Tree line shifts, changing vegetation assemblages and permafrost dynamics on the slope of Galdhøpiggen (Norway) over the past ~4400 years

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An environmental reconstruction based on palynological evidence preserved in peat was carried out to examine late Holocene alpine tree line dynamics in the context of past climatic changes on Galdhøpiggen (Jotunheimen, southern Norway). We analysed a peat core taken from a mire at the present-day tree line (1000 m a.s.l.), c. 450 m downslope from the lower limit of sporadic permafrost. We adopted a combination of commonly used indicators of species' local presence to reconstruct past vegetation assemblages, such as the relative pollen abundance (%), pollen accumulation rate (PAR), and presence of indicator species. Additionally, fossil pollen from the peat sequence was compared to modern pollen from a surface moss polster in order to establish a modern analogue. The results were compared with studies covering the late-Holocene climatic changes in the area. The reconstruction demonstrates that a pine-dominated woodland reached above the present-day tree line at c. 4300 cal. yr BP, suggesting a warmer climate suitable for Scots pine (*Pinus sylvestris*) growth at this altitude. Scots pine retreated to lower altitudes between c. 3400-1700 cal. yr BP, accompanied by the descent of the low-alpine shrub-dominated belt, in response to cooling climatic conditions. The colder period covered c. 1700–170 cal. yr BP, and an open downy birch (*Betula pubescens*) woodland became widespread at 1000 m a.s.l., whilst pine remained sparse at this altitude. From c. 170 cal. yr BP onwards, warming allowed pine to re-establish its local presence alongside downy birch at 1000 m a.s.l.

Keywords: palynology, treelines, permafrost, alpine vegetation, reconstruction

Introduction

Over the past decades, northern mountainous areas have been experiencing the thawing of permafrost and alterations in vegetation patterns in response to increasing temperatures. Such

changes have been recorded on Galdhøpiggen (Jotunheimen, Norway), the highest mountain in northern Europe and the subject of the current study. Previous studies carried out on Galdhøpiggen have recorded the decadal-scale warming of near-surface permafrost (Isaksen et al., 2007) and mean ground temperatures (Isaksen et al., 2011). Models indicate that the lower limit of permafrost has moved upslope by 200 m since 1860, to its present-day altitude of c.1450 m a.s.l. (Hipp et al., 2012). Concurrently, aerial photographs reveal upward altitudinal shifts in vegetation (notably *Betula pubescens*) on the north-facing slope over recent decades (Hallang et al., 2020). At higher elevations, shrub encroachment on Galdhøpiggen has been found to have a larger control over surface CO_2 emissions than geomorphological factors (Hallang et al., 2020).

To understand the response of northern alpine vegetation communities and tree lines to changing air temperatures, it is necessary to examine the patterns of such vegetation shifts over longer time periods. Past alpine tree line movements can assist in identifying warmer and colder periods, and allow inferences about permafrost degradation and aggradation. In turn, examining the long-term vegetation- and permafrost dynamics could contribute to improving our understanding of the role of northern alpine regions in the future carbon cycle. Here, we analyse a palaeoecological sequence in order to gain insight into centennial- and millennial-scale movements of vegetation communities on the slope of Galdhøpiggen in response to past climatic changes.

Alpine regions are particularly suitable for studying vegetation dynamics, as they are sensitive to climatic variations and provide a setting where climatic and environmental conditions vary over short distances. Past palynological studies have used tree lines at their altitudinal limits as proxies to infer past climatic conditions in Norway (Aas, 1969; Barnett et al., 2001; Bjune, 2005; Caseldine, 1984; Eide et al., 2006). Here, we define the tree line as a general boundary area connecting the highest altitudinal patches of woodland on the north-facing slope of Galdhøpiggen (Aas, 1969; Körner, 1999). As the position of alpine tree lines is mainly controlled by temperature, they can be highly sensitive to even a small change in climate (Caseldine, 1984; Eide et al., 2006; Kullman, 2002). For example, tree lines in the Scandes have advanced by hundreds of metres in response to warming since 1950 (Kullmann, 2002). Therefore, a record of tree line trends over several thousand years can provide insight to past climatic changes.

The historic altitudinal movements of vegetation belts can be reconstructed from sedimentary deposits (peat- and lake deposits), whilst modern pollen trapped in moss polsters can be used to calibrate the palaeoecological record. However, an accurate estimation of the past vegetation composition based solely on palynological data is not as straightforward as simple quantification of pollen abundance, due to the differences in pollen production and dispersal methods between species. Here, we adopt a combination of commonly used indicators of local species' presence to reconstruct past vegetation assemblages on the slope of Galdhøpiggen. A peat core with an accompanying surface moss polster was taken from a mire near the present-day tree line at 1000 m a.s.l., 450 m downslope of the present-day lower limit of permafrost. Fossil- and modern pollen were extracted from the peat and moss polster and identified. The interpretation of data is enhanced by combining several approaches: (1) relative pollen abundance (%) is compared with thresholds from the literature; and (2) modern pollen abundance is compared with fossil assemblages. Pollen accumulation rates (PAR) and indicator species provide additional insight to past vegetation composition.

Galdhøpiggen has been the focus of several permafrost- and vegetation studies, which provide comprehensive background condition data over recent decades. Holocene climatic history and variability in the Jotunheimen region have also been extensively studied. Periods of glacial expansions and retreats since the beginning of the Holocene have been inferred from glaciolacustrine sediment cores (e.g. Matthews et al., 2000) and from minerogenic sediment layers in stream-bank mires (e.g. Matthews and Dresser, 2008). Holocene ground temperatures and permafrost extents on Galdhøpiggen have previously been modelled using temperature-monitored boreholes for model calibration (Hipp et al., 2012; Lilleøren et al., 2012). Combining the existing climate reconstructions with local palynological data will contribute to improving the interpretation of changing environmental conditions on Galdhøpiggen over the past ~4400 years.

The specific objectives of this study are: (i) to reconstruct the late-Holocene vegetation assemblages on Galdhøpiggen and describe their patterns of distribution through time; and (ii) to analyse the reconstructed vegetation dynamics to infer the late-Holocene climatic conditions and permafrost limits on Galdhøpiggen.

Methodology

Study site

A 46 cm *Sphagnum* peat core was collected from a small mire (Figure 1) situated at 1000 m a.s.l. on the north-facing slope of Galdhøpiggen mountain in NE Jotunheimen, Norway (61°43'07.4"N, 8°23'58.7"E), approximately 250 m southeast of Raudbergstultjønne Lake. The mire is c. 460 m below the lower limit of discontinuous permafrost, which was most recently estimated at around 1450-1470 m a.s.l. (Farbrot et al., 2011; Isaksen et al., 2011).

The coring site lies approximately on the present-day tree line (Figure 1), near the upper boundary of the sub-alpine vegetation belt (Table 1). The upper altitudinal limit of the mixed pine-birch woodland at 1050 m a.s.l. (Figure 1) represents the 'timber line', or the limit of the continuous forest in the area. This is also the altitudinal limit of *Pinus sylvestris* (Scots pine), both here and in Jotunheimen (Bjune, 2005). The tree line extends up to almost 1200 m a.s.l., and consists of stands of *Betula pubescens* (downy birch). Tree line positions have been related to the temperatures of the warmest month in the area (Körner, 1999) or a minimum of 100 days per year over 5°C (Ellenberg, 1963). Paus (2010) estimated that *Pinus sylvestris* requires minimum July mean temperatures of c. 11°C for growth in central Norway, whilst Nesje and Kvamme (1991) found that mean June-September temperatures of at least 7°C are required for *Betula pubescens*.

Based on data from the Fokstua meteorological station (60 km from site), the 2010-2019 mean July air temperature at c. 1000 m a.s.l. in the area is 11.4°C and the mean growing season (June-September) temperature is 9°C (NOAA, 2020). The mean number of days above 5°C per year was 121 during the past decade, a considerable increase from an annual mean of 110 days during 1950s, 1960s and 1970s (NOAA, 2020).

[Insert Figure 1 here]

The strategic location of the mire was selected to obtain a core with a surface moss polster that would contain a pollen assemblage representative of the vegetation at the present-day tree line. The surface vegetation on the mire is dominated by *Sphagnum* moss and sedges (e.g. *Eriophorum* spp.), with scattered shrubs including *Betula nana* (dwarf birch) and *Salix* (willow) species (*S. herbacea, S. glauca*). The mire is surrounded by a sparse stand of *Pinus sylvestris* c. 260 m to the north, mixed with individual junipers (*Juniperus communis*). Approximately 200 m to the south, scattered stands of *Betula pubescens* are mixed with *Salix*

spp. and *Betula nana*. A birch-dominated mixed woodland is found 500 m to the east of the coring site, whilst the mixed woodland 600 m to the west is dominated by pine. The vegetation belts on Galdhøpiggen are described in Table 1.

Table 1. Vegetation assemblages across altitudinal vegetation belts on Galdhøpiggen, including (a) species characteristic of mature vegetation and (b) pioneer species found in each belt (based on Matthews et al. 2018).

Sub-alpine belt ~ 850–1025 m a.s.l.	**Low-alpine belt** ~1025-1350 m a.s.l.	**Mid-alpine belt** ~1375–1600 m a.s.l.	**High-alpine belt** ~1600-2200 m a.s.l.
Birch woodland mixed with meadowland and stands of pine	Dwarf-shrub heath above the tree line	Grass- and lichen heath with late-snowbed communities; shrubs at lower part of the belt	Discontinuous vegetation cover
(a) *Betula pubescens* *Pinus sylvestris* *Alnus incana* *Juniperus communis* *Empetrum nigrum* *Vaccinium myrtillus* *Vaccinium vitis-idaea* *Salix herbacea* *Salix glauca* *Betula nana* *Gymnocarpium dryopteris* (b) *Rumex acetosella* *Epilobium anagallidiflium* *Plantago lanceolata* *Trifolium repens* *Ranunculus acris*	(a) *Betula nana* *Salix glauca* *Salix lanata* *Juniperus communis* *Empetrum nigrum* *Vaccinium myrtillus* *Vaccinium vitis-idaea* *Vaccinium uliginosum* *Solidago virgaurea* *Hieracium* spp. (b) *Rumex acetosella* *Epilobium anagallidiflium* *Plantago lanceolata* *Trifolium repens* *Poa alpina* *Saxifraga spp.* *Festuca ovina*	(a) *Carex bigelowii* *Cetraria* spp. *Nardus sticta* *Salix herbacea* *Salix glauca* *Salix lanata* *Empetrum nigrum* *Vaccinium vitis-idaea* *Vaccinium uliginosum* (b) *Rumex acetosella* *Epilobium anagallidiflium* *Plantago lanceolata* *Trifolium repens* *Poa alpina* *Saxifraga spp.* *Festuca ovina*	(a) *Poa alpina* *Luzula arcuata* *Ranunculus glacialis* *Saxifraga* spp. *Cetraria nivalis* *Stereocaulon alpinum* *Racomitrium canescens*

Sample collection

A 50 cm Russian peat corer with a 5 cm chamber diameter was used to collect a 46 cm-long core (including a 5 cm moss polster) from the centre of the mire. Whilst the peat layer extended deeper, only the top 46 cm was extracted and analysed for the purposes of this study. The core was wrapped in plastic film and placed in a plastic tube for transportation. Prior to sub-

sampling, the core was stored in dark conditions at 5°C. For laboratory analyses, the core was sub-sampled at one centimetre resolution to produce a total of 46 samples. A modified syringe was used to measure out a known volume (1 cm^3) of peat material per sample. Based on previous studies that estimated the pollen deposition time in moss polsters in Scandinavia (Lisitsyna and Hicks, 2014; Pardoe et al., 2010; Von Stedingk et al., 2008), the 5-cm *Sphagnum* moss polster covering the peat was assumed to represent c. four years of pollen accumulation. To examine the pollen composition throughout the moss, the polster was cut into segments at 1 cm resolution from the top down. To ensure that enough pollen was extracted from each segment, 2 cm^3 of material was measured out for analysis.

To determine the organic matter content and density of the peat, loss-on-ignition analysis was undertaken following the method outlined by Chambers et al. (2011). The core was sub-sampled at 2 cm intervals (covering depths between 16-44 cm due to the lack of sediment in the top 6-15 cm). Samples with known volume (1 cm^3) were dried overnight at 105°C in weighed crucibles to determine the dry weight of each sample. The samples were then ignited at 550°C for four hours to combust all organic matter, cooled to room temperature in a dessicator and weighed again.

Pollen extraction

Pollen extraction followed the standard method by Bennett and Willis (2001). Two *Lycopodium* spore tablets (Batch no. 3862) with known concentration of spores were used per sample as a marker to calculate the concentration of pollen (Stockmarr, 1971). The samples were first treated with hot HCl, humic acids were broken down with hot NaOH and sieving through a 180 μm sieve removed large particles from the peat material. Initial samples were tested with and without the use of hydrofluoric acid (HF). Due to the high organic matter content of the samples, the use of HF was determined to be unnecessary after the trial. All samples were subjected to three minutes of acetolysis to remove polysaccharides. To increase the contrast of pollen grains, 0.2% aqueous safranin was added to stain the pollen. The samples were mounted on glass slides using silicone oil.

Pollen counting

A Leica (DM 2000) light microscope was used at x400 and x1000 magnification to identify and count the pollen. A minimum of 500 total land pollen (TLP) were counted at each depth; the sum includes all pollen taxa and spores (*Sphagnum* and Filicales). Moore (1994), Reille (1992) and a collection of reference slides held in the Department of Biosciences, Swansea University, were used to identify the pollen grains and the spores. Due to their different growth forms and ecological significance, pollen belonging to the genus *Betula* was identified to species level where possible as either *Betula nana*, *Betula pubescens* (Birks, 1968) or *Betula* hybrid (Karlsdóttir et al., 2008). The division was based on visual assessment of pollen combined with measurments of diameter (mean values: *B. nana* = 20.42 μm, *B. pubescens* = 24.20 μm) and pore depth (mean values: *B. nana* = 2.20 μm, *B. pubescens* = 2.81 μm) of individual grains. A number of *Betula* pollen grains that were damaged or deformed and therefore difficult to identify were counted as *Betula* undiff.

Radiocarbon dating and age calibrations

The humin fraction of three peat samples (taken at 10 cm, 24 cm and 46 cm depth) was dated using accelerator mass spectrometry (AMS) radiocarbon dating. The resulting ^{14}C dates for samples taken at depths of 24 cm and 46 cm were converted to calendar ages (cal. yr BP = calendar years before present [1950]) using the calibration software CALIB (8.2) (Stuiver et al., 2021) and the northern hemisphere terrestrial calibration curve IntCal20 (Reimer et al., 2020). The dates were determined using 2σ error (Stuiver and Reimer, 1993) meaning that there is a 95% probability that the reported median calibrated age falls within the estimated age range. The 'greater than modern' ($F^{14}C$) radiocarbon date at 10 cm depth was calibrated using the post-bomb northern hemisphere calibration dataset 'NHZ1' by Hua et al. (2013), and the online calibration resource CALIBomb (available from: calib.org/CALIBomb/).

Pollen diagrams

Pollen relative abundance (%) and concentration (grains/cm^3) were calculated following Bennett and Willis (2001). All pollen diagrams were created using psimpoll (4.27) (Bennett, 2000). Statistically significant pollen assemblage zones based on the relative pollen abundance diagram were determined using binary splitting by sums-of-squares and constrained cluster analysis (CONISS); both methods resulted in the same output (Grimm, 1987). The influx

diagram illustrating the pollen accumulation rates (grains cm^{-2} $year^{-1}$) for nine dominant taxa was created using input files with concentration values and calibrated ages for dated depths. PARs were not calculated for the modern moss polster because the exact age-span of the polster is not known.

Methods of analysis

Detection of Holocene tree line positions and dynamics based on pollen relative abundance is difficult (Aario, 1940; Birks and Bjune, 2010; Seppä and Hicks, 2006). Firstly, estimating the local presence of species through traditional pollen analysis is complicated because the relationships between pollen deposition and vegetation cover are rarely straightforward. Differences in the pollen type, production and dispersal methods of individual plant species, but also atmospheric conditions (e.g. wind speed and dominant direction) and topography will play a role in how and where pollen is deposited for long-term preservation (Jackson and Lyford, 1999). Secondly, *B. pubescens* and *P. sylvestris* have been found to produce less pollen near their altitudinal limits than at lower altitudes in Norway (Eide et al., 2006). Above the tree line, pollen production by local tundra species is similarly low, and pollen records are often dominated by long-distance derived tree pollen (up to 90%), masking the local tundra pollen component (Birks and Bjune, 2010; Pardoe, 2006; 2014).

Being aware of the complications regarding the use of pollen data to delineate past tree lines, and acknowledging the limitation posed by the absence of macrofossil analysis (Birks and Birks, 2000), we do not attempt to determine the exact position of the tree lines at any given time. Instead, we aim to describe the directions of past trends in vegetation cover, and draw general conclusions about the late Holocene environmental conditions on Galdhøpiggen in the context of previous publications. To achieve this, we combine several proxies (relative pollen abundance, PAR, and indicator species) to interpret the pollen data.Relative pollen abundance has been used as an indicator of the presence of local taxa (e.g. Barnett et al., 2001; Huntley and Birks, 1983; Lisitsyna et al., 2011), and pollen percentage threshold values have been estimated for dominant European tree species to differentiate between local and regional pollen (compiled in Table 2). However, the use of relative pollen abundance alone to reconstruct past assemblages in open alpine tundra environments can be misleading, as it cannot distinguish between local and regional pollen (Birks and Bjune, 2010; Prentice and Webb, 1986). For example, Barnett et al. (2001) reported periods of local presence of birch and pine throughout

the Holocene in Leirdalen, Norway (approximately 14 km from our site, at 920 m a.s.l.) based on relative pollen abundance (>10% and 55%, respectively). Conversely, similar relative abundance values of arboreal pollen (15-35% of birch, 20-60% of pine) were recorded in surface moss polsters collected from modern open pioneer communities on a nearby glacial foreland at Storbreen, far from tree cover (Pardoe, 2006).

Similarly, we have used the relative abundance of modern pollen in the surface moss polster (and in the top five centimetres of peat in our core) to establish a modern analogue and allow for comparison with fossil pollen assemblages in the peat. This tested approach allows a direct linkage of present-day pollen and vegetation, which can then be used to make inferences about palaeo-relationships (e.g. Caseldine, 1989; Caseldine and Pardoe, 1994; Jackson, 1991; Pardoe, 1996, 2006, 2014). Surface moss polsters are estimated to represent two to five years of pollen deposition and are considered a good analogue for determining plant community composition within palaeoecological records, but they cannot be used to calculate PAR if the exact age of the moss polster is unknown (Lisitsyna and Hicks, 2014; Pardoe, 2006). Moss polsters are useful for estimating local vegetation composition in tundra environments, where the relevant source area of pollen is relatively small (600-800 m) (Oswald et al., 2003).

To further characterise the Galdhøppigen palaeo-vegetation, we examined pollen accumulation rates throughout the core. PARs represent the net number of grains accumulated per unit area of sediment surface per unit time (Davis, 1969). PARs are not affected by the presence or absence of other (abundant) taxa in the pollen profile, allowing each taxon to be analysed individually over space and through time. Assessment of PARs have been used to determine species' local presence (Kuoppamaa et al., 2009) and to quantify the presence of birch, pine and spruce at their latitudinal limit in northern Fennoscandia (Hicks, 2001). Using a network of pollen traps to estimate deposition rates over 18 years, Hicks (2001) found that the long-term average pollen deposition is an accurate indicator of the local presence, absence and abundance of arboreal species. The PAR threshold values for pine and birch presence from Hicks (2001) are also outlined in Table 2.

Table 2. Threshold values of *Betula pubescens*, *Pinus sylvestris* and *Picea abies* pollen accumulation rates (grains cm^{-2} yr^{-1}) and relative pollen abundance (%) from the literature indicating local and regional presence of arboreal species.

		Betula pubescens	*Pinus sylvestris*	*Picea abies*
Hicks (2001) PAR (grains cm^{-2} yr^{-1})	Not present within 10 km	N/A	<300	<25
	Not present within 1 km	<500	300-500	25-50
	Sparse presence	500-1000	500-1500	50-100
	Open forest	1000-1500	1500-2000	100-300
	Dense forest	>1500	>2000	>300
Huntley and Birks (1983) % values	Local presence	10%	>25%	5%
	Local dominance	25%	>50%	N/A
	Dominant woodland	50%	N/A	N/A
Lisitsyna et al. (2011) *%* values	Regional presence	5%	10%	1-5%

Finally, we have identified several species in our pollen profile that may be indicative of certain environmental conditions. This approach has been evaluated in more detail by Birks et al. (2010), and introduced in more detail in the discussion.

Results

The peat is relatively uniform and consists of well-humified organic matter. The organic matter content is high (87-91%) throughout the tested 41 cm of peat material. The bulk density of the samples ranges from 0.14 to 0.23 g cm^{-3}, showing a gradual decline with increasing depth. The ash-free bulk density (organic matter density) shows a similar decline, from 20 to 12 g cm^{-3}.

The radiocarbon dates for three depths (10, 24 and 46 cm) and calibrated ages are listed in Table 3.

Table 3. Radiocarbon dates and age calibrations using the IntCal20 calibration curve (Reimer et al., 2020) and the post-bomb calibration dataset 'NHZ1' (Hua et al., 2013).

Depth (cm)	Laboratory ref. code	^{14}C Age (years BP)	F^{14}C	Calibrated Age
10	UBA-44553	-	1.0915± 0.0021	2000 ± 1 AD
24	UBA-42480	2872 ± 24	-	2997 ± 76 cal. yr BP
46	UBA-42479	3918 ± 32	-	4332 ± 91 cal. yr BP

An age-depth model (Figure 2) based on linear interpolation between the three dated levels of the core (10, 24 and 46 cm) and the surface was created using the 'clam' (2.2) package (Blaauw, 2010) in R (3.6.3) (R Core Team, 2021). The input file contained both ^{14}C ages and the calibrated F^{14}C date. By default, 'clam' uses the IntCal13 calibration curve from Reimer et al. (2013) for ^{14}C ages. To include the F^{14}C date, we selected the post-bomb calibration curve 'NHZ1' by Hua et al. (2013). The non-^{14}C dates (i.e. at 10 cm and at the surface) were assigned negative values to indicate their departure from 1950 AD to present. For example, the calibrated date at 10 cm is c. 2000 AD, therefore this depth was assigned the value '-50' in the input file. The surface of the consolidated peat core is set at 6 cm, excluding the modern moss polster. Assuming that the 5 cm thick moss polster represents two to four years of accumulation (Lisitsyna and Hicks, 2014) and the core was collected in 2018, the age of the surface was set to 2014 (represented by '-64' in the input file).

[Insert Figure 2 here]

Accumulation rates vary throughout the core. Between 46 and 24 cm, accumulation rates are relatively high, and 1 cm of peat covers 61 years. The rates drop between 24 and 10 cm, where 1cm covers 217 years. The remaining 4-cm section of peat at the top corresponds to only three years of accumulation per 1 cm. This apparently disproportionately high rate of accumulation can be explained by a combination of incomplete decomposition of the less compacted and less consolidated near-surface peat. Direct comparisons between the top and deeper parts of the core should be made with caution (*cf.* Young et al., 2019). In our study we therefore excluded the PARs of the section of the peat core between six and nine centimetres from the influx diagram (see Figure 4). However, as the top five centimetres of peat date post-2000, the relative abundance of pollen from this section can be used in comparison with deeper peat layers.

Zone 1 (4350 - 3430 cal. yr BP)

The relative abundance of arboreal pollen (86-92%) is high in the basal zone of the pollen profile (Figure 3). *Pinus sylvestris* pollen dominates the percentage diagram (45-64%), followed by *Betula pubescens* (20-35%). Both exhibit highest PARs at c. 3670 cal. yr BP (6500 and 3000 grains cm^{-2} $year^{-1}$, respectively). Other arboreal taxa, i.e. *Alnus, Quercus, Sorbus, Ulmus, Juniperus* and *Tilia*, are represented by small quantities of pollen (<3%). The proportions of shrub and herb pollen increase in the upper portion of the zone. The relative abundance of *Empetrum nigrum* pollen increases from 0.2% to 3%, with *Betula nana* and *Salix* pollen following a similar pattern. The highest relative pollen abundance of some herb genera throughout the 4400-year sequence (e.g. Asteraceae, *Filipendula, Rumex*) are recorded in this zone, whilst other genera (e.g. *Valeriana, Plantago*) appear exclusively in this time period. The relative abundance of Filicales spores decreases from 4% to 0.8% in Zone 1, and *Sphagnum* spore abundance increases from <0.5% to 1%.

Zone 2 (3430 – 1690 cal. yr BP)

A sharp decrease in PAR for all taxa is evident in the middle of Zone 2. Arboreal pollen relative proportions drop to the lowest values of the entire profile (77%), before recovering to 91% by 1690 cal. yr BP. *Pinus sylvestris* pollen exhibits a consistently lower PAR (300-2600 grains cm^{-2} $year^{-1}$), and its relative abundance decreases from 57% to 16% by c. 3000 cal. yr BP, recovering to 37% by c. 1690 cal. yr BP. The relative abundance of *Betula pubescens* pollen

fluctuates between 20% and 52% throughout the zone, with PAR comparable to *P. sylvestris.* Shrub pollen abundance increases from 8% to 19% by mid-zone, followed by a decline to 6% by the end of the period. *Betula nana* pollen reaches the highest PAR (500 grains cm^{-2} $year^{-1}$) and relative abundance (14%) in the profile. *Salix*, *Empetrum nigrum* and *Vaccinium* pollen is recorded throughout the period (≤4% each). Herb pollen and spores are present in small quantities in this zone (≤4% and ≤6% respectively). *Epilobium angustifolium* pollen occurs, whilst *Ulmus, Geranium and* Apiaceae pollen are not recorded in the profile after this time period. The relative abundance of Filicales and *Sphagnum* spores both fluctuate between 0.4% and 4%.

Zone 3 (1690 cal. yr BP –2014 AD)

PARs for all taxa remain low. Arboreal pollen continues to dominate the profile (84%-91%). *Pinus sylvestris* pollen exhibits lowest overall PAR (<500 grains cm^{-2} $year^{-1}$) and relative abundance (18-33%). *Betula pubescens* pollen shows higher values (30-52%) and PARs (500-1500 grains cm^{-2} $year^{-1}$) exceed those of *P. sylvestris*. *Picea abies* pollen appears in the profile from c. 800 cal. yr BP (≤1%). Shrub pollen relative abundance shows a slight increase, but remains between 6% and 11%. After an initial drop, *Betula nana* pollen exhibits a steady rise (3-9%) throughout this zone. *Empetrum nigrum* pollen proportion declines from 4% to 1% whilst *Salix* pollen abundance increases to 2%. Herb pollen drops below 1%, but regains values of 3%. The relative abundance of spores declines from 2% to 0.6%. *Sphagnum* spores exhibit the highest values (4%) whilst the proportion of Filicales spores remains consistently low (0.4-2%).

Zone 4: Modern moss polster (~2014-2018 AD)

The relative abundance of arboreal pollen is slightly higher (87-92%) in the modern moss polster compared to the underlying peat of Zone 3. *Pinus sylvestris* pollen abundance is also higher here (34-43%), and comparable to the abundance of *Betula pubescens* pollen (36-42%). *Picea abies* pollen is present throughout the moss at ≤1%. *Quercus* (0.5-2%) and *Alnus* (<0.4%) pollen retain low presence, *Tilia cordata* pollen is recorded again after an absence in Zone 3. Shrub pollen proportion is lower than in peat samples, and remains between 3-6%. Low relative abundances are recorded for *Betula nana* pollen (2-5%), *Empetrum nigrum* pollen (<1%) and

Salix pollen (0.2-2%). Herb pollen abundance remains between 2-4%. Poaceae (1-2%) and Cyperaceae (≤2%) relative pollen proportions are higher than in underlying peat samples. Asteraceae, *Filipendula, Rumex* and Ranunculaceae pollen are present, and Caryophyllaceae is recorded again after being absent in Zone 3. Spores account for 0.5-3% of TLP. *Sphagnum* spores exhibit a lower relative abundance in the moss polster (0-1%), whereas the proportion of Filicales spores is slightly higher than in Zone 3 (up to 2%).

[insert Figure 3 here]

[Insert Figure 4 here]

Discussion

Comparison of present-day vegetation composition with pollen from moss polster and modern peat (2000-2018 AD) The relative abundance of *Betula pubescens* pollen in the modern (post-2000 AD) peat- and moss samples indicates the local dominance of the species (Table 2). *B. pubescens* is undoubtedly a dominant presence in the landscape today, and forms a belt between the mixed forest and the tundra, c. 200 m upslope from the coring site (Figure 1). There is a slight increase in *B. pubescens* pollen abundance between 2000-2014, which could be indicative of the increased abundance or maturation of the species in the area. The rapid warming over the past decades has increased the mean summer temperatures at the tree line by 2°C, and lengthened the growing season by 11 days compared to 1950s-1970s (NOAA, 2020; see Study site). Birch is highly sensitive to temperature fluctuations, because the species grows quickly, reaches maturity early and has a short life span (Aas, 1969). The upslope advancement of *B. pubescens* in response to warming over the past decades has previously been recorded from aerial photographs in the area (Hallang et al., 2020). Whilst the climatic conditions today are favourable for tree growth at even higher altitudes above the tree line, the rapidity of the change has likely resulted in a lag in migratory response, as current species' compositions are often determined by the climate of previous decades (Klanderud and Birks, 2003). Additionally, the response is dependent on the availability of suitable substrate and habitat at higher altitudes for seedling recruitment.

The modern pollen abundance of *Pinus sylvestris* also accurately reflects local presence. *P. sylvestris* is less abundant around the mire compared to *B. pubescens*; the closest pine stand

north of the mire is sparse, and the nearest dense woodland is c. 500 m downslope (Figure 1). There is also evidence of long-distance transported modern tree pollen of *Alnus*, *Quercus* and *Tilia cordata*, which likely originates from further down the valley, as they are not currently found near the sampling site.Whilst the presence of tree species is accurately estimated from the modern samples based on the threshold values in Table 2, the non-arboreal component of the surface moss sample contains some discrepancies. Despite the comparable presence of both *Betula nana* and *Salix* spp. on the surface of the mire around the coring site, *Salix* is under-represented in the moss sample with a mean of 0.5% in the moss (compared to 1.2% in the modern peat) whilst *B. nana* accounts for 3% and 6%, respectively. A similar under-representation of Salix pollen in 4 cm thick moss samples compared to adjacent pollen traps was observed in Lisitsyna and Hicks (2014).

The low presence of *Salix* pollen is unexpected, especially since for mire samples, the non-arboreal component of a pollen profile is often dominated by species from within a few metres of the sampling location, as mosses have the capacity to catch poorly distributed local pollen (Bunting, 2003). A strong correlation has previously been found in Jotunheimen (1150-1500 m a.s.l.) between the abundance of *Salix* in the dwarf-shrub vegetation assemblage and the frequency of *Salix* pollen in the pollen spectra (Caseldine, 1989). However, *Salix* pollen is present throughout the 4000-year peat sequence in comparably small quantities (≤1.6%). Due to the close proximity of the tree line, it is possible that the arboreal component dominates the pollen profile so heavily that it masks non-arboreal species in the profile, suggesting that even the smallest signal of *Salix* pollen could indicate local presence of the species.

Additionally, the previously reported encroachment of shrubs affecting the higher elevations of Galdhøpiggen (≥1550 m a.s.l.) in response to warming in the recent decades (Hallang et al., 2020) is not evident from the modern peat- and moss samples. The shrub cover near the coring site has likely not changed significantly in the past 14 years, and samples from the mire at 1000 m a.s.l. are not reflecting the changes at higher elevations.

Several species that are considered indicative of certain environmental conditions are present in this zone. Previous studies conducted in Jotunheimen demonstrate strong correlations between the abundance of indicator taxa in tundra vegetation and their representation in the pollen spectrum (Pardoe 2006, 2014). Local non-arboreal taxa that produce little amounts of pollen, such as *Empetrum* and *Salix*, were found to be accurate indicators of the composition of local alpine plant communities above the treeline. Kuoppamaa et al. (2009) listed a number

of taxa that are linked to disturbance from land-use change in northern Fennoscandia; the following also appear in our pollen profile: *Epilobium*, *Filipendula*, *Plantago major*, *Ranunculus acris*-type and *Rumex acetosa/acetosella*. In Table 1, we have compiled a list of pioneer species and species characteristic of mature vegetation assemblages on Galdhøpiggen today.

The species dominating the pollen spectra in this zone are largely characteristic of the present-day sub-alpine vegetation belt (Table 1). Several open-ground and disturbance indicators, such as *Rumex acetosa/acetosella* type and *Filipendula* (Kuoppamaa et al., 2009) are also present. The most likely Ranunculaceae species in the area is *Ranunculus acris*, whilst the common Caryophyllaceae species is *Silene dioica*; both occur in the 'tall herb' communities in the sub-alpine belt, and extend into the low-alpine belt (John Matthews, 2021, personal communication). The pollen of both families is found in the moss polster. Poaceae pollen is represented in the moss polster in higher quantities than throughout most of the sequence; the common local Poaceae species is the alpine meadow-grass (*Poa alpina*), another light-demanding pioneer species. The vegetation near the mire was recently disturbed in 2004, when the road leading up the slope was asphalted, creating roadside verges suitable for colonisation by pioneers (Matthews et al., 2018). However, no major disturbance events in the surrounding landscape, such as clearing of the woodland or wildfires, have occurred in the period 2000-2018, and no disturbance indicator is represented by unusually high amounts of pollen in this zone. *Mid-Holocene pine-dominated mixed woodland (c. 4300-3400 cal. yr BP)*

The altitude of the present-day tree line on Galdhøpiggen was covered by a local pine-birch woodland between c. 4300-3400 cal. yr BP. The relative abundance of pine pollen for most of the period exceeds the contemporary values by 50%, and indicates local dominance. PARs are up to 10 times higher than estimated for 2000 AD, and indicate a dense pine forest (Table 2). This suggests relatively warm summer temperatures (likely exceeding contemporary values) at this altitude suitable for abundant pine growth, and the advancement of the pine tree line. Aas and Faarlund (1988) suggest that that pine tree lines were 200 m higher (at 1200 m a.s.l.) in Jotunheimen between (5000-2500 cal. yr BP), and c. 150 m higher than today towards the end of this period.

Further, past climatic reconstructions of the area have indicated a decrease in glacial extent between c. 4000-3000 cal. yr BP (Matthews and Dresser, 2008), and models suggest increased

mean annual ground- and surface temperatures at higher altitudes on Galdhøpiggen (up to 1458 m a.s.l.) that remain above 0°C during this period (Lilleøren et al., 2012; Winkler et al., 2021). Higher temperatures, supported by the high relative abundance and PAR of pine pollen, certainly would have influenced the extent of regional permafrost. Combining the evidence from our pollen study with wider literature, we assume that the lower limit of permafrost reached above 1500 m a.s.l. (Figure 5).

Whilst *B. pubescens* also appears locally present at 1000 m a.s.l., the relative abundance of its pollen remains below the present-day values (2000-2014 AD) throughout. PAR, however, exceeds the modern (2000 AD) value during most of this period (Table 2). The lower relative abundance values could be due to the substantial dominance of pine pollen in the profile, as PARs suggest a more abundant birch presence. Moreover, a study combining pollen data with macrofossil evidence suggests that a subalpine birch zone has prevailed above the pine tree line during the period 9000-2500 cal. yr BP, and despite the advanced pine tree lines, pine did not represent the upper forest limit at any point during this time (Aas and Faarlund, 1988). It is difficult to determine whether downy birch reached above the pine tree line on Galdhøpiggen during this period without incorporating macrofossil evidence, but birch was most likely a component of the pine-dominated mixed woodland at 1000 m a.s.l.

A woodland presence is further supported by the highest relative abundance of shade-preferring Filicales spores (Kuoppamaa et al., 2009). The only common Filicales species at this altitude today is *Gymnocarpium dryopteris,* a fern that prefers shady north-facing slopes and forms a continuous carpet under birch trees (Matthews et al., 2018). The pollen of *Geranium*, which is commonly found in the understorey today, is also present. Other trees were absent from the woodland at this altitude, with *Alnus* pollen being regional, and *Quercus* and *Tilia cordata* pollen derived via long-distance transport (Lisitsyna et al., 2011).

However, several disturbance- and open ground indicating species are also present throughout this period. *Plantago media/major* occurs exclusively during this period, whilst Asteraceae, *Filipendula* and *Rumex acetosa/acetosella* type exhibit their highest relative abundances in the pollen profile, and Poaceae peaks in this zone. Several light-demanding Asteraceae species grow in the sub-alpine and low alpine belts today, including *Hieracium* spp., *Achillea millefolium*, *Solidago virgaurea* and *Gnaphalium norvegicum*. It is also notable that from around 3700 cal. yr BP, there is an increase in light-demanding shrub pollen (*Betula nana, Empetrum nigrum, Vaccinium* spp. and *Salix* spp.) (Robbins and Matthews, 2014). Whilst the

514 shrub pollen might have originated from the surface mire vegetation, the high relative
515 abundance of light-demanding herb pollen suggests that the mixed woodland may not have
516 been as dense as indicated by pine PARs. Overall, the species present during this period are
517 comparable to the mature vegetation assemblages of the present-day sub-alpine belt on
518 Galdhøpiggen (Table 1).

519

520

521 *Pine retreat and descent of the low-alpine zone (c. 3400 – 1700 cal. yr BP)*

522 The progressive decline in relative abundance and PAR of pine pollen between c. 4330-3000
523 cal. yr BP coincides with the gradual decline in modelled temperatures in southern Norway.
524 Modelled July temperatures were 1°C higher in 4500 cal. yr BP compared to present day (1961-
525 1990 mean) values; by c. 3000 cal. yr BP, the temperatures had declined and resembled present-
526 day values (Lilleøren et al., 2012). The heat flow model by Lilleøren et al. (2012) is based on
527 studies examining pollen, macrofossils and chironomids from lake sediments, as well as the
528 deposition rate of speleothems in Scandinavia, and the model is calibrated using modern
529 borehole temperatures, including those recorded on Galdhøpiggen. Climatic cooling during this
530 period is also suggested by the concurrent increase in downy birch pollen at the expense of
531 pine. Relative pollen abundance indicates local dominance and PARs are indicative of open
532 birch woodland for most of this period, suggesting that the conditions became cooler (and
533 possibly wetter), which benefits birch rather than pine.

534 By c. 3000 cal. yr BP, pine pollen reaches its lowest relative abundance in the entire profile,
535 coinciding with the decline of total arboreal pollen to its lowest level. Relative abundance and
536 PAR suggest that pine was not present within one kilometre of the coring site at the time, whilst
537 downy birch retains local dominance. Simultaneously, shrubs collectively reach their highest
538 relative abundance in the entire sequence, suggesting that the landscape at 1000 m a.s.l. was
539 becoming more open.

540 The synchronous increase in light-demanding species that characterise present-day low- and
541 mid-alpine vegetation belts, such as *Betula nana*, *Empetrum*, *Vaccinium* spp., and *Salix* spp.
542 Could indicate a possible descent of the low-alpine vegetation belt in response to colder
543 temperatures. The timing of the pine retreat and shrub encroachment corresponds to a cold
544 period of glacial expansion (Smørstabbtindan IV, 17 km from our site) between 3200-2550 cal.

yr BP (Matthews and Dresser, 2008); and a drop in modelled ground temperatures on Galdhøpiggen by 0.2°C in the low alpine belt, and by 0.5°C in the mid-alpine belt between 4000 and 3000 cal. yr BP (Lilleøren et al., 2012). Moreover, Bjune (2005) reported a decline in arboreal pollen and the opening of the landscape at 1309 m a.s.l. due to cooler conditions in E Jotunheimen between 4950-2700 cal. yr BP.

All shrubs in our profile exhibit relative pollen abundance values that exceed the modern-day values, illustrating a scenario where the sampling site was covered by denser stands of dwarf shrubs at the expense of trees. Furthermore, *Epilobium angustifolium*, a light-preferring species often occurring on sites following disturbance such as windthrow of trees or vegetation dieback due to drought (Myerscough, 1980), appears in the profile at c. 3300 cal. yr BP in small quantities (0.7%). Other disturbance indicators, such as *Rumex acetosa/acetosella* type, Ranunculaceae, Caryophyllaceae (likely *Silene dioica*) and Asteraceae are also present. Simultaneously, the proportion of shade preferring Filicales spores remains low.

The pollen diagram (Figure 3) indicates signs of climatic warming between 2800-1900 cal. yr BP, as the relative abundance of arboreal pollen begins to recover whilst the proportion of shrub pollen declines. The relative abundances of pine- and downy birch pollen indicate local presence of pine and birch dominance. However, the PARs of pine and downy birch remain low between 2500-1700 cal. yr BP, indicating a merely sparse local presence. This could be due to the increase in cooler and more humid periods from 2500 cal. yr BP to present, resulting in depressed tree lines and low pollen production (Aas and Faarlund, 1988). Matthews and Dresser (2008) identified numerous cold periods of glacial expansion in the area from c. 3000 cal. yr BP to present day, including between 2350-1700 cal. yr BP. Modelled July temperatures for southern Norway also decline further, remaining approximately 0.1-0.3°C lower than the 1961-1990 mean from 2000 cal. yr BP until c. 1900 AD (Lilleøren et al., 2012). Such conditions reflect a period suitable for permafrost aggradation and the possible depression of the limit of sporadic permafrost to altitudes lower than today (Figure 5). According to Lilleøren et al. (2012), however, the lower limit of permafrost on Galdhøpiggen never reached below 1200 m a.s.l. during the Holocene, suggesting that our coring site (1000 m a.s.l.) was free of permafrost throughout this period.

[Insert Figure 5 here]

Pine decline and the establishment of birch-dominated open woodland (c. 1700 cal. yr BP-2000 AD)

The topmost zone of the pollen profile covers c. 1700 years, and represents very low peat- and pollen accumulation rates. The relative pollen abundances of the main arboreal species indicate that from 1700 cal. yr BP to 2000 AD, downy birch was locally dominant, whilst pine fluctuated close to the threshold of local presence, remaining regionally present throughout most of this period (Table 2). Relative pollen abundances describe the local arboreal composition in 2000 AD accurately, demonstrating that pine was locally present (26%) and downy birch dominated (36%). PARs, however, are low for both species, fluctuating around the threshold value for sparse presence, and suggest that neither was present within 1-km radius from c. 600 cal. yr BP to 2000 AD. This is clearly an underestimation, as downy birch was locally established in the 1980s, and pine was growing c. 200 m from the coring site by 2000 AD (Hallang et al., 2020). Therefore, the relative abundance of downy birch and pine pollen can be considered as the more accurate indicator of local presence during this period.

The discrepancy between PARs and evidence from the area could indicate that the PARs in the top half of the core are not reliable, and their accuracy might be improved by incorporating more radiocarbon dates. Alternatively, the underestimation of arboreal PARs in the recent millennia could be caused by retreated tree lines and lower pollen production due to continuing cooler temperatures. Based on the consistently low relative abundance of pine pollen, the pine tree line was likely lower than today between c. 1700-170 cal. yr BP, whilst the climatic conditions remained more suitable for downy birch growth at 1000 m a.s.l. This scenario is in accordance with two longer periods of glacial expansion between 1400-750 and 500-0 cal. yr BP (Matthews and Dresser, 2008). The latest cold period also covers the Little Ice Age (LIA), which peaked around 1750 AD to the end of the 19th century in southern Norway (Lilleøren et al., 2012). Lowest simulated ground temperatures occurred c. 250 years BP, and the lower limit of shallow permafrost is estimated to have reached as low as 1250 m a.s.l. (Lilleøren et al., 2012). Unfortunately, due to the coarse resolution of our pollen profile caused by low peat accumulation rates, the effects of the LIA are not detectable. However, our results indicate that 1700-170 cal. yr BP was likely a cold period with a low altitudinal pine tree line and a possibly depressed permafrost limit.

Non-arboreal pollen also signals a more open landscape from 1690 cal. yr BP. The pollen of shrub species indicative of dwarf shrub tundra retains high values from 1690 cal. yr BP to 2000

AD. Light-demanding *Betula nana* is the dominant shrub in the landscape, and *Salix*, *Empetrum* and *Vaccinium* are present throughout. Disturbance-indicating herbaceous species and pioneers, such as Asteraceae, *Filipendula*, Ranunculaceae, Poaceae and *Rumex acetosa/acetosella* type are represented throughout by small quantities of pollen, and *Epilobium angustifolium* is briefly found again at c. 2003 AD. However, none of the disturbance indicator species show significant peaks in the pollen profile at any time. Therefore, in this case, it is difficult to confidently identify significant periods of increased disturbance based on the indicator species alone.

From c. 100 cal. yr BP, climatic conditions became warmer. Hipp et al. (2012) estimated that the lower limit of permafrost on Galdhøpiggen has moved up by 200 m since 1860. In south-east Norway, birch tree lines advanced by 40 m between 1918 and 1969 (Aas, 1969), and an increase in tundra species richness at altitudes between 1600–1800 m a.s.l. on Galdhøpiggen has been recorded between 1930 and 1998 (Klanderud and Birks, 2003). By 2000 AD, pine had established its altitudinal limit at 1000 m a.s.l. alongside downy birch. It is also notable that *Picea abies* pollen appears in the profile at around 800 cal. yr BP, several hundred years later than estimated in other pollen studies in the area (e.g. Barnett et al., 2001), but remains "regional" up to the present day (Table 2). The closest spruce stands are currently c. 2 km from the site, growing at an altitude 200 m lower than the tree line.

Conclusions

The late-Holocene vegetation dynamics on the slope of Galdhøpiggen were reconstructed by employing a combination of indicators of species' local presence. From c. 4350 cal. yr BP until present, the area around 1000 m a.s.l. has been dominated by two arboreal species, *Betula pubescens* and *Pinus sylvestris*. Between c. 4300 and 3400 cal. yr BP, the area was covered by a pine-dominated mixed woodland, suggesting that the climatic conditions were warmer than today.The lower limit of permafrost was likely above 1500 m a.s.l. From c. 3400-3000 cal. yr BP, pine began retreating to lower elevations, accompanied by the descent of the low-alpine shrub-dominated vegetation belt in response to climatic cooling. This was a period of colder temperatures and permafrost aggradation. The colder period continued through 1700 – 170 cal. yr BP, as pine retained a sparse presence, and an open downy birch woodland dominated the landscape at this altitude. The lower limit of permafrost likely reached lower altitudes than today. From c. 170 cal. yr BP onwards, the conditions became warmer and pine had re-

established its local presence at 1000 m a.s.l. by 2000 AD. Downy birch remained locally present throughout this period, and the lower limit of permafrost moved upslope to its present-day altitude of 1450 m a.s.l.

The complementing techniques used to determine the local presence of species here (relative pollen abundance, PAR, and indicator species) can sometimes produce conflicting results, especially when the profile is heavily dominated by arboreal pollen. Therefore, the combined use of several methods still requires an appreciation of the strengths and weaknesses of the individual methods.

Figure captions:

Figure 1. Coring site near Raubergstulen on the north-facing slope of Galdhøpiggen in Jotunheimen. Site location is indicated by a triangle, pine (*Pinus sylvestris*) and birch (*Betula pubescens*) upper altitudinal tree limits are shown in contrasting shades of grey.

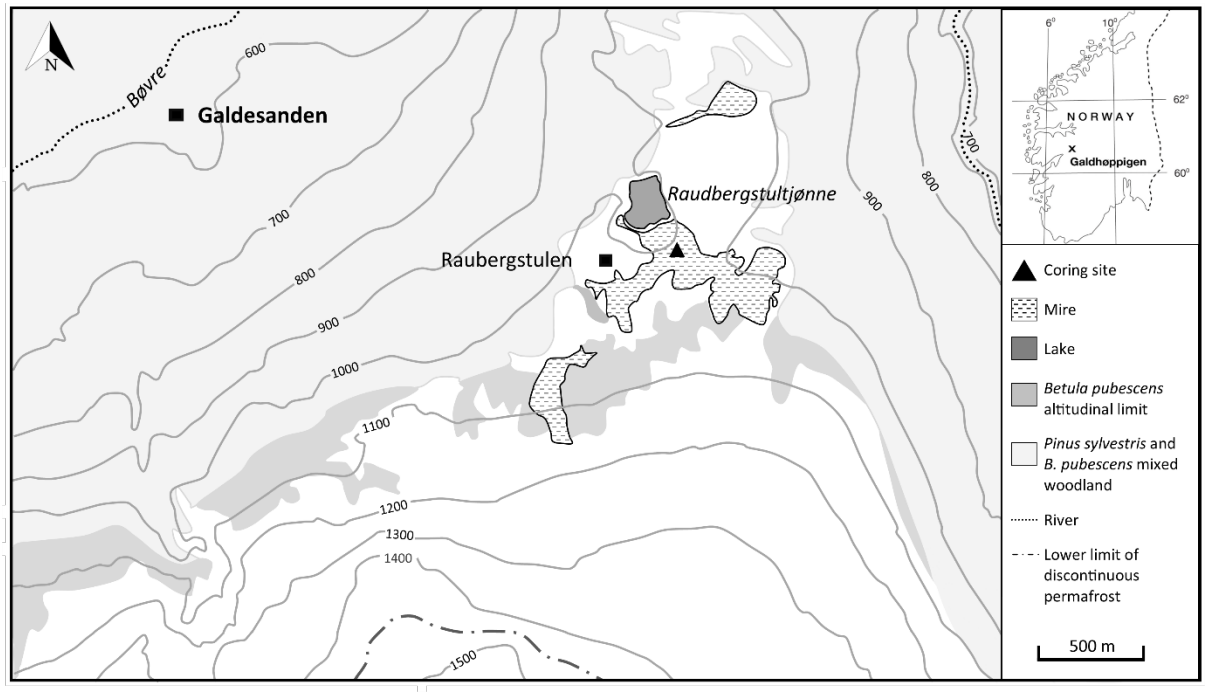
Figure 2. An age-depth model based on linear interpolation between dated levels (10, 24 and 46 cm) and the surface, using the calibration curves IntCal13 and post-bomb curve 'NHZ1'. The model was created using the 'clam' (2.2) package in R (3.6.3).

Figure 3. Pollen diagram summarising the relative abundance (%) of all taxa throughout the peat core. The modern moss polster (top 5 cm) is indicated with a border.

Figure 4. Relative abundance (%), concentration and pollen accumulation rates (PAR) of downy birch (*Betula pubescens*) and Scots pine (*Pinus sylvestris*).

Figure 5. Schematic diagrams illustrating possible vegetation cover and permafrost limits at c. 4300 and 3000 cal. yr BP, and 2000 AD.

664 **Figures:**



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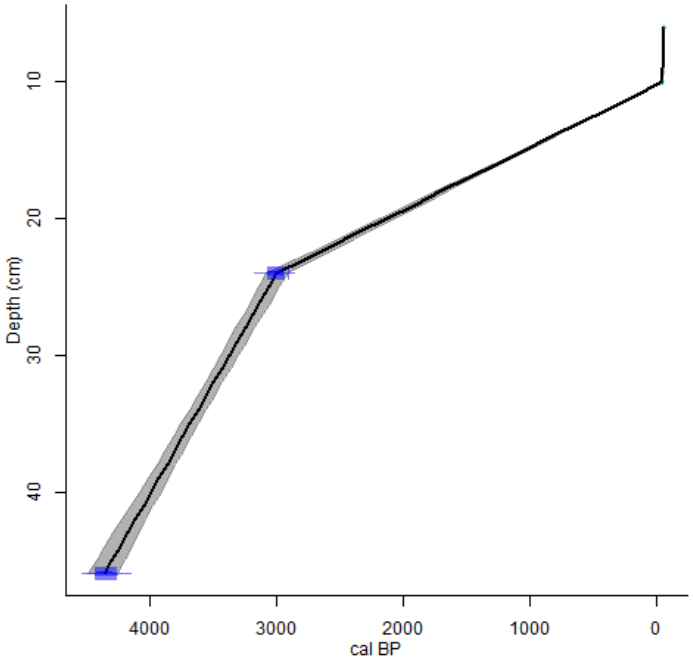

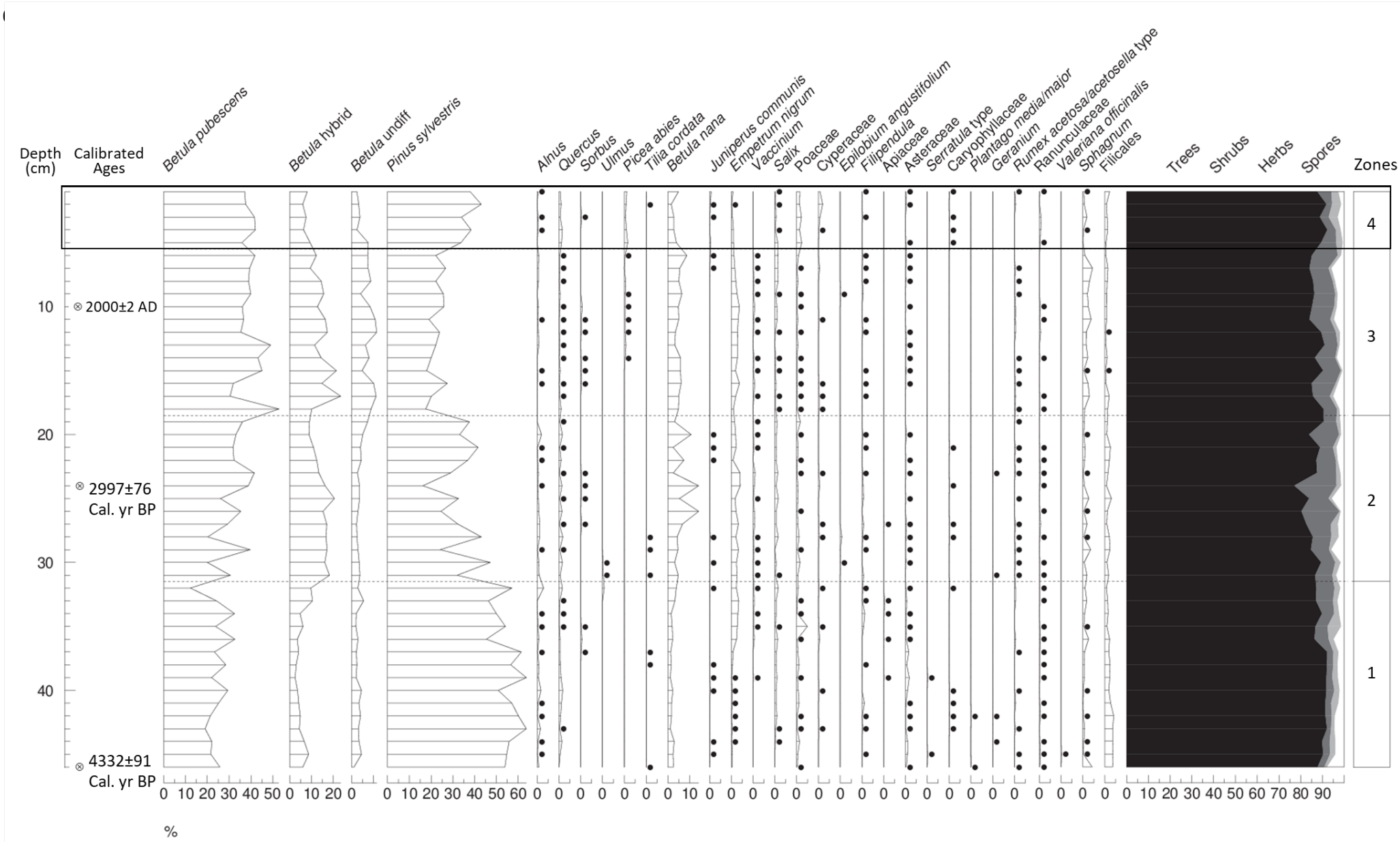
Depth (cm)
Calibrated Ages
Betula pubescens
Betula hybrid
Betula undiff
Pinus sylvestris
Alnus
Quercus
Sorbus
Ulmus
Picea abies
Tilia cordata
Betula nana
Juniperus communis
Empetrum nigrum
Vaccinium
Salix
Poaceae
Cyperaceae
Epilobium angustifolium
Filipendula
Apiaceae
Asteraceae
Serratula type
Caryophyllaceae
Plantago media/major
Geranium
Rumex acetosa/acetosella type
Ranunculaceae
Valeriana officinalis
Sphagnum
Filicales
Trees
Shrubs
Herbs
Spores
Zones
2000±2 AD
2997±76
Cal. yr BP
4332±91
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10
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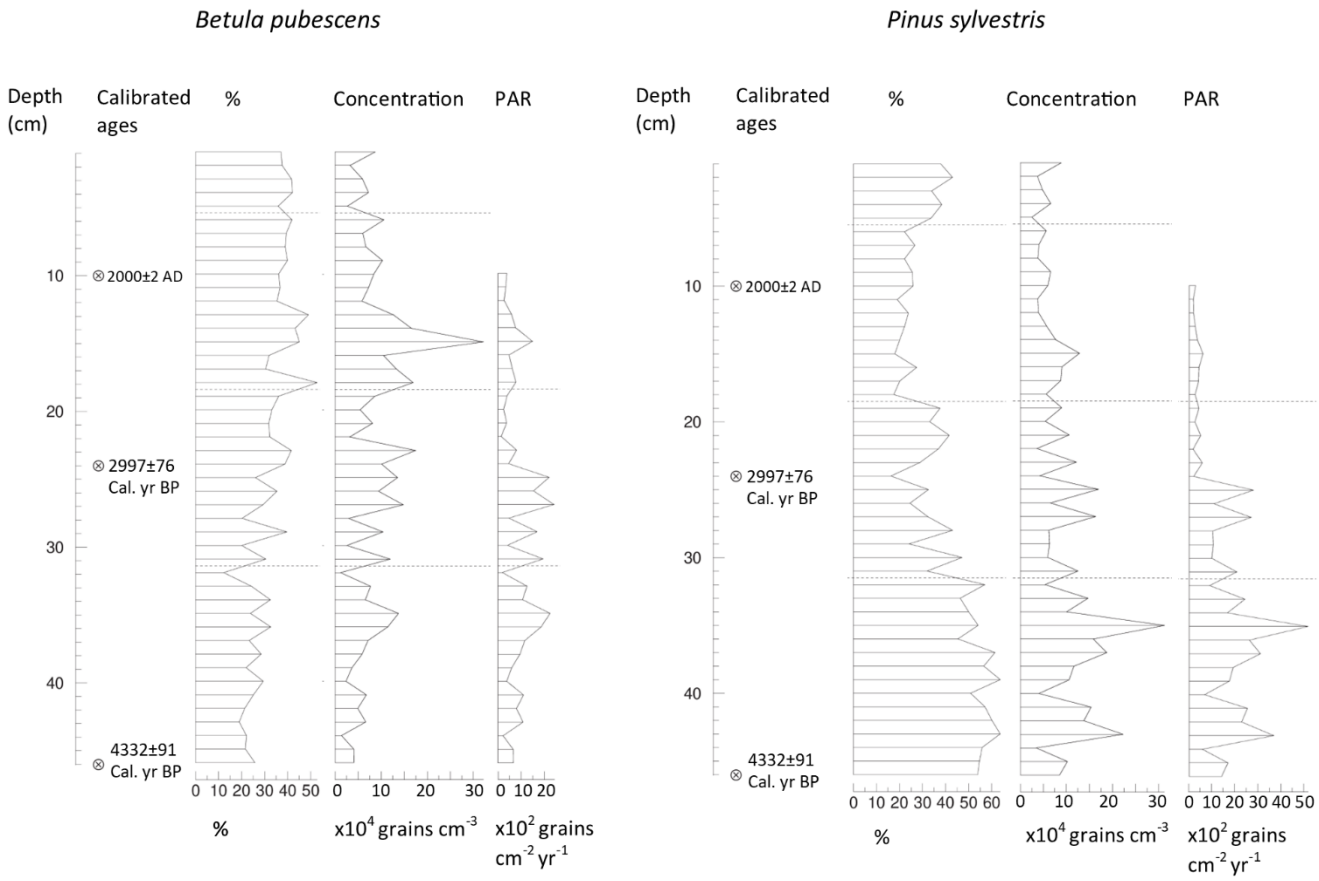
Betula pubescens
Depth (cm)
Calibrated ages
%
Concentration
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20
30
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2000±2 AD
2997±76 Cal. yr BP
4332±91 Cal. yr BP
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Pinus sylvestris
Depth (cm)
Calibrated ages
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Concentration
PAR
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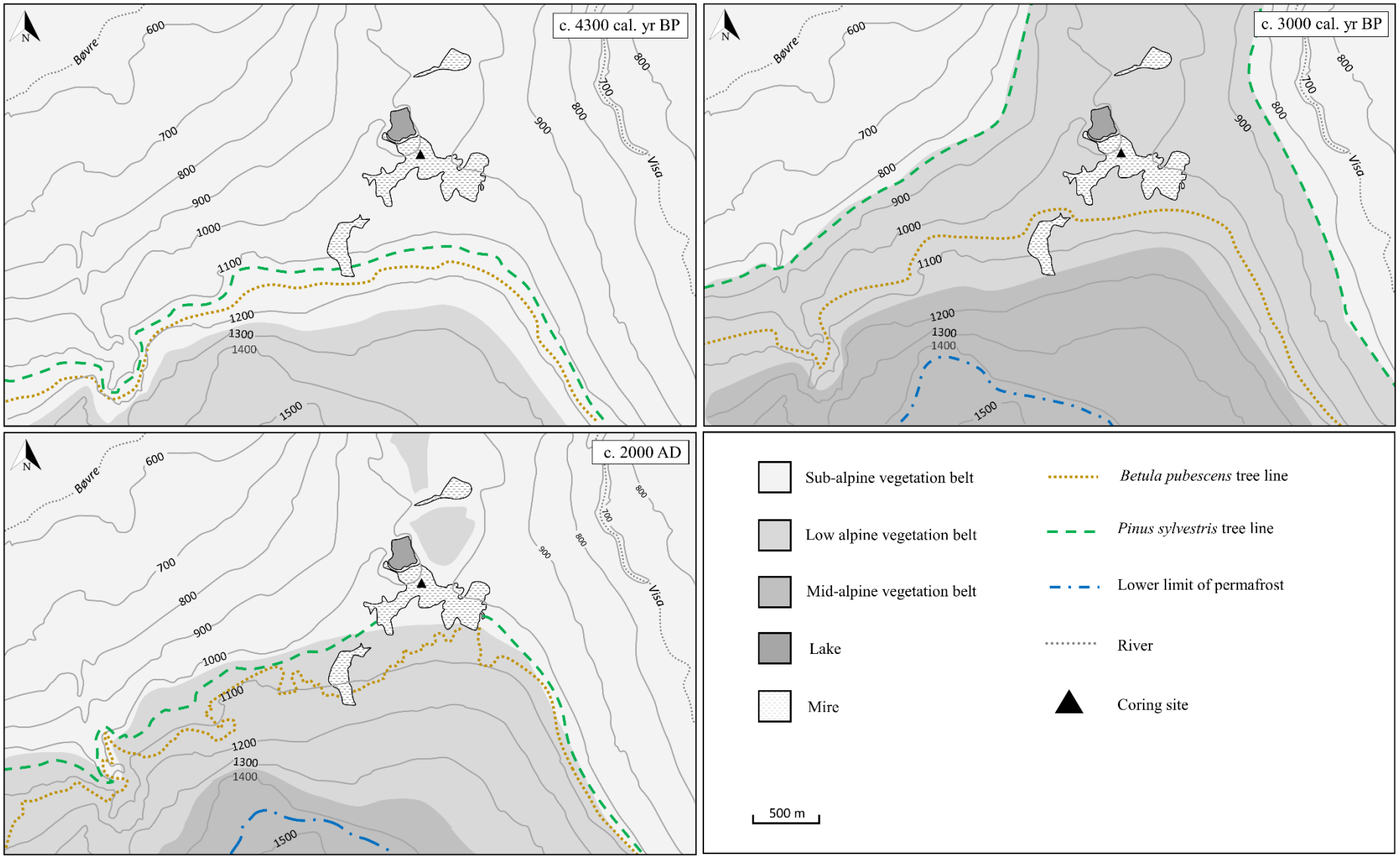
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c. 3000 cal. yr BP
c. 2000 AD
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Bøvre
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1300
1400
1500
Sub-alpine vegetation belt
Low alpine vegetation belt
Mid-alpine vegetation belt
Lake
Mire
Betula pubescens tree line
Pinus sylvestris tree line
Lower limit of permafrost
River
Coring site
500 m

691

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