching 12-13°C. Also, there are various interpretations of the HTM. It has for instance been debated whether an edaphic/ecologic optimum could be more representative (e.g. Høeg *et al.*, 2018) than an optimum based on e.g. maximum July temperatures or growing season. The presence of *H. rhamnoides* during the early Holocene has been linked to the HTM in terms of July temperature (Paus, 2010; Paus & Haugland, 2017). At Stripåtmyrin, the brief occurrence of *H. rhamnoides* could hence indicate traces of the HTM. However, since my peat sequences only covered the last 9600 years, I could not fully assess the Holocene in terms of an early pine maximum.

7 CONCLUSIONS

The pollen analytical investigations from two mires situated at different elevations in eastern Norway illuminate the vegetation and climate dynamics from ca. 9600 cal. yrs BP until present day.

- The study sites were chosen based on e.g. altitudinal position, where Heimfjellsmyren (1097 m a.s.l.) is situated ca. 100m above Stripåtmyrin (990 m a.s.l.). They are also situated close to different present-day ecological ecotones, to better reflect the different tree-line and climate dynamics in both a local and a regional perspective. However, a bigger altitudinal difference would perhaps reflect more variance and hence be more beneficial in determining the local post-glacial (Holocene) dynamics.
- According to the pollen influx estimates, local pine forests were established at least 9600 cal. yrs BP at both study sites.
- A drop in pollen influx values show that pine forests disappeared from the area surrounding Heimfjellsmyren (1097 m a.s.l.) ca. 8150 cal. yrs BP, ca. 3000 years earlier than from Stripåtmyrin (990 m a.s.l.). This could reflect an inaccuracy but could be due to the slightly higher altitude at Heimfjellsmyren.
- Pollen influx estimates suggest that tree-birch forests disappeared from Heimfjellsmyren ca. 8520 cal. yrs BP and from Stripåtmyrin ca. 2300 cal. yrs BP (ca. 6200 years later). They further suggest a regional (non-local) distribution of tree-birch from ca. 1400 cal. yrs BP at Heimfjellsmyren and from ca. 700 cal. yrs BP at Stripåtmyrin. This is incorrect according to present day vegetation in the area and presumably reflect inaccurate extrapolation of age-depth estimates and influx calculations. It could further suggest the presence of trees without pollen production.

- The high pollen influx estimates of pine show traces of HTM in the early Holocene. Yet, the pollen records did not extend beyond ca. 9600 cal. yrs BP and the climate and vegetation dynamics in the early Holocene could not be fully inferred.
- Megafossils confirm local presence of pine 9230 cal. yrs BP near Høvringen (1015 m a.s.l.) and 9260 cal. yrs BP at Raphamn (1055 m a.s.l.) (adjusted for glacio-isostatic uplift).
- Pine forest lines reached at least 1030 m a.s.l. during the early Holocene. This is only 40m higher than present. According to similar studies nearby, they presumably reached at least 1160 m a.s.l.
- The early establishment of pine-forests in the area surrounding both study sites from ca. 9600 cal. yrs BP give evidence of local mean July temperatures of at least 11°C ca. 9600-8200 cal. yrs BP, 0.8-1.1°C warmer than present. From ca. 8200 cal. yrs BP until present day the July mean temperature has presumably been around 8-10°C. Due to the elevational difference between the sites, Heimfjellsmyren presumably had temperatures of ca. 0.6°C lower than Stripåtmyrin. Regionally, mean July temperatures reached at least 12°C.
- The modest traces of the 8200-event ("Finse event") at Heimfjellsmyren (1097 m a.s.l.) reflected by a drop in *A. incana* are too weak to clearly demonstrate the brief cooling. This is presumably because of too low resolution of samples during the pollen analysis due to time restrictions.
- Broadleaved trees such as *Corylus, Quercus* and *Ulmus* reflect favourable conditions and fertile soils in the lowlands during the early Holocene. The asynchronous drop in pollen records (ca. 8200 cal. yrs BP at Heimfjellsmyren and 5300 cal. yrs BP at Stripåtmyrin) suggest a gradual decline regionally.
- The early Holocene climate was rather dry and warm, with a gradual deterioration towards cooler and moister conditions ca. 8200 cal. yrs BP. Mean July temperatures were ca. 10°C ca. 8200-4000 cal. yrs BP, with little change towards the late Holocene and the present.
- Too few megafossils were obtained and dated to reconstruct early Holocene tree-line and forest dynamics. The timing of establishment of tree-birch and pine could hence not be determined. Yet, megafossils give evidence of tree-birch growing at least 1030 m a.s.l. ca. 9080 cal. yrs BP.
- To further investigate the post-glacial (Holocene) tree-line and climate dynamics in the Høvringen area, a higher number of pollen samples should be analysed.

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APPENDIX A – Results from the broken stick model

Stripåtmyrin

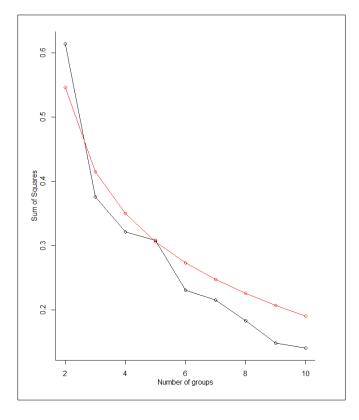


Figure I: Broken stick model (red line) based on cluster analysis of all terrestrial taxa from Stripåtmyrin (990 m a.s.l.). Group by Sum-of-Squares comparing dispersion at various fusion levels to a null model (black line) shows a low turnover and suggests a homogenous dataset.

HEIMFJELLSMYREN

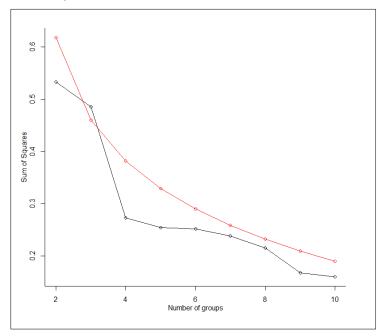


Figure II: Broken stick model (red line) based on cluster analysis of all terrestrial taxa from Heimfjellsmyren (1097 m a.s.l.). Group by Sum-of-Squares comparing dispersion at various fusion levels to a null model (black line) shows a low turnover and suggests a homogenous dataset.

Depth (cm) Age 2 103 10 748 10 748 10 748 10 748 10 748 140 3869 440 3869 4400 60 4490 60 4490 60 4490 60 4490 60 674 10 6977 10 708 10 708 10 708 10 708 10 748 10 748		Artemisia			Junpum,	Stripătmyrin (990 m a.s.l.)					
			Calluna	-type Calluna Asteraceae sect. Cichorium	Filipendula	Hippophae rhamnoides	Melampyrum Populus		Quercus	Quercus Rubus chamaemorus Rumex sect. Acetosa	umex sect. Acetosc
					1.5			0	1.5	3	
								0	0	6.4	
					•			0	4.5	106.3	-
			18.7	7 0	4		0 2.3	0	14	49.1	4.7
								0	13.6	13.6	
					0			1.7	3.3	15.1	
							0 19.3	2.1	10.7	0	
								2.6		0	
							0 9.5	0	12.6	0	
							-	0	0	0	
							0 13.9	0		0	2.3
			2.7					0	2.7	0	
								0		0	
			0	0	2.8			5.5	5.5	0	
130 7765							30.7	0			
140 8038								2.4			
150 8273	3						0 22.1	2.2	4.4		
160 8472								6.5			4.3
165 8560								0		0	6.9
170 8641	1 2.3							0		0	2.3
175 8715								0		0	5.
180 8783	3			3.9				0	0	0	
185 8845								10.3			5.1
190 8902								27.8			13.9
200 9004								0	0		
207 9066								19	0		9.5
210 9091				0 0	0		0 12.7	12.7	0		
220 9166	6 0		5.4					16.2	0		5.
230 9230	0							0	0		
240 9287	7 0			0 0				0	65.2		
250 9337	7 0							69.4	0	0	
260 9384	4							8.7	8.7	0	
270 9429					0			60.3	0	0	
280 9474	4 44.2							44.2	0	0	44
290 9520	0				64.1			32.1	0	0	
300 9568	8			0 0		92		0	0	0	46.2
307 9601	1 50.2	•			0	100.4		200.7	0	0	50.2

APPENDIX B – SUPPLEMENTARY SPECIES LISTS

Stripåtmyrin

Table I: The table lists pollen influx values of all low-abundance taxa used as indicators in the interpretation and discussion which are not displayed in the

pollen influx diagram for Stripåtmyrin (Figure 18).

Table II: The table lists pollen percentage values of all low-abundance taxa used as indicators in the interpretation and discussion which are not displayed in the pollen percentage diagram for Stripåtmyrin (Figure 17).

Depth (cm)	Age	Arnium HdV-261 Botryococcus		Hippuris	Hippuris Menyanthes trifoliata	Pediastrum	Potamogeton -type	Selaginella	Sparganium
7	2 103	3 0	0	0	0	0	0	0	0
10	748	8 0	0	0	0	0	0	0	0
20	1547	7 0	0	0	0	0	0	0.2970297	0
30	2329	9 0	0	0	0	0	0	0.0798722	0
40	3086	6 0	0	0	0	0	0	0	0
50	3809	9 0	0	0	0	0	0	0.97365407	0
60	(4490	0 0	0	0	0.406834825	0	0	0	0
70	5121	1 0	0	0	0.083892617	0	0	0	0
80	5694	4 0	0	0	0	0	0	0	0
06	6211	1 0	0.050658561	0	0.050632911	0	0	0	0
100	6674	4 0	0	0	0	0	0	0	0
107	7 6967	7 0	0	0	0.107526882	0	0	0.10764263	0
110	7086	6 0	0	0	0	0	0	0.0461042	0
120	7448	8 0	0	0	0	0	0	0	0
130	7765	5 0	0	0	0.630630631	0	0	0	0
140	8038	8	0	0	0	0	0	0	0
150	8273	3 0	0	0	0.233535731	0	0	0	0
160	8472	2 0	0	0	0.064641241	0	0	0.06468305	0
165	8560	0 0	0	0	0.159744409	0	0	0	0
170	8641	1 0	0	0	0.134228188	0	0	0	0
175	8715	5 0	0	0	0	0	0	0	0
180	8783	3 0.388349515	0	0	0	0	0	0	0
185	8845	5 0	0	0	0	0	0	0	0
190	8902	2 0	0.347826087	0	0.776531493	0	0	0	0
200	9004	4 0	0	0	0.260756193	0	0	0	0
207	9066	6 0.677200903	0	0	0.112739572	0	0	0	0
210	9091	1 0.765696784	0	0	0.457317073	0	0	0	0
220	9166	0.652883569	0	0	0.217155266	0	0	0	0
230	9230	0 0.134770889	0	0	0.536193029	0	0	0	0
240	9287	7 1.037344398	0.069156293	0	0.754975978	0	0	0	0
250	9337	7 1.615508885	0	0	0.161290323	0	0	0	0
260	9384	4 1.038062284	0	0	0.115207373	0	0	0	0
270	9429	9 0	0	0	0	0	0	0	0
280	9474	4 0	2.446183953	0	0	33.8551859	4.396632367	0	0
290	9520	0 0	2.34375	0	0.18957346	43.75	2.748815166	5	0
300	9568	8 0	3.540669856	0	0	50.9090909	0.947867299	0	0
307	0601	1 0 075075075			C			•	

Table III: The table lists pollen influx values of all low-abundance taxa from	Heimfjellsmyren used as indicators in the interpretation and discussion which	are not displayed in the pollen influx diagram for Heimfjellsmyren (Figure 20).
Table III: The table lists pollen influx va	Heimfjellsmyren used as indicators in th	are not displayed in the pollen influx dia

Depth A	Age Apiaceae	Melampyrum	Asteraceae sect. Cichorium	Filipendula	Potentilla spp.	Thalictrum alpinum	Quercus	Rubus chamaemorus	Ulmus	Rumex sp.	Solidago -type
0	-67	0	0.3	0		0		0.3	1.2		0.3
10	670	0	1	0	1	0	0	1	181.9	0	2.9
15	1056	0	0	0		0	2.4	0	0	0	0
20		0	0	0	0	0	0	0	21.8		237.4
25	1896	21.1	0	0	2.1	0	2.1 8	8.5	69.7	0	4.2 48.6
30		0	4	0	10	0	4	10	7	4	0
40		1.5	1.5			0	1.5	4.5	0	1.5	0
50		0		2.5		0	0 24	24.8	0	S	0
60		0	8.3	0		2.1		2.1	0	2.1	0
70		0	7		2.3 2.3	.3		2.3	0	4.7	0
80						.6		0	0	14.3	0
90			12.6			0		0	0	15.7	0
100		4.7				0		0	0	7	0
110			1.6		0	0	0	0	0	0	0
120						0		0	0	2.3	0
125						0		4.7	0	14.2	0 9.5
127.5	8341	5.7		0	2.9	0		2.9	0	14.3	0
130		0	0			.3		6.3	0	12.5	0 6.3
132.5	8461		11.4	0	3.8	0		7.6	0	11.4	0
135	8520	0	0	0		0	0	0		5.7	0
140	8635		7.8			8.	0	0	0	0	0 3.9
145	8747		15.3	0	0	0	0	0	130.2	7.7	0
150	8858		6.5			0		6.5	0	0	0
160	9080		18.8			0	4.7	0	0	0	0
170			11.8		0 459.7	.7	0	0	0	0	0
180	9479	7.5	14.9	7.5 7.5		0	0	0	0	0	0
195				0		0		10.4	0	0	0
197.5	9623	0		127.7	0	0		0	0	0	0
200	9637			56.3		0	0	19	0	0	0

APPENDIX C – R Scripts for statistical analysis, modelling and pollen diagrams

LINK TO R-CODE IN GITHUB REPOSITORY FOR BOTH STUDY SITES:

https://github.com/Kraakeklo/Master-thesis Appendix-C R-function-and-code.git