Vegetation responses to late-glacial climate changes in western Norway

Odpověď vegetace na pozdně glaciální klimatické změny v západním Norsku

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Dedicated to Kamil Rybníček and Eliška Rybníčková on the occasion of their 80th birthdays

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How fast can vegetation respond to rapid climate change? To answer this question, we require long-term vegetational data and an independent climate record. Both can be obtained from multi-proxy palaeoecological studies involving pollen analysis and plant macrofossil analysis (vegetational data) and chironomid analysis (climate record). Late-glacial climate changed rapidly and passed critical vegetation thresholds in western Norway. The interstadial (Allerød) vegetation at Kråkenes on the west coast was analogous to low- or mid-alpine vegetation in the west Norwegian mountains today. There was a marked vegetational response over ~10 years to the Younger Dryas cooling, even though mean July air temperature, as inferred from the independent fossil chironomid record, only decreased by about 2 °C. Together with the prevailing precipitation, this was sufficient to allow a cirque glacier to develop above Kråkenes Lake during the Younger Dryas. As summer temperatures increased rapidly at the opening of the Holocene, plants responded immediately. Warmth-intolerant arctic-alpines rapidly succumbed. Warmth-tolerant arctic-alpine species expanded until declining as a result of increasing competition. Successional processes proceeded through to damp and dry grassland, the development of tall-fern vegetation, and the expansion of *Empetrum*-dominated dwarf-shrub heath. Tree-birch *Betula pubescens* showed a migrational lag of ~500 years before forming birch woodland. This study illustrates how floristic and vegetational patterns recorded in sedimentary sequences can be interpreted in terms of ecological processes if an independent palaeoclimate record is available; here, from fossil chironomid assemblages from the same sediment core.

Keywords: Allerød, *Betula*, biotic responses, chironomid-inferred temperatures, climate impacts, early Holocene, extinction, Kråkenes, migrational lags, plant macrofossils, pollen, temperature, vegetation dynamics, Younger Dryas boundaries

Introduction

Ecologists are increasingly being asked how will species, vegetation, and ecosystems respond to future climate change, will certain species go extinct, will some species spread and migrate, and will vegetation change in the future into novel assemblages that do not exist today? Dawson et al. (2011) outline an integrated approach to assessing biodiversity responses to climate change. They discuss two main approaches – a mechanistic approach involving ecophysiological and population modelling and experimental manipulations;

and an empirical approach involving climate-envelope modelling, direct field observations and monitoring over time, and palaeoecological studies over a range of time scales. Based primarily on palaeoecological insights, Dawson et al. (2011) propose that there are four major modes of biotic response to climate change: toleration (= persistence through ecological plasticity), habitat shift, migration, and extinction.

High-resolution palaeoecological records can provide unique information on species and vegetation dynamics and their interactions with climate and other environmental changes on time scales from 10 to 10,000 years (Willis et al. 2010). However, to exploit the full potential of the palaeoecological records as a source of information about biotic responses to climate change, it is essential to have not only detailed high-resolution biological data ('responses') and associated reliable chronologies but also climate records ('predictors' or 'drivers') that are independent of the biological responses. Thus the familiar circularity can be avoided of using the biological data of interest to reconstruct the past environment and then using this environmental reconstruction to interpret the observed biological changes (Birks & Birks 1980).

Quaternary palaeoecology has undergone a major revolution in the last 20 years with a proliferation of new approaches and techniques for reconstructing different aspects of the past environment including climate (Flessa & Jackson 2005, Birks 2008). These developments include stable isotopes, organic biomarkers, inorganic geochemistry, new biological proxies such as chironomids, and improved numerical procedures for data analysis and sophisticated modelling techniques (e.g. Birks & Birks 2006, Ammann et al. 2007, Smol 2008, Birks et al. 2012, Jeffers et al. 2012). Thanks to these developments, it is now possible for palaeoecologists to attempt what Deevey (1969) proposed, namely "coaxing history to conduct experiments" and what Flessa & Jackson (2005) describe as "using the geological record as an ecological laboratory" and "understanding the biotic effects of future environmental change" by exploiting "the geological record of ecological dynamics".

This paper adopts a multi-proxy approach to consider species and vegetation responses to late-glacial climate changes in western Norway. It uses taxonomically detailed, fine-resolution pollen and plant macrofossil data with an associated detailed chronology as biological responses and mean July air temperatures inferred from fossil chironomid assemblages using modern chironomid-climate calibration functions as a predictor to interpret the late-glacial floristic and vegetation changes as responses to the rapidly changing late-glacial climate or as responses to biotic interactions. We are thus using the late-glacial as a 'natural experiment' to investigate biotic responses to rapid climate changes.

The summer temperature changes during the late glacial in western Norway were rapid (e.g. Birks & Ammann 2000, Birks et al. 2005a). After deglaciation around 14.7 years ago, a stable vegetation developed in the late-glacial interstadial which at the west coast was analogous to low- or mid-alpine vegetation in the west Norwegian mountains today (Kristiansen et al. 1988, Larsen et al. 1984, Birks 1993, 1994, Birks et al. 1994, Birks & Van Dinter 2010) within a mean July temperature range of 10–5 °C (Dahl 1986, Birks 1994). Rapid climate deterioration with a drop of about 2 °C in summer temperature marking the onset of the

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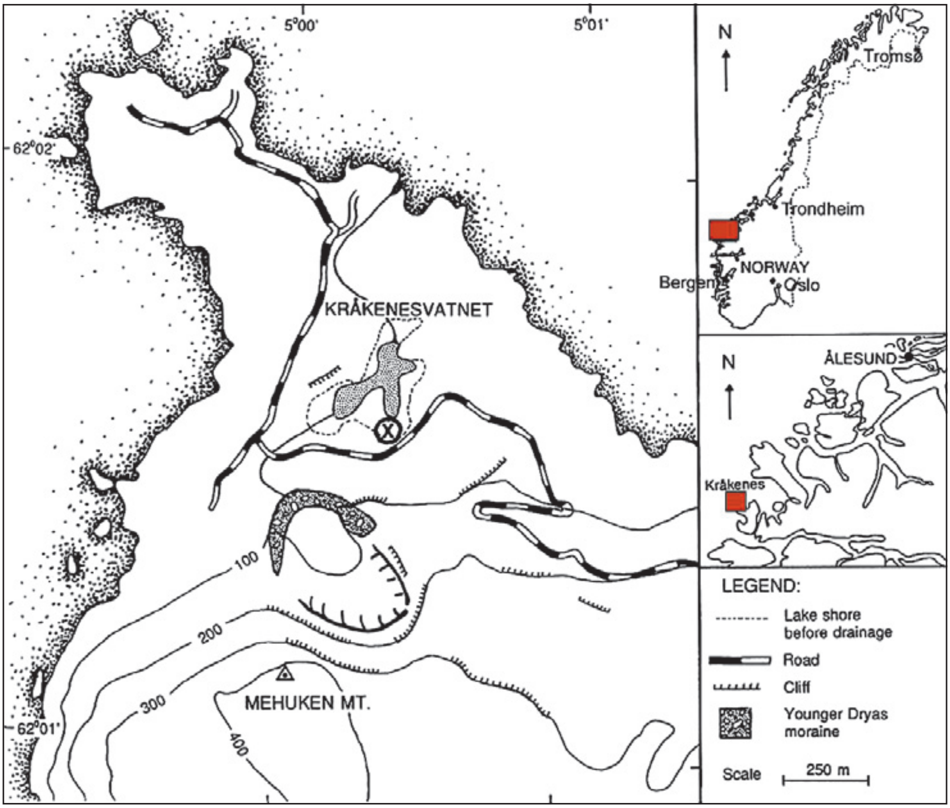
Fig. 1. – (A) Location map of Kråkenes Lake (Kråkenesvatnet) at the foot of Mehuken Mountain. Kråkenes is located on Vågsøy, south of Ålesund in western Norway. (B) Photograph of Kråkenes Lake from the top of Mehuken Mountain showing the Younger Dryas moraines round the cirque. Photo: John Birks. ▶▶

A


5°00'
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KRÅKENESVATNET
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100
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Bergen
Oslo
N
ÅLESUND
Kråkenes
LEGEND:
Lake shore before drainage
Road
Cliff
Younger Dryas moraine
Scale
250 m

B

Younger Dryas cold stadial resulted in the dramatic opening of the vegetation and the destruction of organic soils. The environment and vegetation at the coast then resembled that of the high-alpine zone in the west Norwegian mountains today with mean summer temperatures below 5 °C (Dahl 1986, Birks 1994). At Kråkenes (Fig. 1) a cirque glacier developed in the lake's catchment and glacial advances occurred throughout the region (Larsen et al. 1998). At the opening of the Holocene, glaciers retreated rapidly and the cirque glacier at Kråkenes melted away within about 5 years (e.g. Larsen & Mangerud 1981, Larsen & Stalsberg 2004). Vegetation developed rapidly, culminating in the development of birch woodland some 700 years after the start of the Holocene (Birks & Birks 2008).

The late-glacial and early-Holocene sediments in Kråkenes Lake have been studied in detail. The glacio-lacustrine sediments of the Younger Dryas are remarkable (Larsen & Stalsberg 2004). A high-resolution chronology is available through radiocarbon dates on terrestrial plant macrofossils and Holocene bulk sediment (Gulliksen et al. 1998, Lohne et al. 2013). Numerous analyses of biological proxies have been made, both plant and animal (Jonsgard & Birks 1995, Birks et al. 2000, Birks & Wright 2000a). These include high-resolution pollen and plant macrofossil analyses. The detailed pollen sequence across the Younger Dryas–Holocene boundary is discussed by Birks & Birks (2008). However, macrofossils complement pollen (Birks & Birks 2000). A consideration of the pollen records and macrofossil records together across the lower and upper boundaries of the Younger Dryas stadial will help us address the following questions: what was the vegetation like; how fast did species and vegetation respond to climate changes; what was the role of climate and environment in controlling the vegetation type; and what ecological processes were occurring under moderately stable climate regimes, particularly in the early Holocene. The high temporal resolution of the analyses makes it possible to compare durations of the ecological changes in the past with those of the present.

Methods

The background at Kråkenes Lake

Kråkenes Lake (62°02'N 5°00'E) lies at 38 m a.s.l. on the outer coast of the island of Vågsøy (Fig. 1A) fully exposed to Atlantic storms. It lies at the foot of Mehuken Mountain (438 m a.s.l.) (Fig. 1B) below a cirque that was occupied by a small glacier in the Younger Dryas (Larsen et al. 1984, Larsen & Stalsberg 2004). The sediments in the south-east basin were cored in 1992 with an 11 cm diameter piston corer from the marsh that had developed over exposed lake sediment after the water-level was lowered by 1 m about 100 years ago (Fig. 1A; Birks & Wright 2000b). The bedrock is acidic gabbro and gneiss (Boyle et al. 2013) and the present vegetation is species-poor wet grassland, acid heath, and bog, with a few *Betula* and *Corylus* shrubs growing in the shelter of rock outcrops and crags (Birks & Wright 2000b).

A detailed loss-on-ignition record of the sediments documents the balance between the organic productivity of the lake and its catchment against minerogenic inwash from the catchment. The latter increased when soils were unstable and was dominant during the time when the Younger Dryas cirque glacier was present. The lithostratigraphic and loss-on-ignition changes associated with the start and end of the Younger Dryas are well marked and have been taken to represent its lower and upper boundaries at Kråkenes (Gulliksen et al. 1998, Lohne et al. 2013).

The multi-proxy biostratigraphic analyses of the sediments included pollen and plant macrofossils and chironomids. Pollen results are presented by Birks et al. (2000) and Birks & Birks (2008), aquatic macrofossils by Birks (2000), and chironomids by Brooks & Birks (2000). Detailed terrestrial macrofossil results are unpublished. Rates of change in the proxies are presented by Birks et al. (2000). The botanical analyses were made at high resolution over the lower and upper boundaries of the Younger Dryas to detect fine-scale plant responses to changes in temperature registered by chironomids and loss-on-ignition.

Methods of pollen, macrofossil, and chironomid analyses are described in Birks & Birks (2008), Birks (2000), and Brooks & Birks (2000). Loss-on-ignition is weight loss as a percentage of dry weight after burning sediment for 6 hours at 550 °C. Pollen percentages on samples spanning 0.5 cm were calculated on the sum of terrestrial pollen and spores, which was usually 300–500 grains. Pollen and spore nomenclature and the taxonomic composition of the morphological types follow Ecological and Environmental Change Research Group (2012) except that *Capsella*-type (a small grain form of the *Sinapis*-type) here includes some taxa within *Sinapis*-type such as *Draba, Arabis,* and *Cochlearia*. The pollen sequences were zoned into statistically significant zones and subzones by optimal partitioning and comparison of the partitions with random expectation from a broken-stick model (Birks 2012). The macrofossil samples spanned 1 cm each. The sequences were zoned by eye. Diagrams were plotted on a calibrated age scale using the Tilia software (Grimm 1990).

The abundance of terrestrial plant macrofossils (TPM) (mainly *Salix herbacea* leaves) and the rapid rate of sediment accumulation allowed high-resolution radiocarbon dating of the late-glacial and earliest Holocene sequence. All 118 ^{14}C dates and the age-depth model derived from them are reported in Lohne et al. (2013). The lack of carbonate in the catchment bedrock and till allowed the high-resolution radiocarbon dating of bulk sediment later in the Holocene where TPM became too scarce (Gulliksen et al. 1998, Lohne et al. 2013). The dates on gyttja conform without reservoir effects to dates on TPM where the series overlap (Gulliksen et al. 1998, Lohne et al. 2013).

The mean July air-temperature reconstructions (Tjul) from the fossil chironomid data made from samples spanning 0.5 cm from the same core were made by weighted-averaging partial least-squares regression and calibration (WA-PLS) using a training set of 157 samples of modern chironomid assemblages in surface lake-sediments covering a mean July air temperature range of 3.5–16 °C in Norway and Svalbard (Brooks & Birks 2000, 2001, Heiri et al. 2011). The modern chironomid-July temperature model has a root mean square error of prediction (RMSEP) of 1.1 °C, as assessed by leave-one-out cross-validation (Brooks & Birks unpublished). Sample specific errors of reconstruction for every fossil sample were estimated by aggregated bootstrapping (Juggins & Birks 2012) (1000 cycles). These errors range from 1.1 to 1.4 °C depending on the composition of the chironomid fauna, the number of head capsules counted, and the degree of compositional similarity between the fossil and the modern chironomid assemblages. Although not at such high resolution as the botanical data, we use the chironomid-inferred mean July temperatures (Tjul) and their changes at the boundaries of the YD and during the early Holocene as an independent climatic record against which the observed botanical changes can be compared.

Results

The Allerød/Younger Dryas transition

The macrofossil and pollen data over the AL–YD transition are plotted on a calibrated age-scale in Figs 2 and 3. Note that the pollen sequence is from 927.5 to 919.5 cm depth. The macrofossil sequence is from 938 to 917 cm depth. The AL–YD boundary is defined by lithology and lies at 924.5 cm (12,710±52 cal. yr BP; Lohne et al. 2013). The corresponding pollen zone is placed at 924.25 cm (12,680 cal. yr BP) and the corresponding macrofossil zone boundary is placed at 924.5 cm. Before this boundary, there is a significant pollen-subzone boundary (AL-p a-b) at 925.75 cm (12,735 cal. yr BP) and a macrofossil subzone boundary (AL-m a-b) at 926.25 cm (12,750 cal. yr BP), reflecting changes in the assemblages some 25–40 years before the start of the Younger Dryas. In the pollen assemblage there are changes in the taxa typical of the Allerød. The macrofossil subzone boundary is placed at increases in *Oxyria digyna, Saxifraga rivularis*, and sclerotia of the soil fungus *Cenococcum geophilum* and the loss of *Daphnia* ephippia (Fig. 2). The pollen subzone boundary marks declines in *Betula* and the green alga *Pediastrum* and in *Juniperus* percentages some 10 years before, and rises in Poaceae, *Rumex acetosella*-type, *Oxyria digyna*, *Salix,* and indeterminable pollen and the appearance of *Sagina* (Fig. 3). Loss-on-ignition at 15–20% and chironomid-inferred July temperature (Tjul) values at about 10±1.1 °C are stable in both subzones.

At the start of the Younger Dryas pollen percentages of *Betula, Carex*-type, *Juniperus, Empetrum nigum, Filipendula, Rumex acetosa*-type*,* and *Pediastrum* decrease (Fig. 3). In contrast, percentages of *Salix* and herbs of open-ground and alpine habitats all increase. Macrofossil concentrations of *Salix, Luzula, Oxyria, Nitella*, and *Plumatella* decrease, whereas concentrations of arctic-alpine herbs characteristic of the YD increase or appear in the record. *Saxifraga cernua/S. rivularis, S. cespitosa, S. oppositifolia*, *Papaver* sect. *Scapiflora, Ranunculus glacialis*, *R. hyperboreus,* and *Koenigia islandica* are particularly characteristic of high-alpine habitats today. Chironomid-inferred Tjul decreases rapidly from 9.5±1.3 °C to a minimum of 7.5±1.4 °C over 50 years (1 °C per 25 years) after which the local cirque glacier became active. The mean reconstructed Tjul throughout the YD is around 7±1.2 °C. Loss-on-ignition decreases rapidly from about 20% in the late Allerød to 7% over 50 years and subsequently decreases to stable values between 2–3% during the presence of the glacier.

Younger Dryas / Holocene transition

The macrofossil and pollen results across the Younger Dryas–Holocene transition are plotted on a calibrated age scale in Figs 4 and 5. The lithological boundary is at 756.5 cm depth (11,546±59 cal. yr BP; Lohne et al. 2013). The corresponding pollen and macrofossil zone boundaries are also at 756.5 cm. However, both records have a zone boundary (YD 1–2) some 35 years before the end of the YD, at 762 cm (11,579 cal. yr BP) where significant changes occur in the pollen assemblage and obvious changes occur in the macrofossil assemblage. At this boundary macrofossils of *Draba*-type, *Saxifraga rivularis*, and *Cochlearia* (Fig. 4) and *Capsella*-type and *Sedum* pollen (Fig. 5) show marked declines whereas *Salix* and *Oxyria digyna* pollen and *Salix herbacea, S. polaris, Oxyria digyna,* and *Sagina intermedia*-type macrofossils all increase. Chironomid-inferred

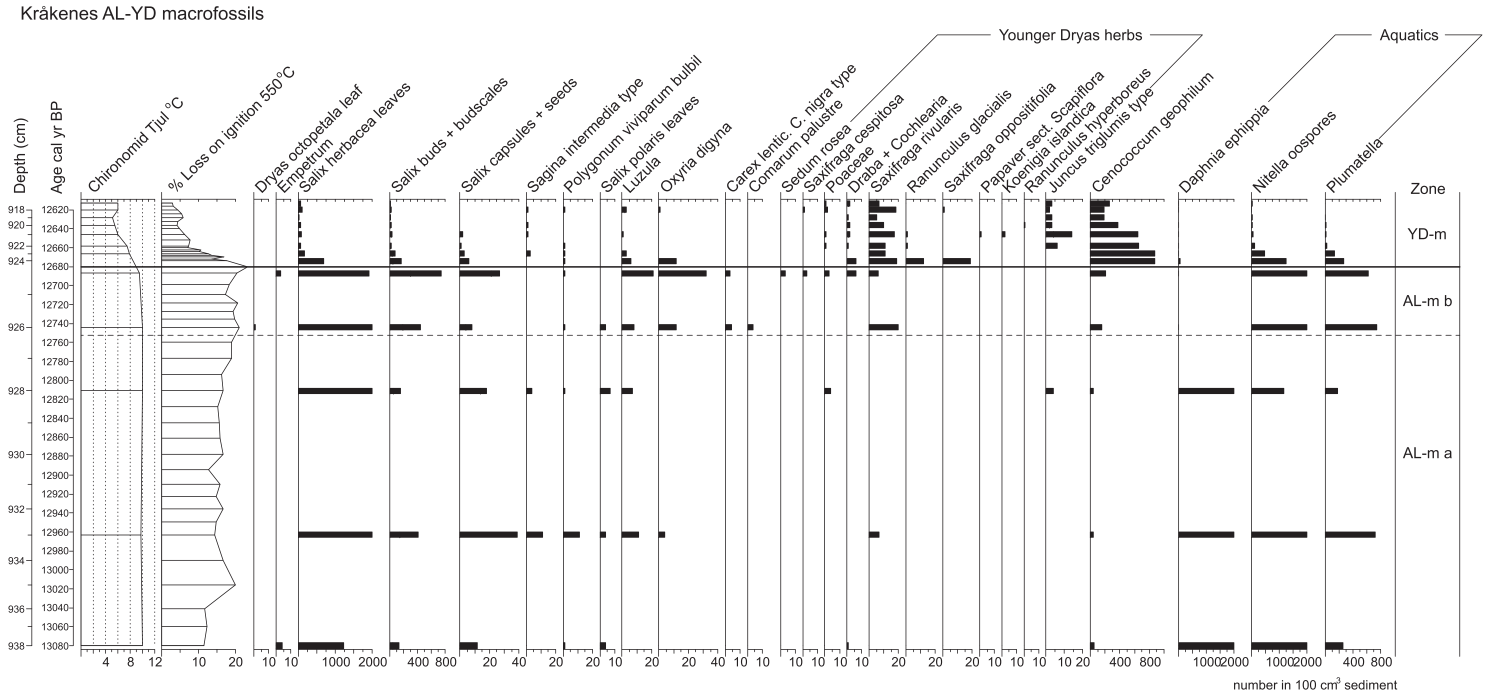

Fig. 2. – Macrofossil diagram across the Allerød–Younger Dryas (AL–YD) transition plotted on a calibrated age scale (years BP). Chironomid-inferred mean July temperatures (Tjul) are derived from Brooks & Birks (2000, 2001). Percentage loss-on-ignition of the sediment is plotted. The zones are placed by visual inspection and denoted by AL or YD and m (macrofossil). The AL–YD boundary is emphasized with a thick line. Values plotted as 2000 mean that the remains were extremely abundant and were not counted. Note the depth range is 917–938 cm. Herbs typical of the Younger Dryas and Aquatic organisms are grouped.

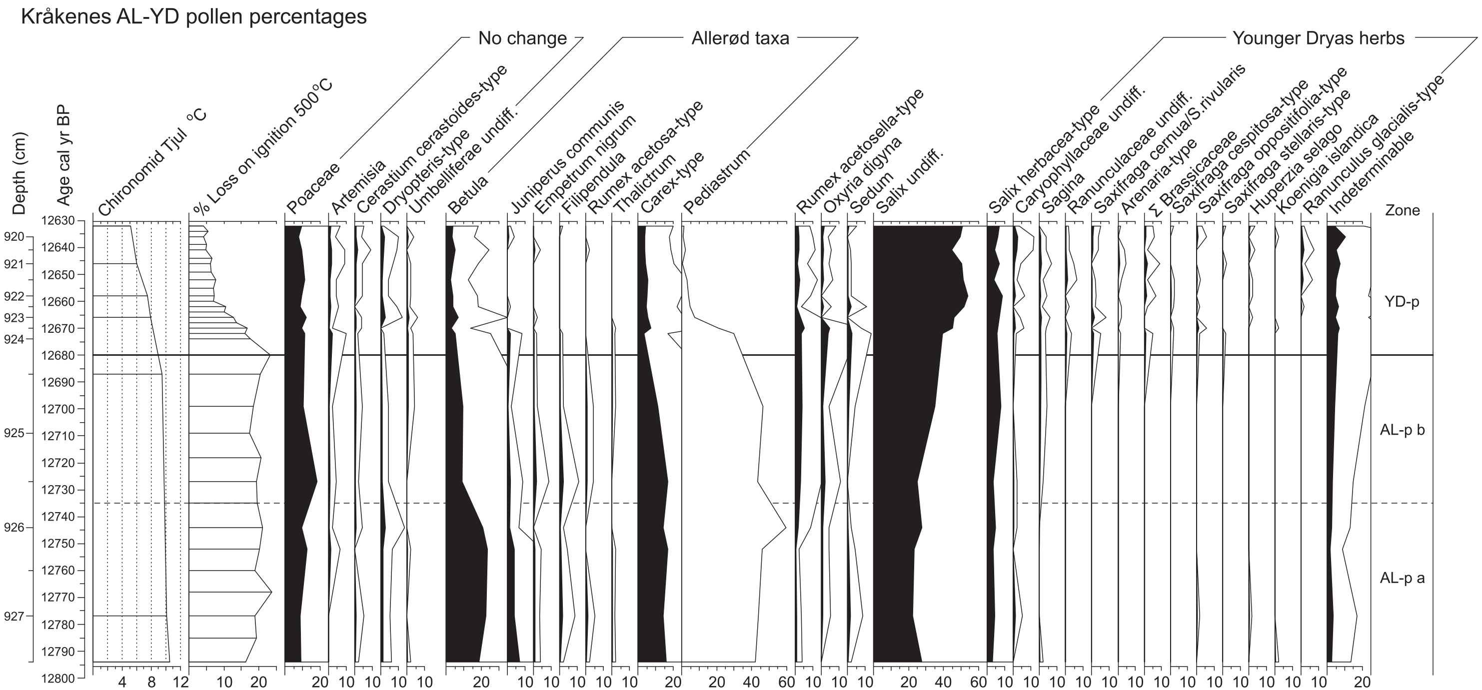

Fig. 3. – Pollen percentage diagram across the Allerød–Younger Dryas (AL–YD) transition plotted on a calibrated age scale (years BP). The curves are shown with x5 exaggeration. The pollen sum is terrestrial pollen and spores. *Pediastrum* values are sum pollen + sum *Pediastrum*. Undiff. = undifferentiated. Statistically significant zones and subzones are denoted by AL or YD and p (pollen). The AL–YD boundary is emphasized with a thick line. Chironomid-inferred mean July air temperatures (Tjul) are derived from Brooks & Birks (2000, 2001). Percentage loss-on-ignition of the sediment is plotted. The taxa are grouped into those that show no change across the boundary, those that are restricted to or are most abundant in the Allerød, and those that expand in the Younger Dryas.

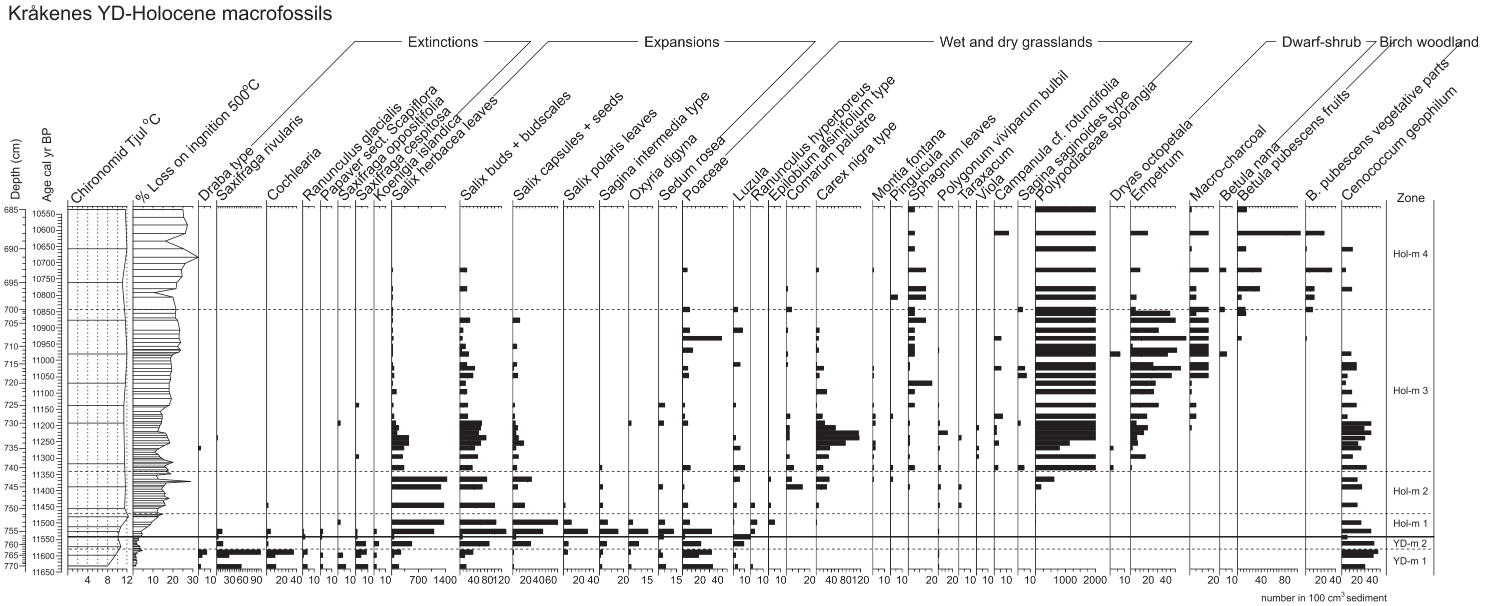

Fig. 4. – Macrofossil diagram across the Younger Dryas–Holocene (YD–Hol) transition plotted on a calibrated age scale (years BP). Chironomid-inferred mean July temperatures (Tjul) are derived from Brooks & Birks (2000, 2001). Percentage loss-on-ignition of the sediment is plotted. The zones are placed by visual inspection and denoted by YD or Hol and m (macrofossil). The YD–Hol boundary is emphasized with a thick line. Values plotted as 2000 mean that the remains were extremely abundant and were not counted. The taxa are grouped into those that become locally extinct at the YD–Hol boundary (Extinctions), those that briefly expand before decreasing (Expansions), and those characteristic of wet and dry grasslands, dwarf-shrub heath, and birch woodland.

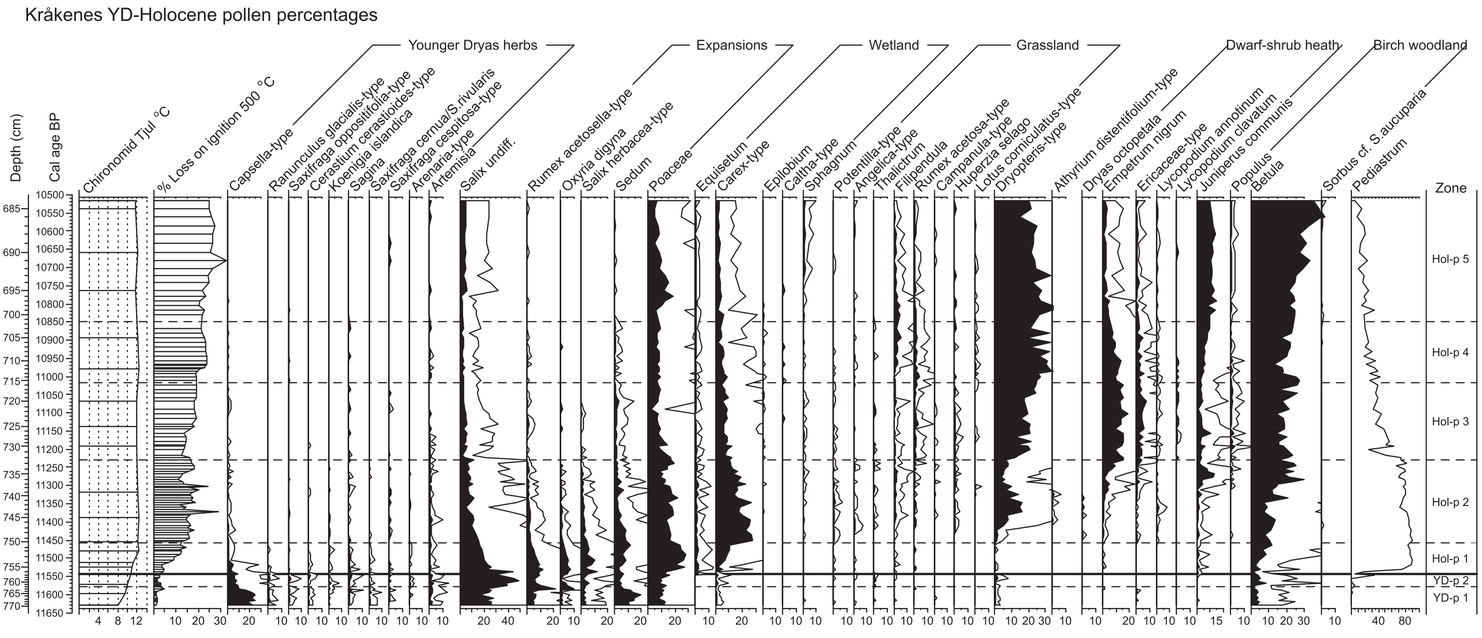

Fig. 5. – Pollen percentage diagram across the Younger Dryas–Holocene (YD–Hol) transition plotted on a calibrated age scale (years BP). The curves are shown with x5 exaggeration. The pollen sum is terrestrial pollen and spores. *Pediastrum* values are sum pollen + sum *Pediastrum*. Statistically significant zones are denoted by YD or Hol and p (pollen). The YD–Hol boundary is emphasized with a thick line. Chironomid-inferred mean July temperatures (Tjul) are derived from Brooks & Birks (2000, 2001). Percentage loss-on-ignition of the sediment is plotted. Undiff. = undifferentiated. The taxa are grouped into those characteristic of the YD (Younger Dryas herbs), those that show a brief expansion at the Holocene boundary (Expansions), and those characteristic of wetland, grassland, dwarf-shrub heath, and birch woodland.

Tjul rises from ~8 to 10 °C in zone YD p/m 1 (11,630–11,579 cal. yr BP) at a rate of 1 °C per 25 years and from 10 to 11 °C in zone YD p/m 2 (11,579–11,547 cal. yr BP) at a rate of 1 °C per 37 years. Loss-on-ignition remains around 2% with a small peak of ~4% at the YD 1–2 boundary.

The Younger Dryas–Holocene boundary is well marked by pollen decreases in *Capsella*-type, *Salix* undiff., many other arctic-alpine taxa, and indeterminable pollen, and increases in *Rumex acetosella*-type, *Oxyria digyna, Salix herbacea*-type*, Sedum,* Poaceae, *Equisetum*, and *Carex*-type, together with a massive increase in *Pediastrum* (Fig. 5). *Salix herbacea*-type and *Sedum* do not decrease here, but later at the end of zone Hol-p 1. The boundary is well marked in the macrofossil record (Fig. 4) by decreases and subsequent local extinctions (Extinctions on Fig. 4) of *Saxifraga rivularis, S. cespitosa, S. oppositifolia, Cochlearia, Ranunculus glacialis*, *Papaver* sect. *Scapiflora,* and *Koenigia islandica* and substantial increases (Expansions on Fig. 4) in *Salix herbacea, S. polaris, Sagina intermedia*-type, *Oxyria digyna,* and *Sedum rosea*. Loss-on-ignition values start to rise at the zone boundary. Chironomid temperatures increase by 1 °C over the first 60 years of the Holocene to ~12±1.1 °C at 752cm (11,485 cal. yr BP), after which they remain remarkably constant around 11.5–12 °C. Present-day mean July temperature at Kråkenes is 12.6 °C (Birks & Wright 2000b).

At 750 cm (11,460 cal. yr BP), both pollen and macrofossil records show decreases in all the arctic-alpine taxa that had persisted or increased in zone Hol-p/m 1, except for *Salix herbacea* leaves (Fig. 4). These continue to occur at high values, corresponding to the maintained values of *S. herbacea*-type and *Salix* undiff. pollen. The next major changes in the pollen diagram (Fig. 5) are at 732 cm (zone Hol-p 2–3) (11,220 cal. yr BP), whereas marked changes in the macrofossil record (Fig. 4) are earlier at 741 cm (zone Hol-m 2–3) (11,340 cal. yr BP). At this point, macrofossils of *S. herbacea* sharply decrease and Polypodiaceae sporangia increase, accompanied by wet and dry grassland taxa and the start of the *Empetrum* record. During zone Hol-p 2, *Carex*-type increases together with pollen of tall herbs and spores of tall ferns (Fig. 5). A peak in *Dryopteris*-type spores is associated with the occurrence of *Athyrium distentifolium*-type. Around 740 cm (Hol-p 3) *Empetrum* pollen becomes abundant, and together with *Juniperus communis* and *Betula* pollen, dominates zone Hol-p 4. A rather ill-defined zone Hol-p 5 starts at 702 cm (10,860 cal. yr BP) where *Betula* percentages exceed 25% (Fig. 5). However, this corresponds to the start of a well-marked macrofossil zone (Hol-m 4) (701 cm, 10,844 cal. yr BP) where *B. pubescens* macrofossils increase and *Empetrum* and grassland taxa decrease (Fig. 4).

Discussion

Responses before the Allerød-YD boundary (13,000–12,710 cal. yr BP, subzones AL a-b)

Allerød chironomid-inferred Tjul are around 10±1.1 °C, but start to decrease at the end of zone AL b. In contrast, loss-on-ignition values remain constant during the Allerød, around 20%. *Salix herbacea* dominates the Allerød, together with *S. polaris*, and a little *Empetrum*, some grassland taxa, and taxa of open ground such as *Sagina intermedia*-type in subzone AL-m b. The pollen assemblage accords with this, with high percentages of *Salix* pollen, some *Empetrum* and *Juniperus,* some tall herbs and grassland taxa, and open-ground taxa such as *Oxyria digyna* and *Sedum*. The assemblage suggests an analogy with closed low- or mid-alpine vegetation in the west Norwegian mountains today with widespread snow-beds lasting well into summer and wet areas of snow-melt (Fig. 6). The lake ecosystem was stable but at an immature stage, with assemblages dominated by *Nitella*, an abundance of *Pediastrum*, and invertebrates tolerant of cool water, such as *Plumatella,* and *Daphnia* (see Birks 2000). *Betula* percentages are relatively high at 20% in subzone AL-p a, but tree-birch macrofossils were absent (Van Dinter & Birks 1996, Birks 2003). Alpine tundra vegetation has low pollen productivity, so long-distance transported *Betula* pollen, probably from southern Scandinavia and the British Isles, is not masked (Birks 1993). The situation was similar to that on Spitsbergen today (Hyvärinen 1970, Van der Knaap 1987) where *Betula* pollen can reach 50%. In such situations, pollen influx gives a better idea of the abundance of *Betula*. The Allerød influx at Kråkenes is extremely low, less than 100 grains $cm^{-2}\cdot yr^{-1}$ (Birks et al. 2000).

Small changes occur in subzone AL b. *Betula* pollen percentages decreased about 70 years before the start of the YD implying that distant birch woodlands were reduced or that spring wind direction had changed. *Juniperus* pollen, probably locally produced, also decreased implying that *Juniperus* shrubs either decreased or their pollen production was reduced by more severe environmental conditions. Both pollen and macrofossils of *Oxyria digyna* increased and the abrupt increase in *Saxifraga rivularis* seeds suggests that snow-meltwater habitats expanded. At the same time, the arrival of increased amounts of *Cenococcum* sclerotia into the lake suggests that soil was becoming destabilized. It is likely that there was a small deterioration in climate, with a decrease in Tjul starting before the major change at the start of the Younger Dryas and possibly an increase in precipitation. Previously continuous vegetation began to be disturbed, allowing open-ground taxa to increase. Open conditions and summer rivulets would have allowed seeds of snow-melt taxa such as *Saxifraga rivularis* to be washed into the lake. It is likely that the AL vegetation was near an ecotone and small environmental changes made a marked ecological impact upon it, particularly in terms of soil stability and increased snow meltwater.

Responses at the Allerød-Younger Dryas transition (12,710±52 cal. yr BP, 924.5 cm)

The lithological boundary at 924.5 cm, where brown silty gyttja is abruptly replaced by grey silt, is the start of the Younger Dryas according to Lohne et al. (2013). They conclude that the transition into the YD took 30 years. The loss-on-ignition values fell rapidly, from ~20% to 7% at 922 cm (over 50 years) and to 2–3% or less as the glacier developed in the catchment.

The pollen-zone boundary is placed at 924.25 cm (Fig. 3) and the macrofossil-zone boundary at 924.5 cm (Fig. 2). These small differences may be a result of different sampling intensity in the botanical records (see Liu et al. 2012). Marked assemblage changes occur in both records. The dramatic declines of *Pediastrum, Nitella,* and *Plumatella* indicate that limnic conditions had become too extreme for their survival. A similar response is shown by other aquatic organisms (Birks 2000), as the water became too cold and turbid to support life. In contrast, percentages of *Salix* pollen increased and pollen of many taxa characteristic of high-alpine or arctic vegetation appeared and persisted in continuous amounts during the YD. Indeterminable pollen, especially degraded and broken pollen, also increased, as the periglacial conditions presumably damaged it mechanically on its way to the lake sediments. The macrofossil record shows a large reduction in *Salix*

Fig. 6. – A modern analogue for the Allerød landscape from the mid-alpine zone in the west Norwegian mountains. Dry rocky slopes bear sparse dwarf-shrub heath. Widespread snow-beds dominated by *Salix herbacea* release melt-water. Irrigated ground supports willow shrubs, grasses, and herbs. Photo: John Birks. ▸▸

Fig. 7. – A modern analogue for the Younger Dryas landscape from the high-alpine zone in the west Norwegian mountains. Extensive snow-beds are dominated by *Salix herbacea*. Open, frost-disturbed rocky ground and extensive open ground irrigated by melt-water are occupied by alpine herbs. A glacier is in the background. Photo: John Birks.

herbacea and associated *Salix* remains, the disappearance of dwarf shrubs and grassland taxa, and the appearance of high-alpine or arctic taxa characteristic of the YD.

These changes suggest that there was a rapid destruction of the Allerød vegetation at Kråkenes from one sample to the next, i.e. over about 30 years. The previous vegetation was destroyed and plants of cold open habitats expanded. The *S. herbacea* mats were disrupted and more temperate dwarf-shrubs and herbs became locally extinct. The opening of the vegetation allowed Allerød soil to be washed into the lake, as witnessed by the large increase in *Cenococcum* sclerotia. *Salix* influx values (Birks et al. 2000) peaked at the zone boundary as pollen from soils was washed into the lake, but then fell to low values. The increased pollen percentages of *Salix* are a result of the very low pollen production of the high-alpine vegetation, as its influx is extremely low in the YD. Taxa such as *Saxifraga rivularis, S. stellaris*-type, *Cochlearia, Ranunculus hyperboreus, Juncus triglumis*-type, and *Koenigia islandica* are typical of snow-meltwater flushes. Other taxa such as *Papaver* sect. *Scapiflora, Saxifraga cespitosa, S. oppositifolia, Huperzia selago*, and *Luzula spicata* grow on well-drained dry gravelly soils, whereas *Ranunculus glacialis, Sedum*, and *Oxyria digyna* prefer damper situations. This mosaic of communities is typical of high-alpine vegetation in western Norway today, especially on moraines and gelifluccted substrates (Fig. 7). The decrease in *Betula* pollen percentages to around 5% at Kråkenes reflects the widespread reduction of birch woodland across northern Europe in the YD. The switch to high-alpine vegetation was extremely rapid (maximum of 30 years). Chironomid-inferred temperatures fell from most probable values of 9.4 °C at the boundary to 7.9 °C in 45 years at 923 cm (1 °C in 30 years) and further to 5 °C in the next 40 years (919 cm) (1 °C in ~15 years). This extremely rapid and severe summer temperature reduction, probably leading to prolonged snow-lie, gelifluction, and permafrost development, caused the rapid response. Conditions probably became analogous to those at the outer coast of Spitsbergen today, where mean July temperatures are around 4–5 °C and vegetation is discontinuous (Birks et al. 2004).

Responses just before the Younger Dryas-Holocene transition (11,580 cal. yr BP, 762 cm)

There are pollen- and macrofossil-zone boundaries at this level, between YD 1 and 2 (Figs 4 and 5). Loss-on-ignition shows a small peak of 4.8% and chironomid-inferred Tjul increased to about 10±1.1 °C. The marked decrease in *Capsella*-type pollen and the con-specific *Cochlearia* macrofossils, together with decreases in *Sedum* pollen percentages and *Saxifraga rivularis* macrofossils and the disappearance of *Draba*-type macrofossils suggest that aspects of the high-alpine vegetation mosaic decreased, possibly due to warming and to less snow-cover. However, other high-alpine taxa continued to be present in zones YD 1 and YD 2, and *Salix* pollen (*S. herbacea* macrofossils) in particular increased. It seems that the warmer summers allowed the vegetation to become denser and more stable, and for *S. herbacea* to become dominant in vegetation analogous to the mid-alpine zone vegetation in western Norway today (Dahl 1986). Zone YD 2 is very short (some 35 years) and probably corresponds with the final melting phase of the cirque glacier that deposited a 3 cm band of unlaminated silt just before the end of the YD (Gulliksen et al. 1998, Lohne et al. 2013). The sensitivity of the vegetation to a rapid 2 °C increase in temperature is remarkable. Temperature was the overall factor controlling vegetation composition and at Tjul of 10 °C the local vegetation was beyond the ecotonal limit for the open, unstable YD vegetation, which was analogous to high-alpine vegetation in the Norwegian mountains today, occurring below summer temperatures of 5 °C (Dahl 1986, Birks 1994).

Responses at the Younger Dryas-Holocene transition (11,546±59 cal. yr BP, 756.5 cm)

This level is the lithostratigraphic and chronological end of the Younger Dryas at Kråkenes (Lohne et al. 2013). Glacio-lacustrine sediments were replaced by lake gyttja with decreasing amounts of silt and increasing amounts of organic matter, as reflected in the loss-on-ignition curve. High values correspond to layers of *Salix herbacea* leaves. Chironomid-inferred Tjul is around 10±1.3 °C in zone YD 2. It increased rapidly to ~11±1.1 °C by 754 cm, over ~35 years, and reached 12±1.1 °C by 752 cm, some 25 years later (~11,485 cal. yr BP). This is a remarkably rapid temperature rise of 2 °C over 55 years. Subsequently, reconstructed Tjul stayed constant through the rest of the early Holocene. Loss-on-ignition also increased from 2 to 10% over the first 50 years of the Holocene and then reached average values fluctuating around 15% until a renewed increase at 712 cm to 25–30%.

The vegetation response is rapid and fascinating (Figs 4 and 5). High percentages of *Salix* pollen are replaced by increased Poaceae percentages. Pollen of arctic-alpine taxa and *Artemisia* became sparse, except for *Oxyria digyna, S. herbacea*-type, and *Sedum*, which increased and remain at higher values. This pattern is seen much more clearly in the macrofossil record. The increase in *S. herbacea* leaves is dramatic. Although many arctic-alpine herbs declined and abruptly disappeared from the record, remains of *S. polaris, Oxyria digyna,* and *Sedum rosea* all increased markedly over a period of 50 years before decreasing to low levels or disappearing after 40 years (11,485 cal. yr BP). These taxa are tolerant of warm temperatures (Dahl 1951, 1998) and, except for *Salix polaris,* can be found at low elevations in western Norway today, in open habitats, such as sea cliffs and coastal rocks. The increase in temperature at Kråkenes allowed them to increase in abundance and density and perhaps colonise newly formed habitats over a very short time while competition was still low. Poaceae seeds remained abundant during this period, but then rapidly decreased with other high-alpine taxa. This suggests that these seeds were derived from alpine grasses, perhaps such as *Phippsia*. In contrast, Poaceae pollen percentages increased during zone Hol-p 1, suggesting that some grasses with higher pollen production expanded with increased temperature. Unfortunately, the identification of Poaceae pollen and fruits is difficult below family level. The high-alpine taxa (e.g. *Koenigia*) that decreased at the boundary are physiologically sensitive to higher temperatures (e.g. Dahl 1963, 1998) and are not generally found growing at low elevations. It would seem that summer temperatures of 10 °C were too high for their growth and survival. Responses in the lake ecosystem were also immediate at the YD–Holocene boundary, as exemplified by the sharp increase in *Pediastrum* percentages (see Birks 2000) and during the early Holocene a fascinating aquatic succession occurred (Birks 2000, Birks et al. 2000, Birks & Wright 2000a).

Vegetation succession in the early Holocene

Chironomid-inferred temperatures remained constant after 11,460 cal. yr BP at Kråkenes. The available sample resolution is unable to reflect any fine-scale changes related to the early Holocene instabilities detected in other parts of Europe. It is also possible that the biota of western Norway may have been insensitive to these changes as they are not obvious in other biological records from the region. Any changes in vegetation were presumably no longer driven by temperature changes but were controlled by other ecosystem processes. After their expansion in zone Hol 1, the warm-temperature-tolerant alpines decreased in the macrofossil record (Fig. 4). Scattered occurrences of macrofossils and pollen are probably derived from plants growing at higher altitudes on Mehuken Mountain in the craggy cirque behind the lake. *Salix herbacea* and *Saxifraga aizoides* still grow on the mountain today and *Sedum rosea* and *Saxifraga oppositifolia* occur nearby on coastal cliffs.

Betula pollen percentages rose in zone Hol-p 1 to about 10%. Presumably, *Betula* trees were spreading once more in northern Europe and south Scandinavia. Influx values are less than 500 grains $cm^{-2}\cdot yr^{-1}$ (Birks et al. 2000) and birch trees were not close to Kråkenes.

Over the next 700 years, the early-Holocene vegetation succession proceeded. Grasslands and flushes, analogous to low- or mid-alpine grasslands and flushes found in western Norway today, replaced the open vegetation of the earliest Holocene, showing that late-lying snow cover had decreased. *Salix herbacea* continued to play a prominent role until its decrease at about 740 cm (11,330 cal. yr BP). Vegetation composition was changed by local expansion of key competitive species, for example tall ferns arrived and expanded to high values by about 11,330 cal. yr BP. The presence of *Athyrium distentifolium*-type spores between 743 and 735 cm (zone Hol-p 2) corresponds with a peak in *Dryopteris*-type spores, suggesting that the first tall fern to expand may have been *A. distentifolium*, a species characteristic of bouldery ground in the low- or mid-alpine zone today. The continued abundance of *Dryopteris*-type sporangia and spores indicates that other tall species colonized, probably *Dryopteris* spp. and *Athyrium felix-femina* that are characteristic of western low-alpine shrub and sub-alpine birch vegetation today. They are often associated with shrub-willows such as *S. glauca*. These willows are represented by continuous low percentages of *Salix* pollen after 11,230 cal. yr BP. Their diagnostic leaves are easily destroyed, but their presence may be indicated by the continued occurrence of other vegetative remains and seeds.

At 736 cm, *Empetrum* colonized the grassland and its pollen reached high values by 733 cm (11,240 cal. yr BP). Its macrofossil remains continued to increase, reaching their maximum abundance by 718 cm (11,050 cal. yr BP). Well-drained substrates must have become sufficiently dry for *Empetrum* to expand and form dwarf-shrub heath. Interestingly, macro-charcoal remains follow the increase of *Empetrum* macrofossils (Fig. 4), suggesting that the climate was dry enough, probably in spring, for natural burning to occur. Thus the climate may have been more continental than it is at present, although we have no means of reliably reconstructing winter temperatures. *Dryas octopetala* is a rare component of the dwarf-shrub heath, rather unexpectedly considering the acid nature of the local bedrock. *Campanula* (*rotundifolia*) may also have grown in drier open ground. However, *Betula nana* seems to have been very rare, with only a few macrofossils being recorded at around 10,800 cal. yr BP. In contrast, it was extremely common in the inner fjord areas during both the Allerød and early Holocene (Birks & Van Dinter 2010). Today it grows near Kråkenes, but on soils with decimetres of accumulated humified peat on the south flanks of Mehuken Mountain. *Juniperus communis* accompanied *Empetrum* in the heaths. However, its pollen percentages increased considerably after the establishment of birch woodland, suggesting that it became a major component of this vegetation. The occurrence of *Populus* (*tremula*) pollen suggests that it grew as low shrubs or small trees in the *Empetrum* vegetation, perhaps in more sheltered rocky areas. However, its percentages decreased after the expansion of tree birch. Pollen production and dispersal may have been reduced by a tree-birch canopy or plants may have been eliminated by competition. Damper soils were also present around Kråkenes Lake, as shown by the continued high abundance of tall ferns associated with shrub-willows and pollen of tall herbs such as *Angelica*-type, *Filipendula*, and *Rumex acetosa* and macrofossils of *Carex* spp. and *Sphagnum*.

The first record of *Betula pubescens* macrofossils is at 708 cm (10,930±98 cal. yr BP; 2σ range 11,026–10,829), after which macrofossils show that tree-birch became well established by 702 cm (10,850 cal. yr BP) and expanded at 698 cm (10,800 cal. yr BP) to form open birch woodland. As a consequence, *Empetrum* decreased, particularly in the macrofossil record, indicating that although it probably remained as an understorey plant, its remains were no longer easily transported into the lake sediments. At this point, macro-charcoal also becomes rare (Fig. 4), suggesting that birch woodland was not flammable or that the climate had become wetter. The records of tall ferns and shrub willows (*Salix* pollen) do not change after the establishment of tree-birch, suggesting that birch could not compete with them or survive on the wet soils they occupied. However, tall ferns probably became dominant in the woodland understorey, as they are today in western Norway, where such vegetation is very typical of damp, mesotrophic sloping conditions. The pollen record of *Betula* is continuous throughout the profile. Percentages were very low in the YD, but gradually increased after the Holocene boundary to around 20% at 735 cm. They increased further at about 700 cm reaching 35–40% at the top of our profile (10,500 cal. yr BP). It is difficult to discern the local arrival of *B. pubescens* from the pollen record, but the macrofossil record is clear. The first tree-birch fruit was recorded at 708 cm and the record became continuous after 702 cm (10,850 cal. yr BP). Birch fruits are well dispersed and can be found above the treeline in trap samples (Birks & Bjune 2010), so the first fruit may have arrived by long-distance dispersal. However, the continuous record implies that birch was present near the lake and this corresponds with zone Hol-p 5 where *Betula* pollen percentages exceed 25% and its influx exceeds 1500 grains $\mathrm{cm}^{-2}\cdot\mathrm{yr}^{-1}$ (Birks et al. 2000).

From the start of the Holocene, flush and mire vegetation occurred round the lake. The *Saxifraga rivularis*-dominated flushes with *Koenigia islandica* were replaced firstly by montane taxa *Ranunculus hyperboreus* and *Epilobium alsinifolium*-type followed by *Montia fontana* with *Pinguicula*. Evidence of mires at the lake margin is provided by varying amounts of *Comarum palustre, Carex nigra*-type, and *Equisetum*. Gradual acidification of the catchment is illustrated by the increase in *Sphagnum* leaves. However, this process is more clearly reflected by biotic and geochemical responses in the lake ecosystem (Birks et al. 2000, Bradshaw et al. 2000, Boyle et al. 2013).

Ecological processes during the early Holocene

The ecological processes leading up to birch woodland establishment after Tjul had stabilized at ~11.5 °C depended on immigration and establishment of the relevant taxa. Most of these arrived very soon after the start of the Holocene, illustrating the rapid dispersal abilities of most species in the early Holocene of western Norway. It is possible that *Empetrum* did not arrive until ~11,270 cal. yr BP. It is dispersed by birds and mammals, which may not have been attracted to the site until food and habitats were available for them. Although temperatures had exceeded its minimum requirements of about 11 °C by 11,500 cal. yr BP (Odland 1996) and ecological conditions were favourable for its establishment, *Betula pubescens* did not become established until about 700 years after the start of the Holocene (Birks & Birks 2008) and expanded to form woodland some 70 years later, within the population doubling time of *B. pubescens*. *B. pubescens* was not present in western Norway during the Allerød or YD (Birks 2003, Birks et al. 2005b) but survived in mainland Europe and the British Isles (Birks 2003). Although its fruits are well dispersed by wind, it took about 700 years after the Holocene temperature rise for it to spread from these distant refugia. A Tjul of 11 °C is at its lower limit for growth in western Norway, so the northwards expansion of the tree-line was slow (Birks et al. 2005a). On freshly deglaciated terrain in Norway today where *B. pubescens* is present on the surrounding hill slopes, succession to birch woodland takes about 200 years (e.g. Matthews 1992, Vetaas 1994, Birks & Birks 2008). Therefore, the likely delay due to migration at Kråkenes was about 500 years. It may be postulated that tree birch colonized as small populations during the Allerød and persisted into the early Holocene. If so, the delay in establishment is more difficult to explain, and when evidence of mean summer temperature and the environment implicated by the rest of the fossil assemblage is considered, this hypothesis is most unlikely (Birks 1994, 2003, Birks et al. 2005b). A comparison of pollen and macrofossil records of *Betula* spp in western Norway also does not support this hypothesis (Van Dinter & Birks 1996). Other hypotheses such as fire and no-analogue climates are discussed by Birks & Birks (2008).

Other ecological processes in the early Holocene involve local extinction, competition, soil development, and succession. The Tjul increase above 10 °C at the start of the Holocene caused the local extinction of several warmth-intolerant arctic-alpine taxa. Soon afterwards, competition from grassland species and the closure of vegetation restricted those taxa that were tolerant of warmer temperatures but not of competition. Competition and succession continued to act as dwarf-shrub heath and tall fern–willow vegetation replaced grasslands, and then tree-birch shaded out dwarf-shrub heath on drier soils. Soil became gradually stabilized, as shown by the gradual decrease in *Cenococcum* sclerotia. In the nutrient-poor catchment, weathered-out nutrients were sequestered in biomass and soil humus or leached and conditions similar to those of today were rapidly reached. Depletion of base cations and accumulation of acid humus is not easy to detect from the terrestrial record, but it is apparent in the aquatic records, both biological (Birks 2000, Bradshaw et al. 2000) and sedimentological (Boyle et al. 2013). The interaction of all these processes controlled vegetation succession until eventual stabilization when open birch woodland on acid soils with a dwarf-shrub heath understorey developed on dry soil and tall ferns and willows occupied damp soil.

The late-glacial and early-Holocene vegetation at Kråkenes reflected the interplay of climate (mean July temperature), immigration, expansion, local extinction, soil development, competition, and succession. Rates of vegetational change in response to temperature changes at the YD boundaries were very fast. Plants responded within about 50 years or less at the boundaries of the YD; previous vegetation was eliminated and new vegetation types were initiated. Usually the species were in common, but the structure and relative composition of the communities changed; the *Salix herbacea* mats were destroyed at the start of the YD, but *S. herbacea* and most of the Allerød taxa persisted through the YD. Likewise at the start of the Holocene, several arctic-alpine taxa were eliminated by the temperature rise, but others increased in productivity until they became restricted by competition from grassland taxa. However, many apparently survived in open habitats, such as on the cliffs of Mehuken Mountain and the coast, through the early Holocene. Such rapid species turnover comparable to that in the early Holocene is seen today during the colonization of recently deglaciated ground in western Norway (Birks & Birks 2008) since the Little Ice Age (Matthews & Whittaker 1987, Matthews 1992), where the timing is comparable.

The initiation of grassland communities took about 50 years after the start of the Holocene and succession within these communities can be detected in the fossil record. The expansion of tall ferns and shrub willows after about 110 years and later of dwarf shrubs caused further abrupt vegetation shifts, to damp-soil *Salix*-fern communities and to dry-soil dwarf-shrub heath. As a consequence, many weakly-competitive herbs of open ground became locally extinct. These kinds of successions can be observed in modern situations on moraines left by retreating glaciers (Fægri 1933, Matthews & Whittaker 1987, Matthews 1992, Vetaas 1994) where their timing can be dated by determining the ages of the moraines.

The birch tree-line eventually advanced as far north as Kråkenes about 700 years after the start of the Holocene. The impact on the dwarf-shrub heath was large. Although taxa were generally not eliminated, the dwarf-shrubs rapidly decreased in abundance in the fossil record over a few decades as they became understorey components with a reduced chance of dispersal of their remains to the lake. In contrast, the *Salix*-fern communities seem to have been unaffected, being resistant to birch invasion.

Conclusions

There are natural uncertainties in the chironomid-based temperature reconstruction (1.1–1.4 °C) and in the age-depth model from the Kråkenes sequence, although the latter could scarcely be improved with radiocarbon dating (Lohne et al. 2013). Even when these are taken into account, our data demonstrate the rapidity with which alpine and sub-alpine vegetation can change under conditions of changing summer temperature, especially if it is near an ecotone and sensitive to temperature changes. Summer temperature itself is a result of summer solar insolation that was greater during the late glacial than today, thus influencing seasonality and sea-surface temperatures. Temperature may not always be the direct cause of the responses, but it influences other environmental factors that may play a driving role, such as frost frequency, permafrost development, continentality, fire frequency, lake-ice cover, and the environmental impact of the local glacier (Birks et al. 2000). In addition, precipitation changes may also play a role. These are more difficult to reconstruct (see Larsen & Stalsberg 2004).

We have demonstrated that rapid vegetation shifts can also occur under constant temperature conditions, driven by the invasion and expansion of keystone species such as tall ferns, dwarf-shrubs, and birch trees. When an ecologically dominant and highly competitive species arrives, the community structure can apparently change very fast. Similar changes can be studied at the present day, but their long duration in comparison to the opportunity for human observation means that chronologically and taxonomically high-resolution palaeoecological studies can provide a link between observed ecological processes and long-term responses to past changes.

The Kråkenes YD–early-Holocene vegetation responses show all the four modes of biotic responses to climate change discussed by Dawson et al. (2011). Persistence or toleration is illustrated by *Carex* spp. and shrub *Salix* spp. Habitat shift is shown by *Salix herbacea* and *Sedum rosea*, both of which occurred in snow-bed vegetation in the YD and earliest Holocene but today are confined in the Kråkenes area to exposed open wind-blasted summit vegetation on Mehuken Mountain (*Salix herbacea*) or coastal cliffs (*Sedum rosea*). Migration was the dominant response of *Betula pubescens* and other trees such as *Populus tremula* and *Sorbus aucuparia* and possibly ericaceous dwarf shrubs. Extinctions at a local scale occurred for arctic-alpines such as *Koenigia islandica, Ranunculus glacialis*, and *Saxifraga rivularis* that do not tolerate temperatures above 10 °C.

Other biotic responses included compositional change, turnover, and assemblage shifts (‘regime shifts’) as a result of species persistence, re-adjustment of abundances, competition, and other species interactions; expansion, for example, following the delayed arrival of *Betula* and other trees; and natural population variability (‘pattern and process’) and local disturbances such as fires. As discussed by Birks & Birks (2008), these responses led to changes in assemblage composition and richness, driven, in part, by climate change and, in part, by long-term successional processes (Willis et al. 2010),

The Arctic and mountain regions of Scandinavia are sensitive to the current global temperature rise and vegetation changes have been recorded, such as the invasion of tundra by shrubs and trees (e.g. ACIA 2004). Our study at Kråkenes demonstrates how rapid vegetational shifts can occur when mean July temperature falls or rises by about 2 °C over ~50 years. The modern temperature increase is slower (about 0.5 °C over 50 years). However, the responses at Kråkenes are an analogue for possible responses to modern global warming and could provide insights into possible types and rates of future vegetation change.

This study at Kråkenes shows how it is possible to use the palaeoecological record as an ecological laboratory, and as a long-term record of ecological dynamics under conditions of rapid climate change, thus providing a means of considering the biotic responses to future climate change.

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Souhrn

Jak rychle může vegetace zareagovat na rychlou klimatickou změnu? Abychom mohli odpovědět na tuto otázku, potřebujeme dlouhodobý vegetační záznam a na něm nezávislý záznam o změnách klimatu. Obojí můžeme získat z paleoekologických studií, které zahrnují více skupin organismů. K rekonstrukci vegetačních změn slouží

zejména pylová analýza a analýza makrozbytků, zatímco analýza zbytků pakomárů slouží k rekonstrukci změn klimatu. Autoři analyzovali tyto skupiny fosilií v často a detailně zkoumaném profilu ze sedimentů jezera Kråkenes v západním Norsku. V pozdním glaciálu se klima v západním Norsku rychle měnilo a v důsledku těchto změn se měnila i vegetace. U jezera Kråkenes, které leží poblíž pobřeží, rostla v interstadiálu Allerød vegetace analogická dnešní vegetaci nižšího a středního alpínského stupně v západním Norsku. Vegetace výrazně zareagovala během zhruba 10 let na ochlazení v mladším dryasu, i když průměrná červencová teplota, odhadnutá z fosilního záznamu pakomárů, klesla jen asi o 2°C. Takový pokles byl totiž v této oblasti s hojnými srážkami dostatečný na to, aby se nad jezerem vytvořil v mladším dryasu karový ledovec. Když pak letní teploty na úplném začátku Holocénu vzrostly, rostliny okamžitě zareagovaly. Alpínské druhy, které tolerují vyšší teplotu, expandovaly, avšak později byly potlačeny kompetičně zdatnějšími druhy. Vývoj vegetace pokračoval směrem k mírně vlhkým a suchým trávníkům, kapradinovým nivám s kapraděmi a papratkami a keříčkovým společenstvům s šichou. Stromová bříza pýřitá (*Betula pubescens*) přišla asi o 500 let dříve, než se vytvořily březové lesy. Výsledky této studie tedy názorně ukazují, jak mohou být floristické a vegetační patrnosti, které jsou zaznamenány v sedimentech, interpretovány ve smyslu ekologických procesů, pokud máme k dispozici nezávislý paleoklimatický záznam. V tomto případě jej poskytl fosilní záznam pakomárů ze stejného vrtu.

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