

# Vegetation responses to rapid climatic changes during the last deglaciation 13,500–8,000 years ago on southwest Andøya, arctic Norway

Ingelinn Aarnes · Anne E. Bjune · Hilary H. Birks ·  
Nicholas L. Balascio · Jostein Bakke ·  
Maarten Blaauw

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**Abstract** The late-glacial vegetation development in northern Norway in response to climate changes during the Allerød, Younger Dryas (YD), and the transition to the Holocene is poorly known. Here we present a high-resolution record of floral and vegetation changes at lake Lusvatnet, south-west Andøya, between 13500 and 8000 cal B.P. Plant macrofossil and pollen analyses were done on the same sediment core and the proxy records follow each other very closely. The core has also been analyzed using an ITRAX XRF scanner in order to check the sediment sequence for disturbances or hiatuses. The core has a good radiocarbon-based chronology. The Saksunarvatn tephra fits very well chronostratigraphically.

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I. Aarnes (✉) · H. H. Birks  
Department of Biology, University of Bergen, Post Box 7803,  
5020 Bergen, Norway  
e-mail: ingelinn.aarnes@bio.uib.no

I. Aarnes · A. E. Bjune · H. H. Birks · J. Bakke  
Bjerknes Centre for Climate Research, Allégaten 55,  
5007 Bergen, Norway

A. E. Bjune  
Uni Bjerknes Centre, Allégaten 55, 5007 Bergen, Norway

N. L. Balascio  
Climate System Research Center, Department of Geosciences,  
University of Massachusetts, Amherst, MA 01003, USA

J. Bakke  
Department of Earth Science, University of Bergen,  
Post Box 7803, 5020 Bergen, Norway

M. Blaauw  
School of Geography, Archaeology and Palaeoecology,  
Queen's University Belfast, Belfast BT7 1NN, UK

During both the Allerød and the Younger Dryas time-periods arctic vegetation prevailed, dominated by *Salix polaris* associated with many typically arctic herbs such as *Saxifraga cespitosa*, *Saxifraga rivularis* and *Oxyria digyna*. Both periods were cold and dry. Between 12450 and 12250 cal B.P. during the Younger Dryas chronozone, the assemblage changed, particularly in the increased abundance of *Papaver* sect. *Scapiflora* and other high-Arctic herbs, suggesting the development of polar desert vegetation mainly as a response to increased aridity. After 11520 cal B.P. a gradually warmer and more oceanic climate initiated a succession to dwarf-shrub vegetation and the establishment of *Betula* woodland after 1,000 years at c. 10520 cal B.P. The overall late-glacial aridity contrasts with oceanic conditions in southern Norway and is probably related to sea-ice extent.

**Keywords** Macrofossils · Pollen · Northern Norway · Arctic vegetation · Late-glacial aridity

## Introduction

Future climate warming is predicted to have large consequences for Arctic ecosystems (e.g. ACIA 2004; ACIS 2008). The extent of regional differentiation will depend on the importance of feedbacks in the arctic (Moritz et al. 2002). In the past large differences in extent, timing and response to climate change at the Holocene Thermal Maximum have been shown (Renssen et al. 2009).

Ecosystems respond differently over even relatively short distances if climate gradients are present. To detect such gradients in the past we need critically positioned and well dated, high-resolution records that cover the same key periods of climatic change. The determination of past

climate and vegetation patterns can provide data to models that can investigate forcings and regional-scale feedbacks. These processes could also play a role in the future developments of the climate system and can be used as constraints for higher resolution models of future climate change that are being developed to enable mitigation and adaptation.

During the Weichselian deglaciation, which started at c. 20000 cal B.P. (calendar years before A.D. 1950), large and rapid climate fluctuations have been documented in ice-cores from Greenland (e.g. Johnsen et al. 2001). At the same time temporal and spatial variability in precipitation and temperature have been documented on a large scale in Europe and the Atlantic region (e.g. Lowe et al. 1995). In Norway there are large climatic gradients today both latitudinally and longitudinally. The presence and magnitude of climate gradients during the late-glacial and early Holocene were mapped by Birks et al. (2005). They documented several well dated terrestrial sites providing late-glacial palaeoecological data, particularly in the south (see e.g. Birks et al. 2000). However, comparable records that cover the same period are sparse in the north.

Although most of Fennoscandia was covered by ice during the last glacial maximum (Svendsen et al. 2004), part of Andøya in northern Norway was deglaciated soon after the last glacial maximum (LGM) (Møller and Sollid 1972; Svendsen et al. 2004). Some of the mountains have been ice-free since before the LGM, some for more than 50,000 years according to Nesje et al. (2007). The potential for obtaining long lake-sediment sequences has been realized from Øvre Æråsvatn, Nedre Æråsvatn and Endletvatnet on northern Andøya which have yielded basal radiocarbon dates of between 22000 and 18000  $^{14}\text{C}$  years B.P. (Vorren 1978; Vorren et al. 1988; Alm 1993).

Andøya is favourably situated to record responses to late-glacial climate changes in northern Norway. Although located at 69°N, it has a relatively warm maritime climate today due to the northern transport of heat by Atlantic and Norwegian coastal currents. Any changes in the strength of the Norwegian Atlantic Current (a northern branch of the Gulf Stream) will affect the climate on Andøya. During the deglaciation there were major changes in the extent of sea ice, activity of the thermohaline circulation and strength of the Norwegian Coastal Current, and wide variations in the position of the polar front (e.g. Koç et al. 1993; Hald et al. 2007). Andøya acts as a terrestrial ‘thermometer’ inserted in the Norwegian Sea, and the late-glacial lake sequences are in an optimal location to study the vegetation responses to large and rapid climate changes.

The late-glacial vegetation history of northern Andøya has been documented by Vorren (1978), Vorren et al. (1988), Alm (1993), Alm and Birks (1991), Vorren and Alm (1999) and Vorren et al. (2009). Major vegetation

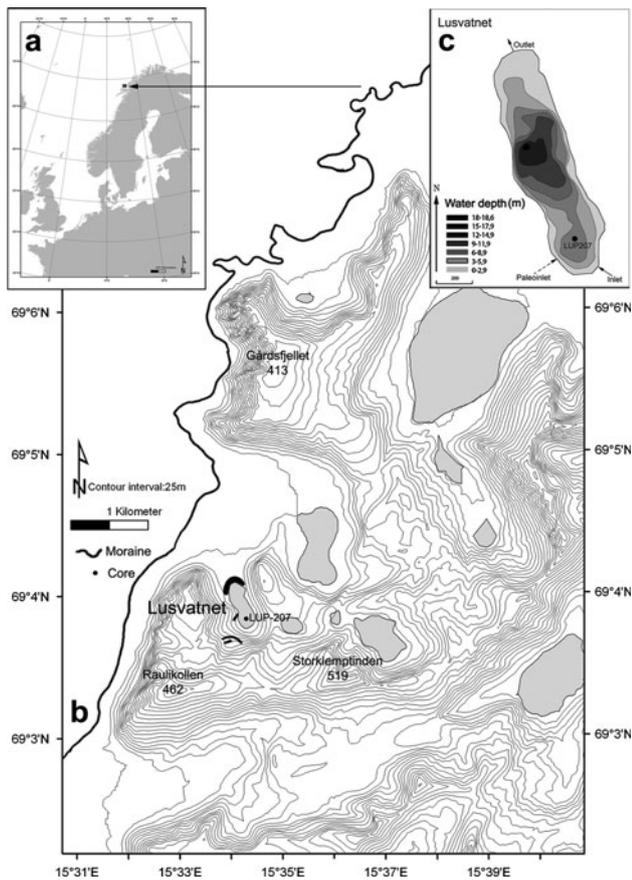
shifts during the deglaciation have been demonstrated based on pollen (Vorren et al. 1988, 2009; Alm 1993). However, all these studies suffer from difficulties in obtaining good chronological control of events and none of the records covers all the key periods of major climatic change (Allerød, Younger Dryas and the onset of the Holocene) in the same sequence due to hiatuses. Many also suffer from problems with low pollen counts leading to weaker interpretations. The Younger Dryas record is weak (Vorren et al. 1988; Alm and Birks 1991). Only data from Vorren et al. (2009) adequately cover parts of the Younger Dryas (from 12300 cal B.P.) where however dating of the sequence was difficult. Two previous studies have included analysis of plant macrofossils (Alm and Birks 1991; Vorren et al. 2009). The records are restricted by the fact that they contain relatively few fossil remains and/or cover relatively short time periods.

In this study we aim to present a record of vegetational changes from a continuous late-glacial lake sediment record from lake Lusvatnet, southwest Andøya, covering all the major late-glacial climatic shifts since c. 13400 cal B.P. and through into the early Holocene. To ensure that the vegetation record could be reconstructed in as much detail as possible, plant macrofossils and pollen were integrated as proxies from the same sediment core with good chronological control and with high temporal resolution in the parts of the record where major changes were expected. We focus here on the vegetation responses to climate changes and discuss possible explanations for the observed changes in the proxy records. We compare our data with previously published studies.

#### Site

Andøya is the northernmost island of the Vesterålen–Lofoten archipelago in northern Norway (Fig. 1). It lies in the northern part of the middle boreal vegetation zone (Moen 1998). However, due to its maritime location, *Pinus sylvestris* is rare and *Betula pubescens* is the major forest component forming a tree-line at an altitude of about 200 m (Fig. 2). Today Andøya has a relatively warm maritime climate for its northern latitude, with a mean July temperature of 11°C, mean January temperature of  $-2.2^\circ\text{C}$ , and mean annual precipitation of 1,060 mm reported from the weather station at sea level at Andenes in northwest Andøya (E-Klima.no).

Lusvatnet (69°04'N, 15°34'E) is a lake close to the southwest coast of Andøya in a sheltered valley at 30 m a.s.l. (Fig. 2). It is dammed by a prominent moraine at its northern end. The lake is surrounded by steep slopes to the south, west and east. The lake has two basins (Fig. 1) separated by an underwater moraine. A stream from a small lake in the east of the catchment drains into



**Fig. 1** **a** Lusvatnet is situated in northern Norway near the south-western coast of Andøya. **b** Topography around Lusvatnet. The coring site and moraines in the catchment are indicated. The bathymetric map (**c**) shows that Lusvatnet consists of two basins separated by a moraine. The core, LUP207, for pollen and plant macrofossil analysis was taken from the inner basin (black dot)



**Fig. 2** Lusvatnet is situated in a sheltered valley with steep slopes on three sides bearing open birch woodland and open towards the sea in the north-west. A white dot marks the coring location in the innermost basin (Photo: B. Kvisvik)

Lusvatnet. There may once have been small cirque glaciers present in the catchment as there are several bowl-shaped depressions cut into the mountain sides surrounding Lusvatnet, bounded by moraines (Fig. 1). Active slope processes occur in the catchment, in particular on the steep north-facing slope at the head of the valley where there are traces of recent avalanche activity. Today, Lusvatnet is surrounded by open *Betula pubescens* ssp. *tortuosa* woodland with a dwarf-shrub understory dominated by *Empetrum nigrum*, *Calluna vulgaris* and *Vaccinium* spp. in drier areas, whilst *Eriophorum vaginatum* dominates the wetter peaty soils especially at the north-west side of the lake. *Equisetum fluviatile* and *Juncus filiformis* grow along the shore of the lake. No submerged aquatic plants were observed.

## Methods

### Coring and sediments

Lusvatnet was surveyed with ground penetrating radar with a frequency of 50 MHz penetrating through the soft sediments in order to map the palaeo-basin and to locate potential sub-aquatic moraines. One 6 m long continuous sediment core (LUP107) was taken from under c. 7 m water in the south basin of Lusvatnet in summer 2007 with a 110 mm diameter piston corer (Nesje 1992) operated from a raft. As this core did not reach the basal sediments, a parallel 5.12 m long core was taken for which the corer was opened at c. 2 m depth in the sediment. The basal sediments were successfully retrieved and this core, LUP207, was used for the investigation. The core was divided longitudinally in the laboratory. One half was used for sediment analysis (loss-on-ignition, XRF and pollen analysis), whilst the second half was used for plant macrofossil analysis. Sediment lithology was described in terms of structure, colour and other visible features (Figs. 3a, b, 4) including a fist-size rock at 457–446 cm.

### Loss-on-ignition (LOI)

Sediment samples of 0.5 cm<sup>3</sup> were taken at 0.5 cm intervals, dried overnight at 105°C, weighed, burned at 550°C for 1 h, and weighed again after cooling in a desiccator (Bengtsson and Enell 1986). LOI was calculated as percentage of dry weight. LOI data are available from the bottom of the core up to 220 cm depth. It is not expected to vary much above this level in the uniform lake gyttja. The LOI curve is presented in the stratigraphic diagrams (Fig. 3a, b).



◀ **Fig. 3** Lusvatnet (LUP207) combined macrofossil concentration and pollen % diagram of all major taxa plotted stratigraphically, plus total pollen accumulation rate (grains  $\text{cm}^{-2} \text{year}^{-1}$ ). Macrofossil concentrations (*histograms*) are shown as numbers in  $50 \text{ cm}^3$  sediment. Macrofossils that were counted on a relative scale (rare, occasional, frequent, abundant) are shown as *grey histograms*. Pollen percentages are shown as sum of terrestrial pollen, spores, and indeterminate pollen (*black silhouettes* with *exaggeration line*  $\times 10$ ). The samples are plotted on a depth scale with a secondary age-scale based on the age-depth model (Fig. 5): **a** taxa predominantly present in the late glacial, **b** taxa mainly present during the early Holocene

XRF core scanning

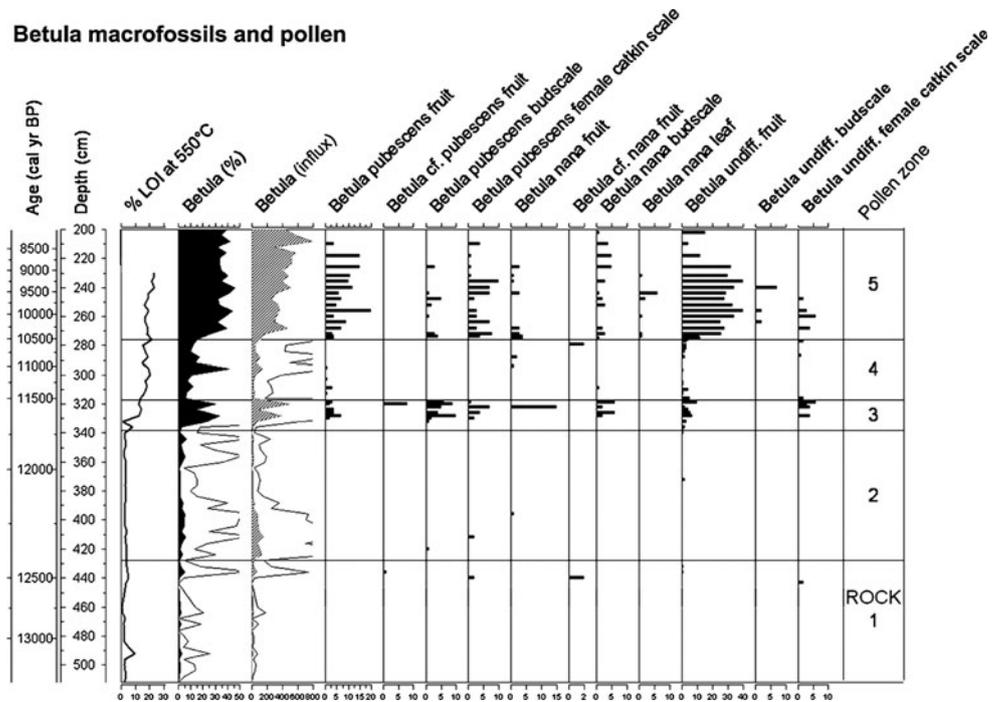
Core LUP207 was scanned using an ITRAX core scanner with a step size of  $200 \mu\text{m}$  ( $n = 14,277$ ) and equipped with a XRF chrome tube for the interval from 227.5 to 512 cm. From the chemical log, the mineralogical and geochemical composition can be inferred. The main purpose of the scanning was to evaluate the stability of the sedimentological environment and detect potential areas in the core where there could be disturbances or hiatuses and to detect and quantify, for example, input of allochthonous minerogenic sediments associated with transport and deposition in the lake basins. The XRF count rate of titanium in distal glacier-fed lakes has been successfully employed to detect glacial erosion (Bakke et al. 2009, 2010), as titanium is present in most bedrock lithologies. Since titanium is redox insensitive, different ratios with redox sensitive elements such as titanium/iron or titanium/magnesium can indicate

any secondary process affecting the lake sediment such as slope wash or periglacial processes.

Plant macrofossil analysis

One half of the core was cut into 1 cm slices. The outer 2 mm of sediment were carefully removed to avoid contamination. The individual plastic bags were stored at  $-20^\circ\text{C}$  to avoid fungus growth that could contaminate potential radiocarbon-dating samples (Birks and Lotter 2003; Wohlfarth et al. 1998). Preparation of macrofossil samples followed Birks (2001). Sample volume was measured by displacement of water. Sediment was dispersed if necessary by addition of sodium pyrophosphate and washed through a  $125 \mu\text{m}$  mesh with a gentle stream of water. Macrofossil remains were picked out systematically from the residue under a stereo microscope at  $12\times$  magnification and identified by visual comparison with modern reference material in the collection at the Department of Biology, University of Bergen, or from macrofossil identification literature (see references in Birks 2001). All macrofossil counts were converted to numbers in  $50 \text{ cm}^3$  sediment. A relative abundance scale was used for fossil remains too numerous to count or that were uncountable as individuals (e.g. vegetative remains). The temporal resolution of the macrofossil data is high during the Allerød (30–40 years) and Younger Dryas (10–20 years) and is lower during the Holocene.

**Fig. 4** *Betula* remains in Lusvatnet (LUP207). *Betula* macrofossil concentrations (*histograms*) as numbers in  $50 \text{ cm}^3$  sediment, *Betula* pollen percentages (*black silhouette*) with *exaggeration line*  $\times 10$ , and *Betula* pollen accumulation rate (grains  $\text{cm}^{-2} \text{year}^{-1}$ ) (*grey silhouette*). The samples are plotted on a depth scale with a secondary age-scale based on the age-depth model (Fig. 5)



**Table 1** Radiocarbon dates from terrestrial plant material from Lusvatnet (LUP207)

Depth (cm)	Lab. code	<sup>14</sup> C age	Material dated	Cal B.P. (min)	Cal B.P. (max)
170–169	Poz-33966	6160 ± 35	Bark	6966	7162
194–193	Poz-33967	6960 ± 40	Bark, twig, leaf fragments	7691	7923
210–209	Poz-33968	7470 ± 40	Leaf fragments, wood	8197	8372
226–225	Poz-33969	6580 ± 40	Leaf fragments, wood	7427	7564
236–335	Poz-30108	8210 ± 50	Leaf fragments, bark	9020	9395
244–243	Poz-33965	8360 ± 40	Leaf fragments	9287	9473
260–259	Poz-33964	8980 ± 35	Leaf fragments, wood	9933	10232
269–268		8995 ± 65	Saksunarvatn tephra	9914	10249
272–271	Poz-24476	9230 ± 50	Leaf fragments	10251	10544
282–281	Poz-30109	9580 ± 50	Bark, <i>Salix</i> bark, wood	10736	11132
295–294	Poz-33963	9640 ± 50	Single <i>Salix</i> twig	10782	11191
316–315	Poz-33915	9910 ± 60	Leaf fragments, wood	11213	11500
319–318	Poz-30107	3420 ± 35	Twig	3576	3824
340–339	Poz-24477	10150 ± 60	<i>Polytrichum</i> , leaf fragments	11409	12054
380–379	Poz-30106	10350 ± 50	<i>Polytrichum</i> , leaf fragments	12010	12406
389–388	Poz-33914	10600 ± 60	<i>Polytrichum</i> , leaf fragments	12413	12659
400–399	Poz-33913	10640 ± 60	<i>Polytrichum</i> , leaf fragments	12426	12693
416–415	Poz-33911	10630 ± 60	<i>Polytrichum</i> , leaf fragments	12424	12683
428–427	Poz-22884	10550 ± 60	<i>Polytrichum</i> , <i>Salix</i> bud, leaf fragments, bark	12222	12644
440–439	Poz-33910	10300 ± 60	<i>Polytrichum</i> , leaf fragments	11827	12394
443–442	Poz-22885	9910 ± 50	<i>Polytrichum</i> , leaf fragments, twig, bark, <i>Salix</i> bud	11216	11601
476–475	Poz-33909	11390 ± 60	Leaf fragments, wood	13129	13386
490–489	Poz-30105	11220 ± 60	<i>Polytrichum</i> , leaf fragments, bark	12916	13278
512–511	Poz-22886	11920 ± 60	<i>Polytrichum</i> , leaf fragments, twig, bark	13592	13960

The age of the Saksunarvatn tephra is included from Birks et al. (1996)

### Pollen analysis

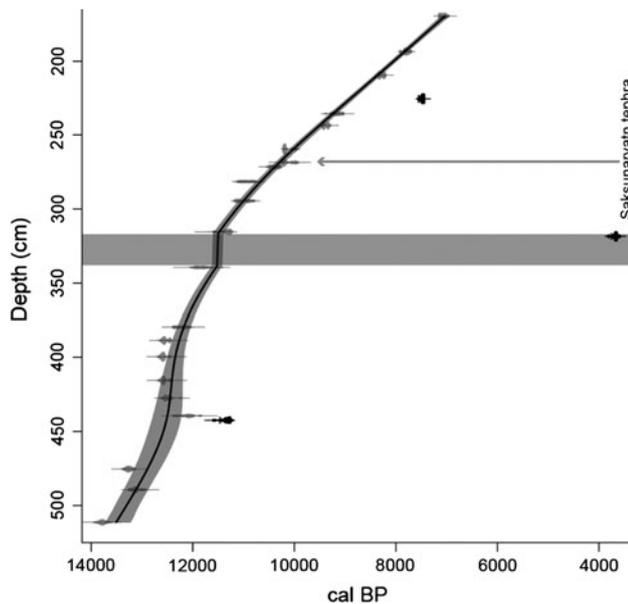
A total of 83 l cm<sup>3</sup> sub-samples for pollen analysis were extracted from the second half of the core. To permit estimation of *Betula* pollen concentration and the calculation of pollen influx (Fig. 4), tablets with a known concentration of *Lycopodium* spores were added prior to preparation (Stockmarr 1971). Each sample was prepared according to standard methods (KOH, HF, acetolysis) described in Fægri and Iversen (1989) and mounted in glycerine. Although the pollen concentrations were low in the minerogenic sediments, at least 200 terrestrial pollen and spores per sample were identified to the lowest possible taxonomic level using keys (Punt 1976–1995; Fægri and Iversen 1989; Moore et al. 1991) and an extensive modern pollen reference collection at the Department of Biology, University of Bergen. Indeterminable pollen grains are included in the calculation sum of total terrestrial pollen and spores.

Stratigraphic diagrams of pollen and plant macrofossil data (Figs. 3a, b, 6 and Fig. 4, the summary diagram of all *Betula* remains) were plotted using C2 (Juggins 2005).

Plant nomenclature follows Lid and Lid (2005). The pollen diagram was zoned by optimal partitioning using the sum of squares criterion (Birks and Gordon 1985) using the program ZONE 1.2. The number of significant zones was determined by comparison with the broken-stick model (Bennett 1996; Birks 1998). A visual zonation of the plant macrofossil data gave similar results, so the zones based on pollen data were used. Where they can be correlated with the Greenland Ice-Core Chronology (GICC05) (Rasmussen et al. 2006), they are named Allerød (GI-1), Younger Dryas (GS-1) and Holocene.

### Chronology

Terrestrial plant remains from 23 selected samples were picked out, cleaned with forceps and brush under the microscope for visible contamination and adhering sediment, and stored either frozen in water or air-dried until sent for AMS radiocarbon dating at Poznan AMS Radiocarbon Laboratory, Poland (Table 1). Calibration of the radiocarbon dates and age-depth modelling were done



**Fig. 5** Age-depth model for LUP207 calculated using a smooth spline. In each date the *solid line* indicates the calibrated ranges and *grey field* around it represents the probability distribution. A section that is probably contaminated is indicated as a *grey bar* and was excluded from the age model. The Saksunarvatn tephra (age from Birks et al. 1996) at 268–269 cm is plotted

using R (R Development core team 2011) and routine Clam (Blaauw 2010). Calibration is based on the IntCal09 calibration curve (Reimer et al. 2009). All ages in the text have been rounded to the nearest 10 years, but it should be borne in mind that their probability ranges are larger than this (Fig. 5).

The age-depth model (Fig. 5) was constructed using a smooth spline run through randomly sampled point estimates from calibrated dates and iterating this process a thousand times. The smooth spline was weighted by the probabilities of the sampled calibrated years (Blaauw 2010). Any models with age reversals were rejected. Three dates (at 443, 319 and 226 cm depths) were considered improbably recent and were excluded from the age model (Table 1).

Dates that are too recent can result from contamination during long-term cool storage of wet macrofossil samples by incorporation of young carbon from, for example, fungi, or contamination from younger material. Low weights of organic material are especially vulnerable (Wohlfarth et al. 1998). It is unlikely that storage factors have affected the samples from Lusvatnet as the core was sampled very soon after collection and all samples were immediately frozen at  $-20^{\circ}\text{C}$  until analyzed. The radiocarbon sample at 319 cm was a single *Salix* twig with a resulting very recent age of 3420  $^{14}\text{C}$  years B.P. A single large macrofossil may not be

contemporary with the surrounding sediment as it could be brought down by the coring process. This date plus sedimentary and fossil data indicates that bulk contamination has occurred between 338 and 317 cm (see results and discussion below) so this interval was taken out of the age depth model. Samples at 226 and 443 cm seem to be around 1,000 years too young compared to the age-depth model. It is possible that these contained a combination of in situ material with some younger material incorporated. At 443 cm, a *Betula pubescens* female catkin scale was recovered (Figs. 3b, 5). As *Betula* is highly unlikely to have grown in northern Norway during the deglaciation it is likely that there has been some down-core movement of material (see below).

To verify the age-depth model, the Saksunarvatn tephra, previously dated to 8930–9060  $^{14}\text{C}$  years B.P. by Birks et al. (1996), was identified at 268 cm and used in constructing the age-depth model (Fig. 5). To find the cryptotephra, samples were collected every cm from 265 to 270 cm and treated according to Turney (1998). Sediment between 2.3 and 2.5  $\text{g cm}^{-3}$  was retained, cleaned in deionized water, mounted on microscope slides in epoxy resin, and glass shards were identified using a polarizing light microscope. A distinct peak in the concentration of glass shards occurred in the sample from 268 to 269 cm where 679 olive green grains were counted. This sample was polished to expose the grain interiors which were analyzed using a Cameca SX50 electron microprobe. Instrument calibration was performed using a series of silicate minerals, synthetic oxides and glass standards. Geochemical results show that all glass shards analyzed fall within the compositional range of the Saksunarvatn tephra identified in other distal locations (Mangerud et al. 1986; Birks et al. 1996; Wastegård et al. 2001) (Table 2).

## Results and reconstruction of ecosystems

### Vegetation development

The micro- and macrofossil biostratigraphic records follow each other closely at Lusvatnet, enabling pollen percentages and plant macrofossil concentrations to be presented together in the same diagrams (Fig. 3a, b). In the discussion pollen and spores are noted with p whilst the macroremains are noted with m. The zonation of Fig. 3 is based on the statistically significant pollen zones. In addition one zone that was not significant according to the optimal partitioning was added (zone 3) as it clearly stands apart from zones 2 and 4, particularly in the macrofossil record (Fig. 3b). The vegetation development will be discussed following these zones.

**Table 2** Geochemical composition of glass shards isolated from LUP207 268–269 cm compared to the Saksunarvatn tephra identified in western Norway (Birks et al. 1996) and the Faroe Islands (Wastegård et al. 2001)

Sample	n	SiO <sub>2</sub>	TiO <sub>2</sub>	Al <sub>2</sub> O <sub>3</sub>	FeO	MnO	MgO	CaO	Na <sub>2</sub> O	K <sub>2</sub> O	P <sub>2</sub> O <sub>5</sub>	Total
LUP-207 268–269 cm	26	48.48 (0.78)	2.93 (0.19)	13.08 (0.29)	14.16 (0.53)	0.25 (0.03)	5.69 (0.43)	10.14 (0.35)	2.57 (0.20)	0.43 (0.04)	0.34 (0.06)	98.07 (0.77)
Wastegård et al. (2001)	16	48.17 (0.49)	2.98 (0.19)	12.73 (0.22)	13.88 (0.50)	0.28 (0.04)	5.61 (0.21)	9.74 (0.21)	2.75 (0.18)	0.44 (0.04)	–	96.58 (0.84)
Birks et al. (1996)	20	49.73 (0.68)	2.81 (0.23)	12.57 (0.47)	13.43 (0.49)	0.21 (0.06)	5.61 (0.79)	10.22 (0.53)	2.67 (0.21)	0.42 (0.08)	–	97.64 (0.99)

*Zone 1: 512–428 cm (c. 13500–12450 cal B.P.)—pioneer species on open ground and snow beds (equivalent to Allerød and early Younger Dryas)*

The sediments of zone 1 are minerogenic grey silts (LOI between 1 and 5%) with some visible sand layers. Seeds of *Saxifraga cespitosa*, *Saxifraga rivularis*, Poaceae and *Luzula*, and leaves of *Salix polaris* are prominent in the macrofossil record while Brassicaceae and *Saxifraga oppositifolia* (m) as well as undetermined moss (m) and *Polytrichum* (m) have a steady presence. *Rumex acetosella*-type and Poaceae dominate the pollen record throughout zone 1. *Saxifraga oppositifolia* (m, p), *S. rivularis* (m), *Oxyria digyna* (m, p), *S. cernua*-type (p), *Beckwithia (Ranunculus) glacialis* (p), *Silene acaulis* (m) and Brassicaceae (p) decrease in the middle of the zone, whereas there is a marked increase in *Luzula* (m) and lesser increases in *Salix* undiff. (p), ferns (m, p), and Caryophyllaceae (p). *Papaver* sect. *Scapiflora* (m) becomes present at irregular intervals from 464 cm (Fig. 3a).

These fossil assemblages can be matched by analogous present-day vegetation assemblages at high elevations in Norway and throughout Svalbard, where *Salix polaris*, *Saxifraga cespitosa*, *S. rivularis*, *S. oppositifolia*, *Oxyria digyna*, *Luzula* spp. and Poaceae are nearly ubiquitous (Benum 1958; Elvebakk 2005). These taxa are present at sea-level in north Norway and they can grow as high as 1,400 m a.s.l. in Troms County today (Benum 1958) but they are increasingly confined to the high alpine zone southwards in the Norwegian mountains (Moen 1998). Their present ecology indicates that they are highly tolerant of long cold, dry winters and also prolonged snow cover.

*Salix herbacea*, *Beckwithia glacialis*, *Oxyria digyna*, *Rumex acetosa*-type and *Saxifraga rivularis* are characteristic constituents of late-snow communities or moister areas influenced by snow melt-water (Benum 1958; Fremstad 1997). The first two species are rare in zone 1. *Saxifraga cespitosa*, *S. oppositifolia* and *Oxyria digyna* have wide ecological ranges, from open gravelly polar desert to more dense mossy vegetation and cliff ledges (Rønning 1996). *Salix polaris*, *Rumex acetosella* and *Silene acaulis* prefer exposed, well drained, open gravelly substrates and are common on fresh moraines, talus slopes and stone fields today (Rønning 1996; Benum 1958). Most of zone 1 is characterised by low total pollen influx (300–600 grains cm<sup>-2</sup> year<sup>-1</sup>) comparable to the present day pollen production in Canadian dwarf-shrub tundra (Ritchie and Lichti-Federovich 1967).

During the first 800 years following the deglaciation at Lusvatnet (13500–12690 cal B.P.; 512–460 cm) there was a mosaic of pioneer vegetation on dry, gravelly open ground interspersed with snow-bed communities in depressions that were regularly irrigated from melting snow. The

assemblage consists mainly of early colonizers of recently deglaciated ground. For example, *Saxifraga oppositifolia*, *S. cespitosa* and *Salix polaris* are characteristic of glacier forelands in high arctic Svalbard (Hodkinson et al. 2003) and in the mountains of southern Norway (Whittaker 1993).

The light grey clay comprising the sediment is typical of melt-water discharge (Matthews et al. 2000) and there was probably a small cirque glacier (see moraines in Fig. 1) still present in the catchment (J. Bakke, field observations) which would have provided silty melt-water in addition to melt-water from snow beds. We suggest that precipitation was low to moderate. A macrofossil record from northern Andøya covering the period of zone 1 indicates open sparse vegetation containing *Papaver* on immature soils (Alm and Birks 1991), but is otherwise similar to the record from Lusvatnet.

After 12690 cal B.P. (460 cm) there was little habitat change as shown by the continued presence of the common taxa *Saxifraga cespitosa*, *Luzula*, Poaceae and *Salix polaris*. *Papaver* sect. *Scapiflora* (m) was present and probably derives from the Fennoscandian endemic *Papaver radicum* agg. (Lid and Lid 2005) typical of polar desert and open gravel substrates (Benum 1958). The fern spores that are recorded after 444 cm were probably derived from tall ferns (*Dryopteris filix-mas*-type (p), Fig. 3b), such as the snow-loving *Athyrium distentifolium* characteristic of boulder fields in arctic and alpine areas. Less *Saxifraga rivularis* and *Beckwithia glacialis* might indicate that there were fewer melt-water habitats, either due to decreased melting of the glacier or, more probably, to less precipitation. This proposed increase in aridity and the abundance of taxa of open-gravel habitats occurred c. 200 years after the start of the Younger Dryas (GS-1).

**Zone 2: 428–338 cm (c. 12450–11520 cal B.P.)—*Salix polaris*, Brassicaceae and *Papaver* (equivalent to the mid Younger Dryas)**

In zone 2 the sediments consist of clay, sand and silt in varying proportions, interrupted by distinct thin gravelly-sand layers at irregular intervals. LOI is low, between 2 and 4%.

*Oxyria digyna* (m, p) almost disappeared and *Rumex acetosa*-type (p) decreased rapidly at the transition to zone 2. *Saxifraga cespitosa* (m) and *Salix polaris* (m) continued to dominate the macrofossil record in increased amounts. *Salix* undiff. (p) and Poaceae (p) are still prominent in the pollen record. *Papaver* and particularly Brassicaceae undiff. (m) show major increases at the transition to zone 2, and are abundant in the assemblage. There are also increases in *Saxifraga rivularis* (m), *Silene acaulis* (m) and *Luzula* (m) at the start of the zone, and a little later in *Saxifraga oppositifolia* (m), *Beckwithia glacialis* (m, p)

and *Artemisia* (p). Other arctic-alpine taxa have more scattered occurrences, such as a variety of Brassicaceae, including *Braya glabella* ssp. *purpurascens* and *Cardamine pratensis* ssp. *angustifolia* (m), and macrofossils of *Silene furcata*, *Minuartia biflora*, *Sagina nodosa* and *Rhodiola rosea* (m). Pollen of arctic taxa is represented by increased percentages of *Salix* undiff., Caryophyllaceae undiff., *Cerastium*-type and *Dryas octopetala*. Spores of *Cryptogramma crista* also occur. *Saxifraga rivularis* (m), *Cerastium arcticum* (m), *Silene acaulis* (m), *Papaver* (m), *Luzula* (m) and Cichorioideae Lactucoidea (p) decreased or disappeared in the middle of the zone (around 12260 cal B.P.). *Betula* pollen and two *Betula pubescens* catkin scales were recorded in zone 2. Of the aquatic plants, *Isoetes lacustris* megaspores were present throughout the zone, but their microspores ceased at 390 cm. *Subularia aquatica* (m) occurred in small amounts up to 360 cm.

The rapid decline in *Rumex acetosa*-type (p) at the transition to zone 2 indicates a harsher environment. This pollen type is probably composed largely of *R. acetosa*, as distinct *R. acetosella* and *Oxyria digyna* were separated. *R. acetosa* is relatively thermophilous and does not grow higher than 1070 m a.s.l. in Troms today (Benum 1958) and is rare on Svalbard (Rønning 1996). *Oxyria digyna* also decreased. Its reduction in glacier forelands is unrelated to successional stages but rather is constrained by moisture availability (Whittaker 1993). Increased environmental severity is also indicated by the abundance of *Salix polaris*, *Saxifraga rivularis* and *S. cespitosa*, and records of high-arctic taxa such as *Braya glabella* ssp. *purpurascens*, *Cardamine pratensis* ssp. *angustifolia*, *Silene furcata* and *Papaver* sect. *Scapiflora*. The major increase in *Papaver* together with increases in *Luzula*, *Cerastium arcticum* (m, p) and *Silene acaulis* (m) indicate an increase in open disturbed ground and stony exposed places with little snow cover (Benum 1958). The very abundant Brassicaceae undiff. seeds are badly preserved and are frustratingly difficult to identify to species level. It is possible that they are *Draba* spp. that are numerous in high Arctic areas (Elven 2007 onwards). They often grow on gravel and several species can be found in the polar desert zone on Svalbard (Rønning 1996). *Luzula* spp. are also a common constituent of polar desert communities (Elvebakk 2005).

The fossil assemblage of zone 2 seems to be analogous to a high arctic vegetation type close to a *Papaver* polar desert that developed due to less precipitation, perhaps combined with lower temperatures. The increase in open dry-ground taxa suggests that the climate was arid and soil disturbance by solifluction was prevalent. However, late snow-beds persisted, shown by the relative abundance of *Saxifraga rivularis* and *Beckwithia glacialis*.

There is also a sub-alpine element in zone 2, represented by *Betula* that is recorded as pollen and macro-remains

(Fig. 4). It is not plausible that *Betula*, even *B. nana*, was growing in an otherwise high arctic environment suggested by the rest of the fossil assemblage, so these remains may have been dispersed over a long distance (see also discussion), or have possibly been dragged down-profile during coring, since the remains are few. Aquatic species *Isoetes lacustris* (p, m), *Subularia aquatica* (m) and *Nitella* (m) were present during zone 2. They are normally associated with sub-alpine environments (Lid and Lid 2005). However, they all grow in Greenland, and *Subularia aquatica* is relatively widespread in the low arctic (Hultén and Fries 1986; Fredskild 1992). At this time, summer insolation was at its maximum. It is possible that the lake was sufficiently warmed in the summer, at least in shallow water, to support some aquatic vegetation.

Between c. 12260 and 11520 cal B.P. in the upper part of zone 2, there is a reduction in *Papaver* and other taxa of dry open ground such as *Luzula* and *Cerastium arcticum*, although remains of other taxa of open disturbed soils continued to be abundant. *Saxifraga rivularis* (m) also decreased in frequency, suggesting a decrease in snow beds or irrigated ground. There may have been less available moisture, perhaps from decreased precipitation and/or less melt-water discharge from the cirque glacier and snowbeds in the large hollows in the surrounding mountains in the catchment, possibly due to colder temperatures and a shorter summer melting period. Although negative evidence should not be relied upon, the aquatic species *Subularia aquatica* (m), *Nitella* (m), and *Isoetes lacustris* (p) disappeared during this interval suggesting that the lake may have become colder or ice covered for longer periods that disrupted the littoral zone. The continued presence of *I. lacustris* megaspores may suggest that this species was able to survive in deeper water unaffected by winter freezing and disturbance at the shore.

#### Zone 3: 338–317 cm (c. 11520 cal B.P.)—contaminated layer

From 338 cm the sediment is organic gyttja containing a narrow layer of gravel. The gyttja layer corresponds to an increase in LOI (up to 15%). Pollen zone 3 is not statistically significant but as the section differs substantially in its macrofossil content from zones 2 and 4, it is delimited and discussed separately.

There are major and abrupt changes in the fossil species composition (Fig. 3b). *Betula* pollen and fruits of both *B. pubescens* and *B. nana* are present in relatively large quantities (Fig. 4), accompanied by marked increases in Cichorioideae Lactuoidae (p), *Filipendula* (p), *Empetrum nigrum* (p) and *Gymnocarpium dryopteris* (p) (Fig. 3b). In addition *Silene dioica* (m) and *Stellaria nemorum* (m) are present in several samples and fern sporangia are abundant

(Fig. 3b). *Isoetes lacustris* (m, p) is suddenly abundant and *Subularia aquatica* (m) is also present after having been absent (Fig. 3b). These increases in sub-alpine taxa are accompanied by marked declines in most arctic taxa (Fig. 3a). At the end of zone 3, the sub-alpine taxa decreased or disappeared and arctic-alpine taxa reappeared.

The macrofossil assemblage in zone 3 is completely different from that of zone 2. Many taxa such as *Silene dioica*, *Filipendula*, and *Stellaria nemorum* are associated with open sub-alpine *Betula* woodland in the Norwegian mountains today (Moen 1998) which implies a minimum mean July temperature of 10°C (Odland 1996).

A sub-alpine assemblage with tree birch arriving suddenly and as early as c. 11520 cal B.P. is unexpected. Early Holocene records from southern Norway show a distinctive terrestrial and aquatic succession over several hundred years (Birks 2000; Birks et al. 2000; Birks and Birks 2008). We consider three hypotheses to explain the Lusvatnet record.

First, the assemblage we see in the fossil record could be real. If so, there would have to have been a very rapid warming and instant vegetation response with the immediate consequence that the arctic species that are no longer present in the record were outcompeted. Rapid warming is known from Greenland starting at c. 11650 cal B.P. (Rasmussen et al. 2007). Close to Andøya from c. 11800 cal B.P. sea surface temperature fluctuated between 3 and 10°C until c. 11500 cal B.P. (Ebbesen and Hald 2004). It is highly unlikely that such a cold climate could support the presence of trees. In addition these species would have to come from somewhere instantly which is unlikely considering that it took approximately 700 years before *Betula* trees arrived after the Younger Dryas in western Norway at Kråkenes (Birks and Birks 2008). In addition, it is hard to explain the subsequent demise of woodland and its replacement by an assemblage containing many of the arctic-alpines characteristic of zone 2 above 317 cm in zone 4.

Second, it is possible that the lack of succession could result from a hiatus in the sediment so that the succession is not registered in the fossil record. If so, the pollen and macrofossil curves as well as the sediment stratigraphy should show abrupt changes. However, at the start of zone 4 there is also a rapid transition where the assemblage present in zone 2 returned and the sub-alpine assemblage of zone 3 disappeared as rapidly as it arrived, which cannot be explained by a hiatus.

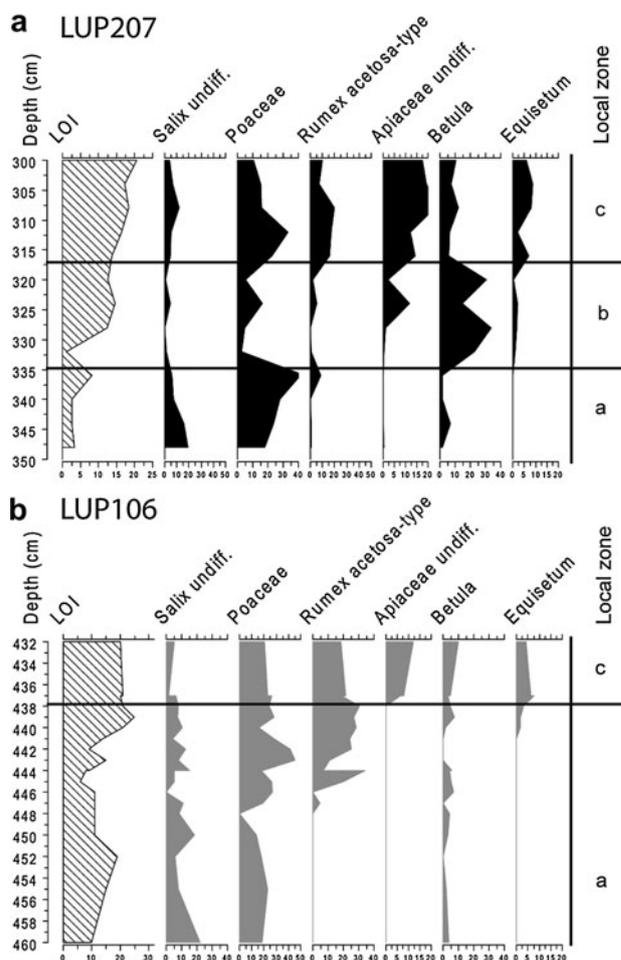
A third possibility is that there is contamination in the core by younger sediment containing a Holocene species assemblage. Sediment cores obtained by piston samplers are likely to be contaminated round the outside. Pollen and plant macrofossils of both terrestrial and aquatic taxa show exactly the same pattern in zone 3 so both would have to be equally contaminated. However, pollen samples were taken

from the middle of the core and should thus not be affected by external contamination. Further, the likely result of exterior contamination in the fossil record would be a combination of in situ deposited and contaminated material, but specifically arctic taxa are totally absent in zone 3.

Alternatively, the contamination was deposited as a unit during coring. We can hypothesise that the piston corer pulled down a unit of sediment and deposited it at a point. There is a fist-sized rock present in the core (Fig. 3) and during the coring process there were difficulties getting the corer past a point that may have been related to the rock. Alternatively, the start of coring below the sediment surface could have trapped young sediment which was released when the corer hit the harder minerogenic late-glacial sediments. At 319 cm at the end of zone 3 there is a highly anomalous young radiocarbon date (Table 1; Fig. 5) that supports this hypothesis that a block of younger sediment was pulled down.

To test this hypothesis, 19 pollen samples were analysed from a core (LUP106) taken from the outer basin of Lusvatnet from a time-correlative section. Apiaceae pollen is characteristic of the early Holocene in Lusvatnet (Fig. 3b) and at another nearby site on Andøya (Vorren et al. 2009). Since the rise of Apiaceae closely follows the proposed contaminated section it was used as a stratigraphic marker to correlate LUP207 and LUP106 (Fig. 6). There is a similar pollen composition with mostly *Salix* and *Poaceae* in LUP106 and LUP207 in zone a, corresponding to the end of Zone 2 (Fig. 6). Below 340 cm in LUP207 there is a distinctive undisturbed sand layer below which are sediment layers with clear boundaries through to the lowermost part of the core (e.g. Fig. 3a). There is no evidence of any disturbance in this part of LUP207. Towards the top of zone a, the LOI curve in LUP106 shows a 10 cm long decrease in contrast to the abrupt increase in LOI in LUP207 zone b (corresponding to Zone 3). The distinctive *Betula* rise and *Poaceae* decline of LUP207 zone b cannot be seen in LUP106 (Fig. 6). In addition, key species indicative of zone 3 in LUP207 like *Gymnocarpium dryopteris* and *Isoetes lacustris* were not found at all in LUP106. If we exclude the anomalous section from LUP207, these species do not arrive until later, above zone c. The sediment composition of Zone 3 in LUP207 is unique to that core and is not repeated in LUP106. In zone c, after *Betula* declined in LUP207 (Fig. 6) pollen composition is similar in both cores including low amounts of *Equisetum*, *Betula* and *Salix*. This evidence supports the hypothesis that bulk contamination has occurred in LUP207.

The Saksunarvatn tephra was found at 268–267 cm (Table 2). The dates by Birks et al. 1996 fall between two dates at 272–271 and 260–259 cm (Table 1) and fit well into the sequence of dates in this interval. This indicates that the upper part of the core is unaffected by contamination.

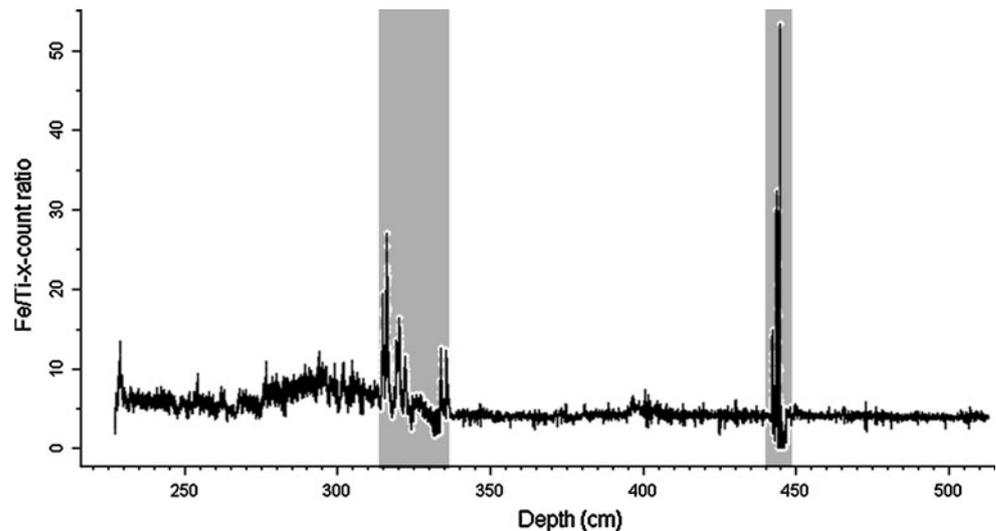


**Fig. 6** Investigation of the proposed contamination in core LUP207: **a** key pollen taxa typical of zones 2, 3 and 4 from LUP207 (black silhouettes) with % loss on ignition (LOI). Local zone *a* is the end of zone 2, local zone *b* is zone 3, and local zone *c* is the beginning of zone 4; **b** pollen data from 19 samples covering the same time period in a core from the outer basin of Lusvatnet (LUP106; grey silhouettes) and LOI. Only local zones *a* and *c* can be distinguished

The ratio between iron and titanium (Fe/Ti-ratio) shows low values throughout most of LUP207 (Fig. 7), indicating that most of the core, both the lower minerogenic part and the upper gyttja dominated part (Fig. 3a), were deposited without the influence of any secondary processes prior to deposition. The short section from 441.5 to 447.0 cm in the lower part of the core shows a distinct peak in the Fe/Ti-ratio (Fig. 7) that corresponds to the presence of the rock (Fig. 3a) clearly reflecting the local disturbance in the core.

There are several peaks in the Fe/Ti-ratio (Fig. 7) between 312.5 and 334 cm, as well as a general increase in the Fe/Ti-ratio lasting until c. 270 cm. The increase is interpreted as a change in sedimentation pattern with more minerogenic input originating from increased early Holocene slope wash or other catchment processes that eroded

**Fig. 7** The ratio between Fe and Ti in LUP207 plotted on a depth scale. Grey areas mark where sediment disturbance may have occurred



glacial deposits along the valley sides before they were stabilised by vegetation development, especially in such a steep catchment as Lusvatnet (Fig. 1). Sediment accumulation rate gradually decreased from 20 to 29 years per cm between 330 and 270 cm and LOI is relatively constant suggesting that the amount of inwash was small and balanced by the increasing organic productivity in the lake and the catchment. If the minerogenic sediments have been exposed sub-aerially, the effect of redox processes could potentially cause the small enrichment in iron compared to the titanium concentration that can be seen in this interval (Fig. 7). The anomalous peaks in the Fe/Ti-ratio between 312.5 and 334 cm indicate disturbances in the core related to contamination. Combined with the evidence from tephra and the pollen analyses from LUP207 and LUP106, this leads us to believe that the core is contaminated by a block of sediment comprising zone 3, but that the rest of the core is still intact, both above and below the contaminated area.

#### Zone 4: 317–276 cm (c. 11520–10520 cal B.P.)—early Holocene succession

At 317 cm mosses become visible in the surface of the gytja. There are no further visible sediment changes. LOI is relatively stable in zone 4 around 20%.

At the start of zone 4 many arctic species reappeared, such as *Saxifraga cespitosa* (m), *S. rivularis* (m), *Oxyria digyna* (m, p) and *Beckwithia glacialis*-type (p), and then gradually disappeared between 304 and 296 cm (c. 11240–11050 cal B.P.). *Salix polaris* (m) and *Silene acaulis* (m) were present until 289 cm (c. 10870 cal B.P.) (Fig. 3a). Poaceae (p, m), Apiaceae undiff. (p), *Equisetum* (p) and *Rumex acetosa*-type (p) increased markedly in early zone 4, but then declined. They were replaced around 296 cm (c. 11050 cal B.P.) by large increases in fern

sporangia (reflected in the increases in *Cryptogramma crispa* (p), *Dryopteris filix-mas*-type (p) and *Gymnocarpium dryopteris* (p)), *Empetrum* (m, p), and *Vaccinium*-type (p), followed by *Salix herbacea* (m) and *Betula nana* (m). Through zone 4, *Betula* pollen increased and there are a few scattered *Betula pubescens* fruits present (Figs. 3b, 4). These, and a spike of *Betula* pollen, may also be results of contamination from above.

The continuous turnover of species during the early Holocene is typical of succession in post-glacial landscapes (Matthews 1992; Birks and Birks 2008). The first early Holocene assemblage is a combination of arctic species such as *Saxifraga cespitosa*, *S. rivularis* and *Oxyria digyna*, and cold tolerant lowland species such as *Rumex acetosa*-type and *Equisetum*. *Rumex acetosa*-type (p) could represent *Rumex acetosa* ssp. *alpestris* that is very common in northern Norway today, and grows chiefly at higher altitudes in grassy communities (Benum 1958). *Equisetum* (p) may represent *E. fluviatile*, a lake-shore species, present at Lusvatnet today. High amounts of Poaceae pollen suggest a widespread grassland community with tall herbs such as *Rumex acetosa*. As *Saxifraga cespitosa* and *Oxyria digyna* were still present some open, gravelly ground was still locally available, presumably at higher elevations on the steep rocky terrain above the south end of the lake.

That *Rumex acetosa* and *Equisetum* are present at high altitudes in northern Norway today (up to 1,260 m a.s.l.) (Benum 1958) and that arctic species were still present in early zone 4 suggest that there was no immediate rapid temperature increase, but rather an increase in moisture. More precipitation and warming temperatures would increase soil development and allow a more continuous vegetation cover to develop. The peak of *Salix herbacea* (m) around 280 cm (10710 cal B.P.), previously very rare at Lusvatnet, suggests an increase in snow cover. A thin soil

layer could support a grass-rich community that would gradually out-compete the alpine-arctic taxa of open ground. *S. cespitosa*, *Oxyria digyna* and *S. rivularis* declined some 200 years later as *Vaccinium*, ferns and *Empetrum* started increasing. That *Salix polaris*, an arctic species (Benum 1958; Rønning 1996), did not disappear until c. 10900 cal B.P. suggests that the climate was still relatively cool until the plant was locally exterminated by temperature increase. Arctic taxa may have found refuge from rising temperatures and competition on the steep, north-facing cliffs at the head of Lusvatnet. The combination of *Salix polaris* and Apiaceae was also found by Vorren et al. (2009) at Nedre Årsvatnet during the period c. 11400 to 11050 cal B.P. where Apiaceae was thought to derive from *Angelica archangelica*-type associated with a low arctic environment (Vorren et al. 2009).

The major increases in *Vaccinium*, *Empetrum* and fern species and the presence of *Betula nana* fruits, combined with the decrease in Poaceae and disappearance of most arctic species in late zone 4, indicate the replacement of grassland by dwarf-shrub heath around 11000 cal B.P. *Betula nana* is usually under-represented by macrofossil remains even when present locally and its remains have limited aerial transport (Birks and Bjune 2010), so it is probable that *Betula nana* thickets were present. In Andøya today dwarf-shrub heaths occur on dry, well drained, wind-exposed soils in flat areas near the sea on the west coast. Vorren et al. (2009) found that *Empetrum* became established in northern Andøya at c. 11050 cal B.P. together with *Cryptogramma crispa*. A similar development was found near Tromsø (Fimreite et al. 2001).

Even though a few scattered *Betula pubescens* fruits were recovered it is doubtful that *Betula* woodland was present. Fruits are normally derived in large amounts from local woodland. Single macro-remains can be wind dispersed considerable distances beyond the tree-line (Birks and Bjune 2010). This is how new colonies of tree birch become established after climate warming or habitat creation. *Betula* pollen influx at c. 100 grains  $\text{cm}^{-2} \text{year}^{-2}$  (Fig. 4) is well below the mean values expected in arctic-alpine heaths (350–500 grains  $\text{cm}^{-2} \text{year}^{-1}$ ) (Seppä and Hicks 2006; Birks and Bjune 2010).

*Nitella* (m) is almost the only aquatic macrophyte present during zone 4. *Nitella* is a rapid colonizer and is well known to be a pioneer species following deglaciation (e.g. Birks 2000; Birks and van Dinter 2010). It is uncertain why isoetids, present during the late glacial, did not reappear. *Potentilla*-type (p), probably representing *Comarum palustre* as one seed was determined, is present at irregular intervals from c. 10900 cal B.P. *Plumatella* (statoblasts) are frequent at the start of zone 4 representing the development of an aquatic ecosystem. They decline around 310 cm (c. 11370 cal B.P.), shortly after *Cristatella* (statoblasts)

become present (Fig. 3b), indicating that the climate was becoming warmer. *Cristatella* is distributed up to or just above the tree-line at present broadly following the 10°C July isotherm (e.g. Birks et al. 2000).

#### Zone 5: 276–200 cm; (c. 10520–8060 cal B.P.)— establishment of *Betula* woodland

At c. 10520 cal B.P. (276 cm) at the transition to zone 5 there is a large increase in both *Betula* pollen percentages and influx and *B. pubescens* macrofossils (Fig. 4). Throughout the zone, *Betula* pollen % values remain relatively stable until the top of the record. However in the macrofossil record *B. pubescens* catkin scales decreased from 236 cm (c. 9130 cal B.P.) and *B. pubescens* fruits decreased around 210 cm (c. 8390 cal B.P.), suggesting a thinning of the woodland, but as *Betula* pollen influx values remain above 250 grains  $\text{cm}^{-2} \text{year}^{-1}$  there is probably a continuing local presence of birch at least on the lower slopes of the catchment (Seppä and Hicks 2006; Jensen et al. 2007). Tall herbs such as *Filipendula* (m, p) and Brassicaceae (m) (that could be *Cardamine pratensis*) grew in damp areas. *Juniperus communis* (p) increased whilst *Vaccinium*-type (p), *Equisetum* (p) and *Empetrum nigrum* (p) rapidly declined, probably becoming poorly represented as they became understory species. Abundant fern sporangia correspond to high percentages of *Dryopteris filix-mas*-type (p) and *Gymnocarpium dryopteris* (p) but *Cryptogramma crispa* (p) declined quickly to low values (Fig. 3b).

*Pinus sylvestris* (p) percentages rose after c. 9780 cal B.P. (252 cm) but its pollen influx does not reach 500 grains  $\text{cm}^{-2} \text{year}^{-1}$  needed to infer its local presence (Seppä and Hicks 2006). This is followed by increases in *Sorbus*-type (p) at c. 9670 cal B.P. (248 cm) and *Alnus* (p) from c. 9000 cal B.P. (228 cm). No macrofossils from any of these trees were found. *Alnus* pollen is continuously recorded at Lusvatnet from c. 9000 cal B.P. but the influx values are too low to indicate local presence. Other studies have shown that it invaded regionally between c. 9600 and 8600 cal B.P. probably in response to increased humidity and temperature (Seppä and Birks 2001; Seppä et al. 2002; Jensen et al. 2002; Bjune et al. 2004; Bjune and Birks 2008; Seppä et al. 2008; Vorren et al. 2009). The *Alnus* pollen at Lusvatnet is probably derived from these distant populations.

In the lake, *Nitella* (m) declined after the start of zone 5, as did the abundance of moss (m), *Plumatella* and *Cristatella*, whereas *Chara* (m) and *Isoetes echinospora* (m, p) increased followed by a large increase in *I. lacustris* (m, p) at c. 9130 cal B.P. (232 cm). Occasional *Subularia aquatica* seeds were present. Brassicaceae seeds were badly preserved and difficult to identify. It is possible that the increase of

Brassicaceae represents *S. aquatica* on gravel substrates in the littoral zone which is a typical part of macrophyte succession in the early part of the Holocene (Birks 2000). The subsequent reduction in *S. aquatica* may mean that gravel shores were reduced by higher water level, or plant communities were buried by organic sediment. It may also have been reduced by increased wave action initiated by stronger westerly winds in a more oceanic climate. The shores at Lusvatnet are quite steep today (Fig. 2), so there would probably have been a narrow littoral zone. Alternatively it may also have suffered competition from *Isoetes lacustris* that became abundant in the fossil record as Brassicaceae (m) decreased in the middle of the zone.

In zone 5 starting at c. 10520 cal B.P., open *Betula* woodland (probably *B. pubescens* ssp. *tortuosa*) became established and there is little change through the rest of the profile. It had a fern-rich field layer with tall herbs such as *Filipendula* and *Salix* shrubs on moister soils and dwarf shrubs and *Juniperus* in drier areas, much like the vegetation on the lower slopes around Lusvatnet today.

## Discussion

### Comparison of pollen and plant macrofossils

Our record from Lusvatnet illustrates the desirability of using both plant macrofossils and pollen from sediments to minimise problems and deficiencies associated with either proxy (Birks and Birks 2000; Birks 2003). Few studies have utilized the full potential of both proxies from the region we study here. When analyses of proxy records are conducted separately by independent researchers it is simultaneously a way of validating results and of uncovering potentially erroneous identifications or other problems.

The two proxies reflect the vegetation at different scales. Pollen is expected to reflect regional and local vegetation. In environments with a generally low pollen production and for situations without modern analogues influx data are valuable for interpreting pollen data (Hättestrand et al. 2008 and references therein). Macrofossils are well known to reflect local vegetation in treeless (Ryvarden 1971, 1975; Glaser 1981) and in temperate environments (e.g. Wainman and Mathewes 1990), and even at patch scale in a lake (Zhao et al. 2006). However, in the Lusvatnet record pollen and macrofossil taxa follow each other surprisingly closely in terms of changing abundance and the timing of their appearance and disappearance (see for example *Saxifraga oppositifolia* and *Isoetes lacustris*, Fig. 3) at least during Allerød and YD. But pollen is nearly always present beyond the stratigraphic macrofossil occurrences. Most probably this concordance is due to the small closed catchment with steep slopes and the relatively small basin

size of southern Lusvatnet (Figs. 1, 2). When the basin size and catchment are small, the pollen source area decreases (e.g. Prentice 1985; Sugita 1994). The congruence between proxies is probably also improved by the high resolution analyses that were possible due to the high sedimentation rates as well as high influx of macrofossils at the coring site.

Pollen and macrofossil records from the same site complement each other. The lower taxonomic determinability of plant macrofossils improves inferences from pollen (e.g. Birks and Birks 2000) that can be vital for ecological interpretation, for example, *Salix* undiff. pollen in Lusvatnet. Ecologically important taxa not in the pollen record can be added such as *Saxifraga cespitosa*, *S. rivularis* and *Papaver* sect. *Scapiflora*. Modern surface samples show that herb taxa such as *S. cespitosa* are rarely represented as pollen although plants are present (Pardoe 2001). On the other hand, *Artemisia* and *Dryas octopetala* and many lowland species such as *Juniperus communis*, *Vaccinium*-type and trees other than *Betula* in Lusvatnet are present only in the pollen record providing valuable additional information to the plant macrofossil data.

At Lusvatnet macrofossils enhanced the reconstruction greatly during treeless situations whilst pollen contributed much to the reconstruction of forested environments. In treeless situations, such as the late-glacial, it is unwise to rely solely on pollen percentages due to the increased influence of long-distance transported pollen (Birks and Birks 2000). The Lusvatnet macrofossil record reveals the arctic flora as a species-rich community and it most probably represents the flora and vegetation well. On the other hand, after the establishment of *Betula* in the early Holocene at the transition to zone 5 (Fig. 3b), the macrofossil record reflects few, if any, changes in the terrestrial vegetation. In contrast, the pollen record shows variations in abundances and the regional invasions of different tree species such as *Alnus* and *Pinus*. The insensitivity of the macrofossil record in the early Holocene may be because macrofossils are deposited more easily into the lake in a treeless environment than in a situation with undergrowth and aquatic vegetation that filter the remains before they reach the deposition point (e.g. Birks 2001 and references therein). In addition macrofossil remains of thermophilous deciduous trees are often either hard to identify (bark, bud scales) or are easily broken down (leaves) (Birks 2003; Eide et al. 2006), adding to the probability that the species will not be represented in the macrofossil record although it was present in the catchment at the time. It is obvious that ecosystem reconstruction benefits from data on both plant macrofossils and pollen.

Macrofossils are produced in much smaller quantities than pollen, and for some species only a single seed was found in the core. Changes in the abundance of pollen may

reflect gradual changes, whereas many macrofossil changes often seem to be abrupt. They may reflect an abrupt change better than pollen, or abruptness might be an effect of taphonomy, as pollen also reflects regional changes in the lake catchment and beyond. The wider representation of many herbs as pollen is probably due to larger numbers and the wider pollen source area from where pollen is transported by wind and by water into a lake, whereas macrofossils are mostly derived from areas near the lake shore or from steep slopes by water transport.

The local presence of high pollen producers like tree-*Betula* is difficult to determine from pollen alone, especially as pollen of tree birch and *B. nana* are difficult to distinguish with precision. Figure 4 shows all *Betula* remains, enabling a more secure inference of when tree-*Betula* was locally present. In zones 1 and 2 a few macrofossils of *B. nana* and *B. pubescens* were found. Pollen percentages and influx rose slightly but are too low (<200 grains cm<sup>-2</sup> year<sup>-1</sup>) to indicate local presence (Seppä and Hicks 2006). However, near the tree-line pollen productivity may be reduced and therefore influx may be a poor guide to local presence as it can be below the expected values even though macrofossil remains are relatively abundant (Eide et al. 2006). The scattered macroremains may have been transported long-distance. Occasional fruits have been found in modern samples above the tree-line (Birks and Bjune 2010) and long-distance transport, in particular by wind blowing over ice and snow, of plant remains has been demonstrated (e.g. Ryvarden 1975). During zone 4 there is a large increase in *Betula* pollen percentages but there is no notable increase in influx values that remain well below the threshold for locally present birch. Only a few scattered macroremains were found. Modern surface samples have shown that when tree *Betula* is locally present it produces macrofossil remains, particularly fruits, in large amounts (Birks and Bjune 2010). Macrofossils and pollen influx rise rapidly and consistently at the transition to zone 5 (Fig. 4). This is the first point in the record (apart from the contamination comprising zone 3) where both proxies support the presence of tree-birch in the catchment.

#### Cold dry Allerød; cold and drier Younger Dryas

The late-glacial ice-core chronozones (Rasmussen et al. 2006) can be delimited at Lusvatnet using the age-depth model; the Allerød period, GI-1, c. 14000 to 12900 years B.P., coincides with lower biostratigraphic zone 1 (510–476 cm); the Younger Dryas period, GS-1, c. 12900–11650 years B.P., (476–345 cm), coincides with upper zone 1 and zone 2 (476–338 cm). Throughout, a similar floral assemblage is dominated by arctic-alpine herbs such as *Saxifraga cespitosa* and by *Salix polaris*, suggesting

rather small vegetational and environmental differences. Modern analogues are with vegetation growing in cold and arid conditions, such as on northern Norwegian mountains and on Svalbard. Reconstructed conditions in the adjacent Nordic Seas show extensive sea-ice cover during this whole period (Ślubowska-Woldengen et al. 2008).

If we go into more detail in the Lusvatnet record we see changes in the proportions of taxa in mid-zone 1, near the start of Younger Dryas. From c. 12700 cal B.P. snow-bed species started to decline whilst polar desert species such as *Papaver* and *Saxifraga cespitosa* are more numerous, indicating increased aridity and perhaps slightly lower temperatures. Maximum aridity continued from 12400 cal B.P. until c. 12260 cal B.P. (388 cm). The lack of cirque glacier activity in southern Andøya also reflects arid conditions (Paasche et al. 2007). However, lack of cirque glacier development has not been confirmed in the Lusvatnet catchment and Younger Dryas glacier activity is documented from several sites on the island (J. Bakke et al. field observations). After c. 12260 cal B.P. instability increased perhaps due to increased precipitation or melting of permafrost.

The other records from Andøya indicate that YD cooling was marked by a reduction in *Oxyria digyna* pollen percentages and influx (Vorren et al. 1988; Alm 1993). However, the radiocarbon dates for the period are rather uncertain, which makes detailed comparison difficult. Records from north of Andøya also suggest that there may not have been a large Younger Dryas cooling in northern Norway. In Troms, a pollen record was interpreted as showing that an *Artemisia-Saxifraga oppositifolia* pioneer vegetation during the Allerød and early part of YD was followed by a Cyperaceae–*Oxyria*–*Salix* phase, thought to indicate a cold, wetter, and less harsh mid Younger Dryas (Fimreite et al. 2001). This record has few dates and the exact timing of change during the YD is difficult to evaluate. At Jansvatnet near Hammerfest (70°N) aridity prevailed through the late glacial. Allerød vegetation was sparse and it became even sparser during the Younger Dryas (H.H. Birks et al. submitted). The floral assemblage was similar to but less diverse than that from Lusvatnet.

The presence of sea-ice through much of the year is probably the cause of the late-glacial aridity. A marine record from Andfjorden, adjacent to Andøya (Ebbesen and Hald 2004), shows that sea-surface temperatures decreased from c. 6°C in the Allerød to around 2–4°C during the early YD. In the SW Barents Sea (72°N) there was only a minor drop in summer sea surface temperature (SST) from 2 to 3°C during the Allerød to 1–3°C during the Younger Dryas (Chistyakova et al. 2010) and sea-ice cover remained extensive over the Nordic Seas throughout (Aagaard-Sørensen et al. 2010). Fresh melt-water input during the Allerød period led to the increased formation of sea-ice and increased albedo. Resulting lower temperatures and

anticyclonic conditions slowed the inflow of Atlantic water and blocked a moisture-carrying westerly airflow leading to low precipitation that resulted in aridity on the adjacent land. After c. 12000 cal B.P., SST fluctuated, showing a gradual rise up to the end of the YD (Ebbesen and Hald 2004).

This climatic situation at Andøya contrasts with that in southern Norway where records suggest major vegetation changes between the Allerød and Younger Dryas (AL–YD) time periods (e.g. Birks et al. 1994, 2005). South of 60°N Allerød sediments commonly contain *Betula* and *Salix* pollen whilst *Artemisia* and *Sedum* pollen were dominant in the Younger Dryas (e.g. Birks 1994; Karlsen 2009). Macrofossil records consistently show that tree-birch was absent and Allerød vegetation was dwarf-shrub heath with *Betula nana* or dominated by *Salix herbacea* (Birks 1993, 2003; van Dinter and Birks 1996). In mid-Norway, around 62°N the Allerød was also treeless. At the oceanic coast *Salix herbacea* was widespread with some *Empetrum* and *Juniperus communis* (Birks et al. 2000) whereas inland in the more continental inner fjord climate, dwarf-shrub heath with *Betula nana* predominated in the lowlands (Birks and van Dinter 2010). A temperature drop of about 2°C (Birks and Ammann 2000; Karlsen 2009) combined with plentiful winter precipitation (Larsen and Stalsberg 2004) was sufficient to cause the Younger Dryas ice-sheet to re-advance in mid-Norway and a cirque glacier to form at Kråkenes (Larsen et al. 1998).

#### Vegetation responses to early-Holocene warming

In Greenland ice-core records there is a gradual increase in temperatures from c. 11500 until around 10000 cal B.P. (Rasmussen et al. 2006). A gradual increase is also seen in SST reconstructions from the Nordic Seas (Hald et al. 2007). The vegetation at Lusvatnet immediately responded to the warming at the start of the Holocene (zone 4; 317 cm, 11520 cal B.P.) as can be clearly seen in the large increase in *Rumex acetosa*-type pollen. However, it took c. 450 years before *Empetrum-Vaccinium* heath developed, whereas on newly deglaciated moraines today the full development of dwarf-shrub heaths can take as little as 200 years (Matthews 1992). This suggests that the early Holocene climate was cool and soil development was slow. *Salix polaris* did not die out until c. 10900 cal B.P. At Kråkenes (62°N) (Birks and Birks 2008) dwarf-shrub heath development took a similar time as at Lusvatnet (370 years), suggesting the vegetation responses between sites were quite similar, and thus probably also the local climate development. It took c. 1,000 years after the start of the Holocene for *Betula pubescens* woodland establishment at Lusvatnet, which is slower than at Kråkenes where *Betula* arrived after c. 700 years. The delay at Lusvatnet could be

related to either a long migration lag or a slower succession rate in the arctic (Hodkinson et al. 2003; Robbins and Matthews 2010). During the Early Holocene, several cold oscillations have been recorded in Greenland ice (Rasmussen et al. 2007) and have also been documented in Lyngen (Bakke et al. 2005), near Andøya. At Lusvatnet there is no clear evidence of any response in the vegetation to cooler phases in the early Holocene.

#### Conclusions

- Pollen and plant macrofossil records follow each other very closely in the Lusvatnet sequence. Pollen contributes most to the understanding of the Holocene while plant macrofossils give a more detailed record of late-glacial species presences and abundances. Both proxies are needed to accurately reconstruct vegetation changes through the deglaciation.
- At Lusvatnet there is little difference in the Allerød and Younger Dryas floral assemblages and environments. Both periods are dominated by high arctic herbs and the climate was cold and dry.
- Changes in the abundances of the components of the late-glacial assemblage indicate that aridity increased during the Younger Dryas at 12690 and was most intense between 12450 and 12260 cal B.P.
- Oceanicity began to increase after 12260 cal B.P. and this continued through the early Holocene, related to the reduction in sea-ice cover and the movement north of the polar front. Temperature increased slowly after the start of Holocene, allowing the persistence of arctic-alpine taxa until 10900 cal B.P. Thereafter, oceanicity increased and dwarf-shrub heath expanded. Following the immigration of tree birch at c. 10520 cal B.P., open woodland developed similar to the vegetation today.
- Vegetation responses to climate changes through the deglaciation and into the Holocene differ between southern and northern Norway. In the north, the responses to the YD cold period are smaller and happen later than in southern Norway. The late-glacial vegetation at Lusvatnet was dominated by *Salix polaris* whereas in the south *S. herbacea* prevailed, reflecting the aridity in the north and the oceanicity (abundant snow-beds) in the south. Initiated at the Holocene transition, the vegetation succession from an arctic-alpine community to the formation of *Empetrum* dwarf-shrub heath to *Betula* woodland was slower in the north than in the south.

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