

Using species attributes to characterize late-glacial and early-Holocene environments at Kråkenes, western Norway

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Abstract

Aim: We aim to use species attributes such as distributions and indicator values to reconstruct past biomes, environment, and temperatures from detailed plant-macrofossil data covering the late glacial to the early Holocene (ca. 14–9 ka).

Location: Kråkenes, western Norway.

Methods: We applied attributes for present-day geographical distribution, optimal July and January temperatures, and Ellenberg indicator values for plants in the macrofossil dataset. We used assemblage weighted means (AWM) to reconstruct past biomes, changes in light (*L*), nitrogen (*N*), moisture (*F*), and soil reaction (*R*), and temperatures. We compared the temperature reconstructions with previous chironomid-inferred temperatures.

Results: After the start of the Holocene around 11.5 ka, the Arctic-montane biome, which was stable during the late-glacial period, shifted successively into the Boreo-arctic montane, Wide-boreal, Boreo-montane, Boreo-temperate, and Wide-temperate biomes by ca. 9.0 ka. Circumpolar and Eurasian floristic elements characteristic of the late-glacial decreased and the Eurosiberian element became prominent. Light demand (*L*), soil moisture (*F*), nitrogen (*N*), and soil reaction (*R*) show different, but complementary responses. Light-demanding plants decreased with time. Soil moisture was relatively stable until it increased during organic soil development during the early Holocene. Soil nitrogen increased during the early Holocene. Soil reaction (pH) decreased during the Allerød, but increased during the Younger Dryas. It decreased markedly after the start of the Holocene, reaching low but stable levels in the early Holocene. Mean July and January temperatures show similar patterns to the chironomid-inferred mean July temperature trends at Kråkenes, but chironomids show larger fluctuations and interesting differences in timing.

Conclusion: Assigning attributes to macrofossil species is a useful new approach in palaeoecology. It can demonstrate changes in biomes, ecological conditions, and temperatures. The late-glacial to early-Holocene transition may form an analogue for changes observed in the modern arctic and in mountains, with melting glaciers, permafrost thaw, and shrub encroachment into tundra.

KEYWORDS

assemblage weighted means, biome reconstruction, chironomids, early Holocene, Ellenberg indicator values, environmental change, late glacial, macrofossils, species attributes, temperature reconstruction

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1 | INTRODUCTION

Understanding past vegetation responses to rapid climate warming may help to predict future responses to the climate warming that has been on-going since about 1950. Arctic and alpine ecosystems are sensitive to environmental changes (Chapin et al., 2005). Increases in temperature and growing season are promoting growth of shrub vegetation (ACIA, 2004, Chapin et al., 2005; Keenan & Riley, 2018). These changes can boost soil microbial activity by increasing *N* mineralization and nutrient availability. Consequently, productivity is increasing in the arctic. However, little is known with certainty about how long-term climate warming affects environmental factors such as soil nutrients, soil moisture, soil reaction, and light demands, and how these interact during ecosystem responses.

The last-glacial to Holocene transition is the best studied analogue for the on-going climate warming in cold regions. The rapid climate warming during the last-glacial to Holocene transition resulted in rapid biotic responses in northern Europe (Birks & Birks, 2008, 2014). Plants quickly re-established and expanded into deglaciated areas as the Scandinavian Ice Sheet retreated. Both the magnitude and direction of change are comparable with changes observed during the last 100 years and can thus be considered as a past analogue for what might be expected for future ecosystem changes in the north (Birks & Birks, 2008; Stivrvins et al., 2016).

Much can be learned from the past about the biotic responses to climate, changes in soils, and natural vegetation succession. Reconstructions of past biomes from the last glacial maximum (LGM) to 14.0 ka show how widespread steppe and tundra biomes began to change around 14.0 ka in response to broad-scale climate warming (Binney et al., 2017). The west-Norwegian coastal area became ice-free around that time and lake sediment records started to accumulate, laying down archives of rapid ecosystem transitions reflecting complex interactions of changes in temperature, precipitation, and soil conditions.

Past vegetational and environmental changes can be reconstructed from fossil pollen or macrofossil assemblages using knowledge about species-specific optima and tolerances to the environment. However, to reconstruct biotic responses to environmental changes, the latter should be reconstructed from independent lines of evidence. Past climates are commonly reconstructed using modern training sets and transfer functions (Birks, Lotter, Juggins, & Smol, 2012; Birks & Seppä, 2010; Birks, ter Braak, Line, Juggins, & Stevenson, 1990). However, relevant modern training sets are not available for all proxies and the application of species attributes *sensu* Hill, Preston, and Roy (2004) (including indicator values or ecological indices) is an alternative approach (Diekmann, 2003). Each species has its optimum, which can to some extent be characterised by ecological indicator values. These have been widely used in modern ecological studies to investigate environmental changes or ecosystem ('bioindication') quality along gradients where there are no real environmental measurements (Diekmann, 2003). Ellenberg (1974), Ellenberg et al. (1991), Landolt (1977), Preston and Hill (1997), and Hill et al. (2004) have assigned ordinal values for species preferences, for example, to soil conditions, light, and geographical distributions.

One of the first applications of Ellenberg indicator values to palaeoecological data was by Wasylkova, Starkel, Niedziatkowska, Skiba, and Stworzerwicz (1985) to a Holocene macrofossil sequence with human impact in Poland. Birks (1990) derived and applied indicator values for pollen types to estimate the extent of human impact in the last 6000 years. Jonsgard and Birks (1995) used indicator values for light, temperature, continentality, soil moisture, soil nitrogen, and soil reaction to reconstruct environmental conditions from fossil mosses during the late glacial at Kråkenes, western Norway. Kuneš, Odgaard, and Gaillard (2011) used Ellenberg indicator values for light and soil reaction to assess vegetation and environmental changes inferred from pollen assemblages during different interglacial periods in Denmark. Mortensen et al. (2011) applied Ellenberg indicator values for light, soil reaction, and soil nitrogen to assess environmental changes from late-glacial macrofossil assemblages in Denmark. Ecological indicator values of diatoms have also been used to reconstruct changes in aquatic conditions (Battarbee, 1986; Battarbee et al., 1984; Flower, 1986; Renberg & Hellberg, 1982).

The Kråkenes site on the west-Norwegian coast has been investigated using a multidisciplinary approach to explore the late-glacial and early-Holocene ecosystem and environmental changes between 14.0 and 9.0 cal years BP (Birks & Ammann, 2000; Birks, Battarbee, & Birks, 2000). A phase of colonization by pioneer arctic-alpine plants and animals after deglaciation was followed by a cold stable Allerød (AL) period. In the following colder Younger Dryas (YD) period, both landscape and vegetation were destabilized and a glacier developed in the catchment. A Younger Dryas to Holocene (YDH) transition led into the warmer early Holocene (EH), resulting in a marked vegetation succession.

Late-glacial pollen assemblages often have no modern analogues and contain well-dispersed taxa such as *Betula* and *Artemisia* (Birks, 2003). Macrofossils are more reliable indicators of local vegetation (Birks, 2000, 2003, 2014; Birks & Birks, 2000) and hence of local environment. No no-analogue macrofossil assemblages have been recorded so far (Birks, 2003) in spite of the fact that false absences can occur due to taphonomic processes, taxon representation often being skewed, and the numbers of the same taxon between samples being variable.

In this study, we revisit the detailed macrofossil data from Kråkenes, western Norway, to reconstruct local changes in biome and environment through the late glacial to the early Holocene using the attribute approach. Our aim is to apply this approach to these palaeoecological data, to determine if it enhances our understanding of the late-glacial and early-Holocene environmental conditions and terrestrial ecosystem processes at Kråkenes. We use attributes of species' present-day geographical distributions to reconstruct changes in major biomes. We reconstruct past January and July temperatures using species' modern optimum temperatures and compare these results with an independent proxy, chironomid-inferred mean July temperature. We reconstruct soil conditions (nitrogen, moisture, reaction) and light availability using Ellenberg indicator values as listed for plants in the British Isles by Hill et al. (2004). These values are generally similar to the values of Ellenberg et al.

(1991), but some have been adjusted for the British Isles (Hill, Roy, Mountford, & Bunce, 2000).

2 | METHODS

2.1 | Site

Kråkenes Lake (62°02'N, 5°00'E, 38 m a.s.l.) fills an irregular basin with a present-day inflow from the higher-lying cirque on Mehuken Mountain to the south and an outflow to the north to the sea. It has been described by Birks et al. (1996), Birks and Wright (2000) and Larsen, Eide, Longva, and Mangerud (1984). The palaeoecology of the late-glacial and early-Holocene sediments has been extensively investigated using both terrestrial and aquatic proxies (Birks, Battarbee, & Birks, 2000). An important proxy is the detailed plant-macrofossil record used in this study.

Ages are given in calibrated kiloyears before present, designated by ka. Sediment chronologies are provided by radiocarbon dating. Radiocarbon years are not equivalent to sidereal years. Therefore, they have been calibrated (IntCal13) by Reimer et al. (2013) to years before present (BP). For historical reasons and by convention, present is taken as AD 1950. Lohne, Mangerud, and Birks (2014) estimated precise calibrated ages BP for the Younger Dryas boundaries in the Kråkenes sequence: Allerød (AL)–Younger Dryas (YD) $12,737 \pm 31$ cal yr BP; YD–Holocene (H) $11,546 \pm 58$ cal yr BP. The base of the sequence is dated to ca. 14 ka (Lohne, Mangerud, & Birks, 2013). The deglacial phase lasted about 100 years before AL vegetation developed (Birks & Birks, 2013). Here, we delimit a short YD–H transition (YDH) from the start of the Holocene to 11.2 ka (the expansion of *Empetrum*). We delimit the early Holocene (EH) from 11.2 to ca. 9.0 ka, the top of our record. Tree birch (*Betula pubescens*) arrived at Kråkenes at 10.8 ka (Birks, 2015; Birks & Birks, 2008, 2013).

Birks (2000) described the macrofossil method, and Brooks and Birks (2000) described the method of chironomid analysis.

2.2 | Data

We base our reconstructions on applying the values of attributes for the British Isles by Hill et al. (2004) and for Scandinavia by Helvik, Orbán, Aronsson, and Birks (2014) and H.J.B Birks (personal communication) to the plant-macrofossil data from Kråkenes. The total Kråkenes data set is unpublished, but selected data are presented by Birks (2015), Birks and Birks (2008, 2013), and Lohne et al. (2013). The data are numbers of macrofossils in 100 cm^3 of sediment (concentrations) or abundance estimates for uncountable vegetative parts. Only terrestrial taxa are considered in this study because aquatic taxa were almost lacking during the late-glacial period. In total, there are 122 samples and 58 taxa.

2.3 | Geographical distributions

Major biome preferences for species are defined using geographical distributions of each species in the Kråkenes data. Hill et al.

(2004) used two biome categories. E1 represents the phytogeographical boundaries of 10 major biomes that form a more-or-less north–south transect in Europe. E2 is the eastern-range limit and trend in seven distribution types from Oceanic to Circumpolar. These phytogeographical categories were first defined by Preston and Hill (1997) for the British and Irish flora. Helvik et al. (2014) expanded them to include the native flora of Denmark, Færoes, Norway, Svalbard, Sweden, and Finland. We use Helvik et al.'s values here.

2.4 | Environmental variables

Selected environmental variables during the late glacial and early Holocene are reconstructed using Ellenberg indicator values for light (*L*), soil moisture (*F*), soil nitrogen (*N*), and soil reaction (*R*) from Hill et al. (2004) and H.J.B Birks (personal communication). Following Hill and Carey (1997), we regard changes in soil nitrogen as changes in above-ground productivity. Schaffers and Sýkora (2000) considered that changes in soil reaction are closely correlated to calcium values, which influence changes in soil pH.

July and January temperature optima for each taxon are derived from the PLANTATT database (Hill et al., 2004). These values apply to the British Isles. The mean temperatures were calculated from the mean temperatures of all 10-km grid squares in which each species occurs. These are therefore mean temperatures, not limiting temperatures, so their use over-estimates the limiting temperatures, and probably also the 'optimum' temperatures from a Scandinavian perspective. We attempt to minimise this bias by plotting temperatures derived for the Kråkenes data as deviations from the overall mean of the reconstructions.

Some Scandinavian taxa lack temperature optima, and these were estimated by predicting mean values based on other variables present using the package mice in R (van Buuren & Groothuis-Oudshoorn, 2011). Because macrofossil counts can be highly variable and may represent biases due to differences in macrofossil representation (Birks, 1973), we performed reconstructions on the Kråkenes data using two alternative data sets: (a) log-transformed concentrations; and (b) a five-point scale for each taxon. The concentration values were assigned to five ordinal categories, abundant, frequent, occasional, rare, and present that took account of the representation of each taxon, i.e., if it produced many or few macrofossils per plant, and if the propagules were well or poorly dispersed and preserved. The ordinal values were converted into a semi-quantitative scale of percentages. Since the results of both analyses showed very small differences, we used log-transformed concentrations.

2.5 | Assemblage-weighted means

To reconstruct past biomes or investigate changes in environment based on changes in the macrofossil assemblages, we used community-weighted means (CWM; Diekmann, 2003). Macrofossil assemblages do not directly reflect plant communities (Birks, 2014),

so in this paper we refer to the means as assemblage-weighted (AWM). Estimates for a biome or an environmental variable are derived by weighted average calibration (ter Braak, 1987). The estimate for biome or environmental variable *x* in a sample of interest is an average of the indicator values for *x* for all taxa present in the sample and the weights are the relative abundance values of the taxa in the sample. Absent taxa have zero weight (ter Braak, 1987).

The AWM July and January temperatures are compared visually with mean July temperature reconstructions based on chironomid assemblages (CT-jul) from the same Kråkenes core (Birks, 2015; Brooks & Birks, 2000). We also present CT-jul as deviations from the mean of the data set, so that we can compare the temperature anomalies.

Patterns and trends of AWM biomes and environments are summarised using generalised additive models (GAM) with cubic regression splines. Boxplots summarise the variability in the four periods; Allerød (AL), Younger Dryas (YD), Younger Dryas–Holocene transition (YDH), and early Holocene (EH). All analyses used R version 3.5.3 (R Core Team, 2019), and plots are made using ggplot2 (Wickham, 2016).

2.6 | Nomenclature

Nomenclature of species attributes (floristic elements, optimal temperatures, and indicator values) follows Hill et al. (2004). Plant nomenclature follows Mossberg and Stenberg (2018).

3 | RESULTS AND DISCUSSION

We use the species attribute approach to infer past biome and environmental changes and to reconstruct July and January temperatures during the late glacial and early Holocene. We combine the results and their discussion in the following subsections.

3.1 | Major biome reconstruction

The major biome reconstructions (E1; Figure 1a) show that the late-glacial plant assemblages (14.0–11.5 ka) are comparable to the Arctic-montane and Boreo-arctic montane biomes. Starting in the YDH (11.5–11.2 ka) they shift from the Boreo-arctic montane biome to more temperate biomes in the EH (11.2–9.1 ka; Figure 1a: values

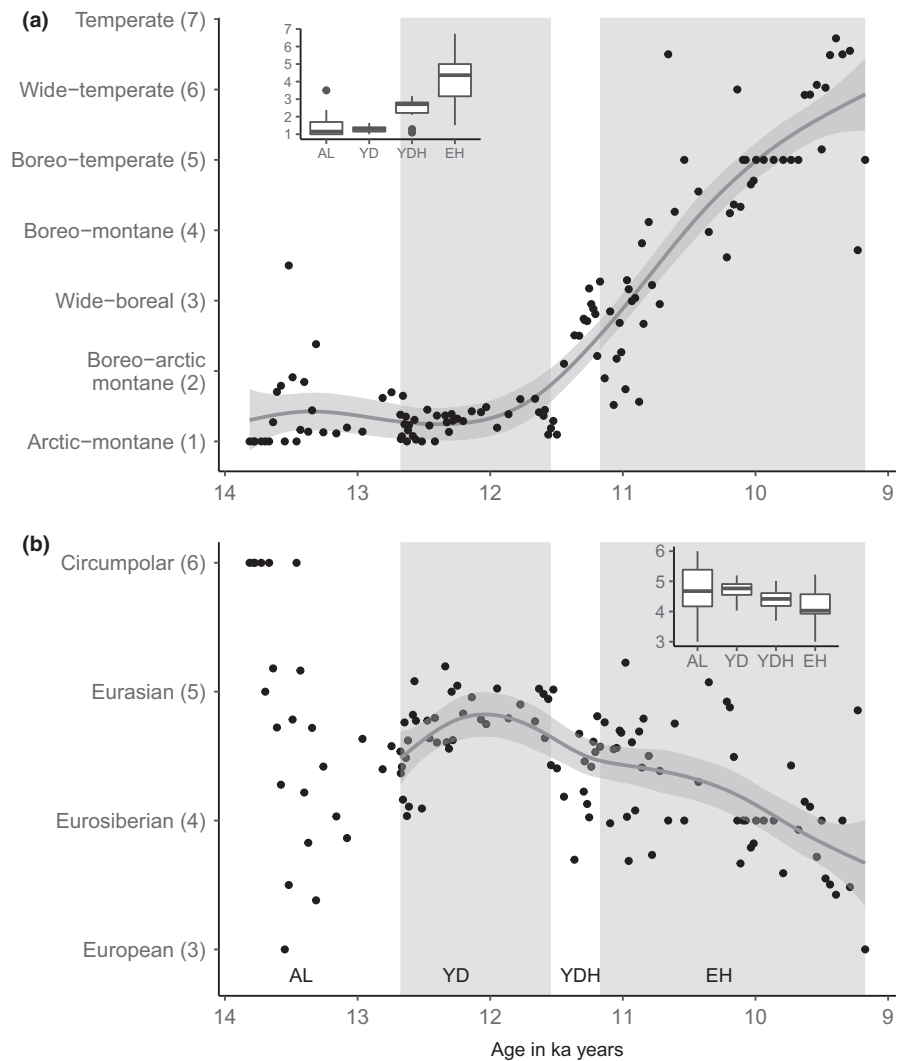


FIGURE 1 (a) Major biome reconstructions based on E1. (b) The phytogeographical elements (E2) based on the eastern limits of species. The grey and white background delimits the boundaries between the time periods AL, YD, YDH, and EH. The numbers after each geographical attribute and in the inserted boxplots follow Hill et al. (2004)

between 1.0 and 6.7). Continentality reconstructions (E2) that are based on the modern eastern limit of the species (Preston & Hill, 1997; Figure 1b) show that taxa belonging to many elements are scattered in the AL (14.0–12.7 ka). The Circumpolar element is exclusive to the early AL within the deglacial period. Although the Circumpolar element is included in the E2 attribute of eastern limits by Preston and Hill (1997) and Hill et al. (2004), it includes taxa in both oceanic Arctic and continental Arctic environments. It is therefore not a reliable indicator of continentality (see Berg, Welk, and Jäger 2017 for a detailed analysis of phytogeographical continentality). The AL flora clearly consisted of taxa that are today phytogeographically diverse in terms of their eastern limits (European to Circumpolar). These plants are widespread arctic and circumpolar pioneer species of open ground, some of which extend far to the east. Arctic circumpolar herbs are good colonisers and they were rapidly able to colonise the deglaciating landscape. Other taxa such as *Empetrum* also occurred, contributing to the predominately Eurosiberian assemblage. Because of this diversity, we do not fit a GAM for the AL in Figure 1b. As the AL progressed, more Eurosiberian species expanded, such as *Salix herbacea* that dominated the widespread snow-bed-dominated vegetation.

The macrofossil assemblage in the YD (12.7–11.5 ka) is closely analogous to the Arctic-montane biome (Figure 1a) with very

little variability. Most species have Eurasian distributions (Figure 1b). Many of them are widespread arctic-alpines characteristic of unstable wet gravel and sand irrigated by snowmelt, or drier, well-drained substrates (Birks, 2015). At about 11.5 ka, there was a sharp shift in the assemblage analogous to the Arctic-montane biome to more southern Boreo-arctic montane and Wide-boreal biomes (Figure 1a). At the same time, Eurasian species increased (Figure 1b).

During the YDH transition (11.5–11.2 ka) there is a trend towards the Eurosiberian element. The EH (11.2–ca. 9.0 ka) becomes dominated by this element by 9.0 ka. At about 10.8 ka tree birch immigrated (Birks & Birks, 2013), some 700 years after the start of the Holocene and some 440 years after CT-jul reached its lower limiting temperature of 11°C (Birks, 2015; Birks & Birks, 2008). The assemblage came to resemble ever more temperate biomes (Figure 1a) and the succession results in a high variability during the period. At the same time, the assemblage became increasingly oceanic (Figure 1b) as arctic species disappeared and species that are more southerly today immigrated.

3.2 | Environmental reconstructions

Figure 2 shows that changes in light demand (L), soil moisture (F), productivity (N) and soil reaction (R) show different, but complementary

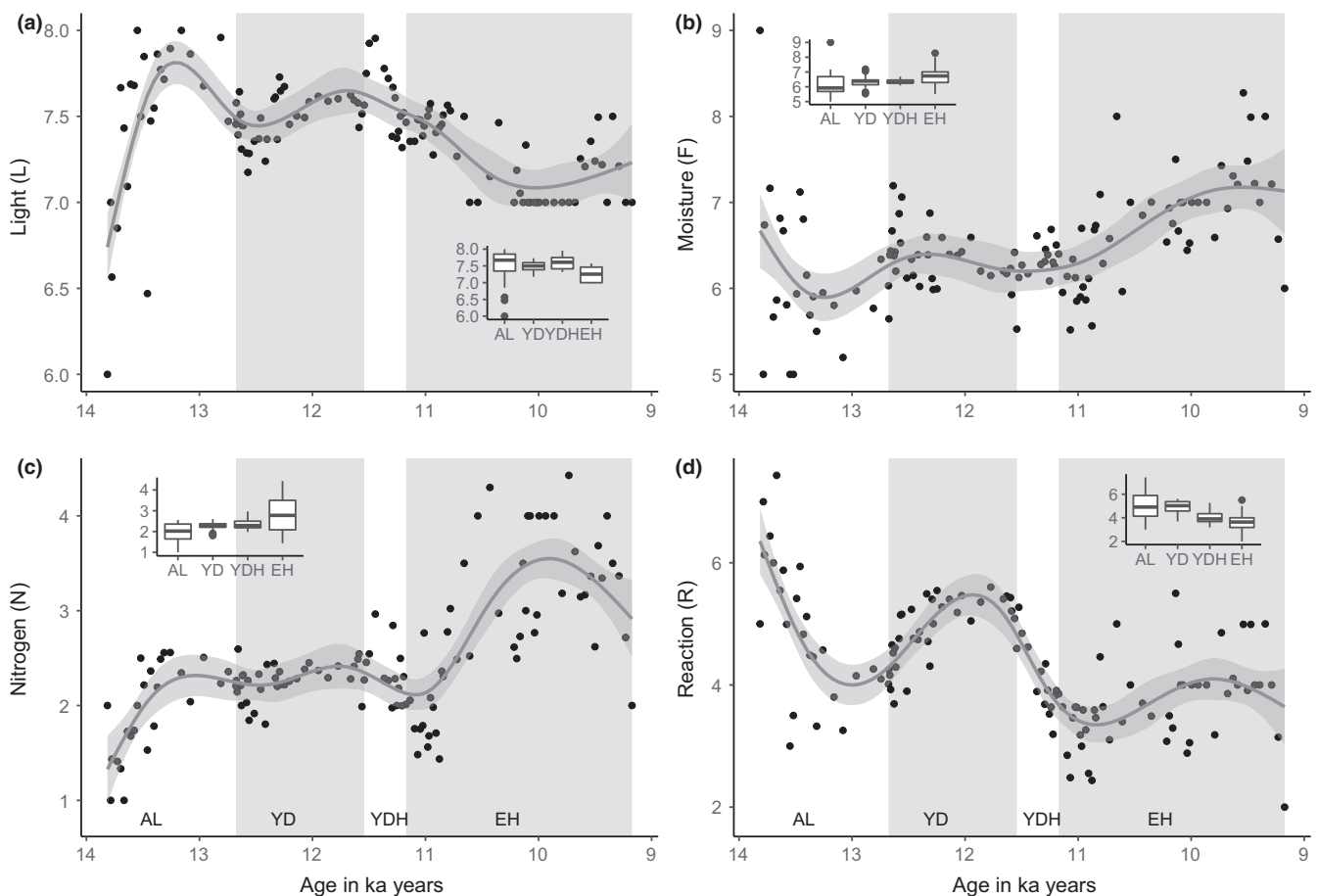


FIGURE 2 Environmental changes in (a) light demands (L), (b) soil moisture (F), (c) nitrogen (N), and (d) soil reaction (R). Box plots show the variability in each period. The grey and white background delimits the boundaries between the time periods AL, YD, YDH, and EH

responses. Box plots show the median and range of variation for each period. Light demand (Figure 2a) was 6 at 14.0 ka and it rapidly increased to higher values of 8 during the AL as vegetation became established. The relatively low value at 14.0 ka is mostly due to the abundance of *Saxifraga rivularis* that is given a value of 6 by Hill et al. (2004). It should probably be given a higher L value in Scandinavia, as it is a plant of more open unshaded habitats. Light values remained very high during the YD but began to decrease during the YDH to lower values in the EH. As the shrub and tree canopy developed, light demands decreased as more shade-tolerant species expanded.

Soil moisture (Figure 2b) was relatively high during the whole period. It is slightly lower in the AL, but in reality, there was very little true soil and much of it was frozen and subject to gelifluction. Most of the terrain would have been minerogenic and well drained, or snow-covered and fed by snow and ice meltwater.

Many species occurred in the YD that are characteristic of wet, snow-meltwater habitats, such as *Koenigia islandica* and *Saxifraga rivularis*, which contribute to the relatively high AWM soil moisture values. The increase in soil moisture during the EH is likely to be a result of organic matter accumulation in the soil with increased moisture-holding capacity, as well as higher precipitation (Larsen & Stalsberg, 2004). The values show high variability during the AL and during the EH.

Productivity (Figure 2c) was low during the AL, YD, and YDH, but during the EH it rapidly increased to a maximum at ca. 10.0 ka before decreasing slightly. However, the variability was very high during the EH. As soils and taller woody vegetation developed, increasing N-values are interpreted as a marked increase in productivity as inorganic N was metabolised even though the pH (Figure 2d) was low in the EH.

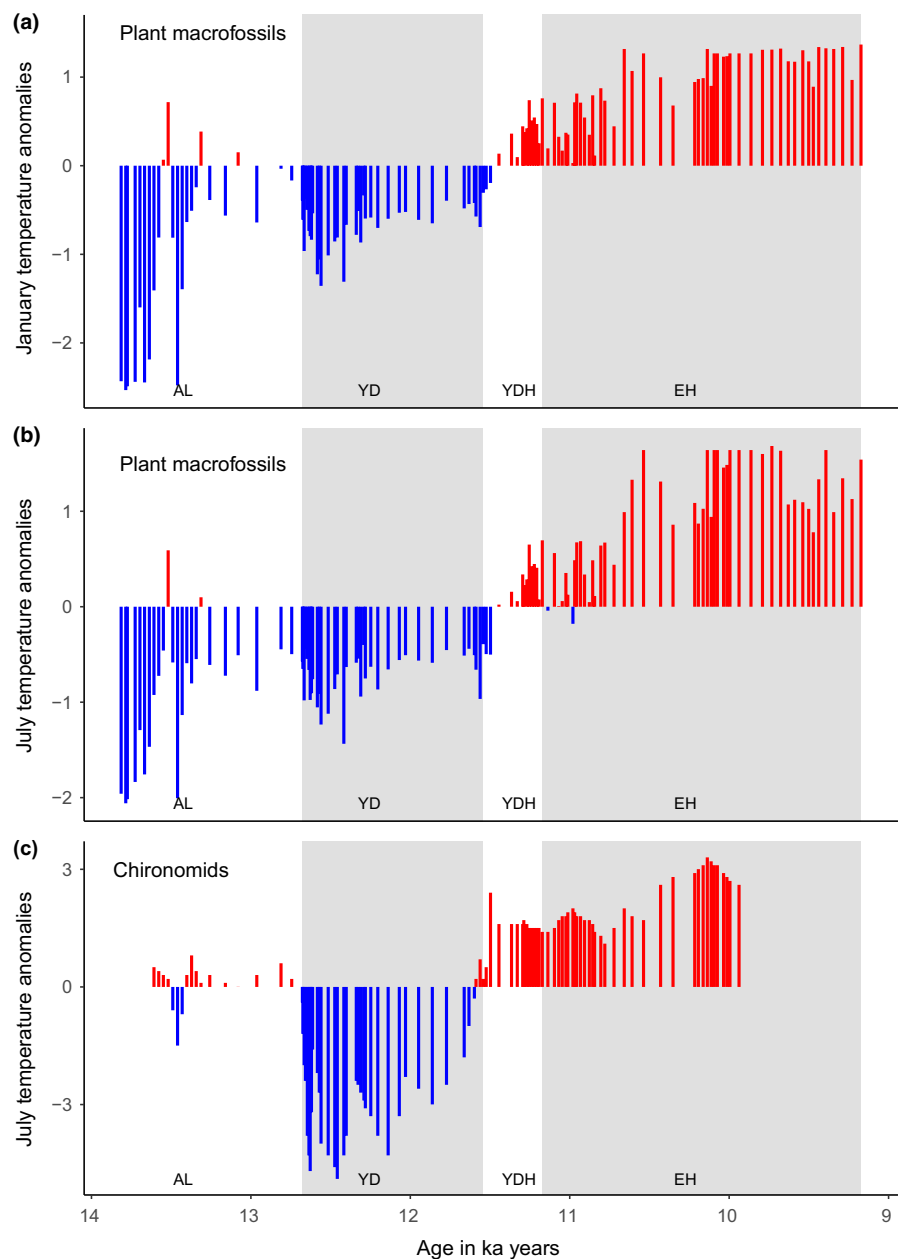


FIGURE 3 Temperature anomaly reconstructions based on plant macrofossils and chironomids: (a) mean January temperature anomalies based on plant macrofossil assemblages; (b) mean July temperature anomalies based on plant macrofossil assemblages; and (c) mean July temperature anomalies based on chironomid assemblages from the same sediment core calculated from Brooks and Birks (2000). The grey and white background delimits the boundaries between the time periods AL, YD, YDH, and EH. The anomalies are deviations from the mean of each reconstruction [Colour figure can be viewed at wileyonlinelibrary.com]

Soil reaction (Figure 2d) shows dynamic changes. It was highest just after deglaciation in the early AL but soils became markedly more acid during the AL. It rose to high values again in the YD, reflecting increased soil instability. The sharp decrease in pH during YDH is mostly due to chemical weathering and leaching of the fine mineral fraction of the soil in the warmer climate, resulting in depletion of the soil nutrient and base-cation pool (Boyle et al., 2013). At the same time, diatom-inferred pH in the lake fell from ca. 7.0 to ca. 6.8 (Bradshaw, Jones, Birks & Birks, 2000) as the source of basic ions from the catchment was steadily depleted. The rapid decline during the YDH led to low values during the Early Holocene. The sequestration of nutrients in the terrestrial vegetation and the lake sediments in addition to the acidification resulted in extreme depletion of nutrients in the lake from ca. 10.8 to 10.2 ka (Birks, 2000). The acidification in the soils after the start of the Holocene is also reflected in the geochemistry of the lake sediments as weathering, leaching, and organic-acid accumulation proceeded (Boyle et al., 2013) and in the decrease in diatom-inferred pH in the lake from around 6.8 to an average of 6.5 during the EH (Bradshaw, Jones, Birks, & Birks, 2000).

In general, all environmental factors show relatively high variability during the AL (Figure 2) which may be due to the dynamic vegetation and ecosystem development, from pioneer plants to a closed, stable *Salix herbacea*-dominated community analogous to low-alpine vegetation in the Norwegian mountains today (Birks, 2015).

3.3 | Mean July and January temperature reconstructions

Climate reconstructions as temperature differences from the overall mean (Figure 3) based on the plant macrofossil assemblages show similar patterns for mean winter (mean = 2.1°C, Δt = 3.9°C) and summer temperatures (mean = 12.8°C, Δt = 3.7°C) (Figure 3a, b). The temperature anomalies decreased during the AL. At the start of the YD they increased rapidly. Then temperatures warmed slightly and stabilised below the mean. There is a marked warming at the beginning of the YDH, with January temperatures reaching the mean a few decades before the July temperature. After about 11.3 ka temperatures remained stable above the mean until a marked increase occurred at about 10.7 ka.

The overall patterns of plant-macrofossil temperature reconstructions are similar to the temperature trend shown by CT-jul (mean = 9.9°C, Δt = 8.2°C; Figure 3c). However, the chironomid-inferred temperature fluctuations are greater and show some marked differences. Temperatures are around the mean at the start of the AL, and show a large rapid drop at the end of the AL and into the YD. They show that slow warming started at ~12.2 ka in the second part of the YD. July temperatures increased gradually until they reached the mean at the start of the Holocene when they showed a rapid increase to stable temperatures with an anomaly of about +1.5°C during the YDH. They increased again in the EH at about 10.5 ka, about 200 years after the increase in the macrofossil-inferred temperatures.

Birks and Ammann (2000) showed that mean July temperatures reconstructed from macrofossils and pollen data were about

5–7°C during the late glacial with little difference between the AL and the YD. They rose to about 8°C at the start of the Holocene, reached 11°C by about 10.9 ka, and present-day temperatures of 12.5°C by about 10.0 ka in the early Holocene. The range of about 7.5°C is less than the range of 8.2°C in the chironomid-inferred mean July temperature record. The CT-jul estimates also show larger changes, falling rapidly from about 9°C in the AL to about 5°C at the start of the YD. They rose gradually during the last half of the YD reaching about 10°C at the start of the Holocene. They then rose rapidly, reaching about 11°C by 10.7 ka and 12.5°C at about 10.5 ka (Birks, 2015).

Both AWM January and July temperatures reconstructed from the macrofossil data using temperature means from the British Isles (Hill et al., 2004) were very cold after deglaciation (ca. 14.0 ka), but warmed substantially into the AL, reaching stable values about 0.5°C below the mean (Figure 3a, b). The apparent increase in temperature probably reflects the immigration of plants to the area. This contrasts with the chironomid-inferred mean July temperatures that were more or less steady close to the mean throughout the AL (Figure 3c). Temperatures in both records decreased sharply at the start of the YD, and a cirque glacier developed above the lake. As glacial meltwater entered the lake, the effect on the chironomid assemblage was very marked, and inferred temperatures were 3.0–3.5°C below the mean, whereas macrofossil-inferred temperatures decreased by about 0.5°C. The AL already contained many arctic-alpine species that continued to be present or expanded during the YD. Although the AL soils were destroyed by frost action and the vegetation became analogous to high alpine vegetation in the Norwegian mountains today (Birks & Birks, 2013), species turnover was not large and hence the temperature reconstructions show relatively small decreases.

At about 12.0 ka, in the mid-YD, temperatures in all the records increased slightly. The macrofossil-inferred temperatures then remained more or less stable at 1–1.5°C below the mean. This warming caused the partial withdrawal and subsequent stillstand of the cirque glacier in the middle of the YD (Hauge, 1995). Bakke et al. (2009) also documented a change after 12.0 ka that they interpreted as a flickering of atmospheric and oceanic circulation during the second half of the YD. CT-jul rose during the last 300 years of the YD, reaching the mean at the end of the YD.

At the start of the Holocene (11,530 cal yr BP, Lohne, Mangerud, & Birks, 2014) CT-jul rose rapidly at an initial rate of 1°C in 55 years, reaching 11°C at 11,490 cal yr BP and then 12°C by ca. 11,000 cal yr BP (Birks, 2015). Bakke et al. (2009) also showed a sharp temperature rise at the start of the Holocene similar to that in the chironomid record.

The corresponding rise in the macrofossil-inferred temperatures was also rapid but lagged by about a hundred years. At the start of the Holocene, many arctic-alpine species expanded due to the increased temperature and lack of competition (Birks, 2015; Birks & Birks, 2008, 2013). It took time for new species to immigrate and expand and for arctic-alpines to be outcompeted by the development of closed grassland. Importantly, the temperatures are inferred

from the macrofossil assemblages, which at that time were not in equilibrium with the rapidly changing climate. There were other migrational lags of later keystone species such as *Empetrum* and *Betula pubescens*, documented by Birks (2015) and Birks and Birks (2008) at Kråkenes, and by Mortensen et al. (2011) in Denmark. Shorter lags between deglaciation and arrival and expansions of trees have been detected further south and longer lags to the north of Kråkenes (Birks, 2015). Hence, the temperatures inferred from the terrestrial ecosystem are not directly comparable to the temperatures inferred from the chironomid record during the transition periods.

Chironomids respond largely to air temperatures and thus react quickly to any regional temperature changes (Birks, 2015; Brooks & Birks, 2000). Terrestrial conditions warmed slowly after the start of the Holocene, as ice and snow had to melt and it takes a long time for soil to warm sufficiently for plant growth. Besides soil warmth, slow vegetation responses might have been exacerbated by unstable and infertile soils and immigration lags. The importance of soil fertility for the support of productive vegetation is emphasised by Mortensen, Henriksen, and Bennike (2014).

Macrofossil-inferred temperatures remained stable at about 0.5°C above the mean until they increased at about 10.7 ka, (Figure 3). This reconstruction is probably influenced by the arrival of tree birch around that time. Thereafter, the vegetation was stable and both mean January and July temperatures reflect this stability. In contrast, chironomid-inferred mean July temperature rose again later, at about 10.5 ka.

3.4 | Use of species attributes for reconstruction

Using species attributes to reconstruct past climate and environment represents a simple way to summarise complex palaeoecological data using similar metrics to those used in modern ecological studies. However, there are issues using AWM that need to be taken into consideration, such as calibrations (ter Braak, 1987). AWM can be biased if there is a highly uneven distribution of indicator values. Species indicator values have been criticized as being subjective, being based on field experience and not actual measurements, and species may change their responses or tolerances over time, space, or during their life cycle (Diekmann, 2003). For example, Ellenberg values for soil reaction can be difficult to assign as species can show geographical variations in their tolerance to acid or calcareous soils. Schaffers and Šykora (2000), ter Braak (1987) and ter Braak and Gremmen (1987) discuss the numerical properties and robustness of indicator values in environmental calibration (=reconstruction), whereas ter Braak and Barendregt (1986) provide a theoretical justification for using weighted averaging calibration (=AWM) with both presence/absence and quantitative abundance data. Attributes such as indicator values are presented on an ordinal scale. For weighted averaging to be useful, the ordinal scale and hence the indicator values should be chosen so that most species show fairly symmetric response curves. In such a situation, the AWM is an informative and robust semi-quantitative biotic index (sensu Ellenberg, 1948) (ter Braak, 1987).

The inference of the reconstructions in this study is supported by other studies. A study of the fossil mosses from the same core at Kråkenes (Jonsgard & Birks, 1995) using ordination, modern indicator values, and altitudinal ranges showed similar results to those from the macrofossils. The major driver was temperature. Late-glacial climate was cold but warmed considerably in the Holocene, soil moisture was high throughout, continentality was intermediate, light intensity decreased in the Holocene, and overall soil reaction was skewed towards low values.

Similar patterns of vegetation development occurred at other sites during the late-glacial–Holocene transition across northern Europe (Birks & Birks, 2014). Climate, especially temperature, drove the overall changes. From south to north in Norway and on a European scale, precipitation played an important role in determining vegetation development (Birks, 2015; Birks & Birks, 2014) but it was never limiting at Kråkenes (Birks, 2015). Here the plant assemblage indicates a cool/cold wet and snowy environment during the late glacial, with the development of a glacier in the Younger Dryas (Birks, 2015; Birks & Birks, 2013; Larsen & Stalsberg, 2004). The early-Holocene plants all indicate that there was adequate precipitation. The rapid rise of temperature initiated a terrestrial vegetation succession at the start of the Holocene (Figure 3; Birks & Birks, 2008, 2013). Grassland developed, followed by *Empetrum* heath and damp *Salix* shrub–tall fern vegetation. This succession is analogous to the increased shrub growth in the arctic today following the global rise in temperature (ACIA, 2004). Results indicate that climate drivers are mediated by local site factors such as time of deglaciation, species migrations, soil development, base status (soil reaction), soil nutrient content, and light intensity, as discussed by, for example, Mortensen et al. (2011, 2014).

4 | CONCLUSIONS

Attributes derived from modern ecological preferences and biogeographical distributions of species found in Quaternary sediments can provide valuable information for the reconstruction of past environment and climate. They are especially useful where modern quantitative data for reconstruction are lacking, such as for plant macrofossils (Birks, 2014).

Biogeographic and environmental attributes applied to the plant-macrofossil data from Kråkenes have shown how major biomes changed at the Holocene boundary from Arctic-montane in the late glacial to Boreal and Temperate biomes as the Holocene progressed. Taxa with Circumpolar and Eurasian distributions were increasingly replaced by Eurosiberian and European taxa during the Holocene. Reconstructed soil conditions showed important changes in reaction, nutrient status, and moisture varying with the amount of freezing, and later with increased organic content. The acid bedrock meant that acidification occurred during the AL, and more markedly in the YDH and EH.

The temperatures based on AWM are biased towards warmer values as they are derived from the species means of the modern

climate in the British Isles (Hill et al., 2004). Therefore, we calculated deviations from the mean temperatures for the sequence. Even if revised climatic optima were available for each taxon for Scandinavia, the patterns would probably remain similar. The trends in mean January and mean July temperature are similar. Chironomid-inferred mean July temperatures from the same core show a similar pattern, but with some differences due to quicker response times of aquatic chironomids compared to terrestrial vegetation.

The vegetation of Arctic and mountain regions is changing in response to present-day global climate warming. Shrubs and trees are expanding northwards and upwards (ACIA, 2004; Grytnes et al., 2014; Kaplan et al., 2003; Steinbauer et al., 2018). The response of vegetation to the late-glacial to Holocene warming was rapid. It provides an analogue for the effects of present-day warming in arctic and mountain regions where the rate of temperature rise is comparable to that from the late-glacial to the Holocene at Kråkenes.

The attribute approach to the interpretation of palaeoecological plant-macrofossil data has given extra insights into the biome analogues that are not readily detectable from the data themselves. Reconstructions of soil nitrogen (productivity) and soil reaction (pH) are particularly novel and more insight has been gained into soil moisture changes. It has been possible to make mean July and mean January temperature reconstructions from the plant-macrofossil data, which was previously impossible due to the nature of these data (Birks, 2014). The differences from an independent mean July temperature reconstruction from chironomid data show the effects of immigration lags and soil development. The attribute approach has greatly enhanced the interpretations from the macrofossil data themselves, and has shown how valuable its use can be in palaeoecological investigations.

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AUTHOR CONTRIBUTIONS

VAF and HHB developed the idea, interpreted the results, and contributed to writing the manuscript. HHB collected and prepared the macrofossil data. VAF assembled species attributes and performed data analyses.

DATA AVAILABILITY STATEMENT

Primary data, prepared data, attribute values, and source codes are stored with the authors.

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