Engels, Stefan (2021) The influence of Holocene forest dynamics on the chironomid fauna of a boreal lake (Flocktjärn, northeast Sweden). Boreas 50 (2), pp. 519-534. ISSN 0300-9483.

Stefan Engels: The influence of Holocene forest dynamics on the chironomid fauna of a boreal lake (Flocktjärn, northeast Sweden)

There is a notable lack of palaeoecological records, particularly quantitative palaeoenvironmental reconstructions, for northeast Sweden. Here I use a lake sediment record from lake Flocktjärn to reconstruct Holocene terrestrial vegetation change and lake ecosystem dynamics, and to study the relationship between these components of the environment. After a period in which the vegetation around the lake is characterised by boreal forest, thermophilous arboreal taxa such as *Ulmus* establish in the Flocktjärn area from 6000 cal. a BP onward. *Picea* becomes abundant from 2930 cal. a BP onward, in line with results from other records from the region. The chironomid fauna of the lake shows high turnover before 7700 cal. a BP, after which an assemblage dominated by taxa indicative of shallow, warm and relatively nutrient rich conditions establishes. A transition to chironomid taxa that are indicative of slightly lower temperatures and lower nutrient levels occurs at 5260 cal. a BP. A chironomid-inferred mean July air temperature record shows unreliable inferences for the record pre-dating 7700 cal. a BP, a Holocene Thermal Maximum with temperatures around 14 °C between 7700-5260 cal. a BP, and temperatures around 12.5 °C between 5260 cal. a BP and the present. A numerical comparison between upland vegetation change and chironomid faunal dynamics for the first time shows that either vegetation change directly impacted on the chironomid fauna of the lake, or alternatively an external factor impacted on both the terrestrial and the aquatic ecosystem, resulting in concurrent changes in both parts of the ecosystem. This novel evidence of ecosystem connectivity is of vital importance to landscape management, as ongoing climate and land use change is likely to lead to increased pressure on lake ecosystems.

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Climate change and land use change, including large-scale vegetation change through e.g. deforestation, are among the most important threats to the natural environment (Steffen *et al.* 2015), and are already impacting on ecosystem functioning and biodiversity (Hallmann *et al.* 2017; Ripple *et al.* 2017). Lakes and other freshwater habitats are amongst the most strongly impacted ecosystems, with e.g. high biodiversity loss reported (Dudgeon *et al.* 2006). It is unclear how continued and increased pressure on lake ecosystems will affect their functioning across the 21st century and beyond.

Palaeoecological records can be used to reconstruct the response of ecosystems to external drivers such as climate change, and can provide new insights into ecosystem functioning on a range of timescales (Willis & Birks 2006; Engels *et al.* 2020). A high number of palaeoecological studies are available for Scandinavia (e.g. Kaufman *et al.* 2020). Many of these records are based on botanical proxies (e.g. pollen, macroremains), together providing a detailed reconstruction of vegetation change across the Holocene (e.g. Giesecke 2005; Barnekow *et al.* 2008; Seppä *et al.* 2009a). Increasingly, palaeoecological studies have focussed on aspects other than vegetation development and have started to employ a wider range of proxy-indicators (e.g. Birks & Birks 2008).

Chironomids (non-biting midge) are holometabolous insects, meaning they have four different life stages: egg, larve, pup and imago or adult. The larval stage of most chironomid species is aquatic, and chironomids can be encountered in virtually all freshwater habitats across the world (Brooks *et al.* 2007). Chironomids are often the most abundant macroinvertebrates in a lake, and they play a critical role in lacustrine food webs, thus contributing to processes essential for lake ecosystem functioning (Hölker *et al.* 2015). Parts of the chironomid larval exoskeleton preserve well in lake sediments, and the analysis of subfossil chironomid remains provides information on ecological, environmental, and climatic developments on a range of timescales (e.g. Brooks 2006).

Temperature is a key variable affecting the chironomid life cycle, and distribution patterns of chironomids in lakes are directly related to ambient air and surface water temperatures (Eggermont & Heiri 2012). Using chironomid-climate calibration datasets (e.g. Brooks & Birks 2001; Nazarova *et* *al.* 2015) and numerical inference models (e.g. Birks *et al.* 2010), chironomid records have been widely used to reconstruct mean July air temperatures (T_{jul}). Chironomid-inferred temperature (CI-T) records now exist for many sites across the globe and cover time-intervals across the last glacial/interglacial cycle and beyond (e.g. Engels *et al.* 2008, 2010; Axford *et al.* 2009; Plikk *et al.* 2019). Whilst T_{jul} is an important driver of chironomid distribution patterns in both space and time (Engels *et al.* 2014, 2020), other environmental factors such as acidity (Brooks *et al.* 2007), trophic levels (Brooks *et al.* 2001), hypolimnetic oxygen (Quinlan & Smol 2001) and lake depth (e.g. Engels *et al.* 2012) also impact on the chironomid fauna of a lake. Chironomid-inferred temperature records and other quantitative climate reconstructions are especially numerous for the Lateglacial period (e.g. Brooks & Langdon, 2014; Heiri *et al.* 2014) as well as for the Holocene (e.g. Brooks *et al.* 2012). However, whilst many quantified palaeoclimate records are available for Scandinavia, there is a surprising lack of Holocene records available for northeast Sweden (Seppä *et al.* 2009b; Kaufman *et al.* 2020).

In addition to providing single-parameter reconstructions of past environmental conditions, palaeoecological records can be used to explore changes in ecosystem functioning using a more holistic approach. For instance, recent studies focus on spatiotemporal trends in taxonomic and/or functional diversity (e.g. Nevalainen & Luoto 2017; Robroek *et al.* 2017; Engels *et al.* 2020), on tracing past changes in the food web (van Hardenbroek *et al.* 2010), and on the interactions between different parts of the ecosystem through studies of past tipping points (e.g. Laug *et al.* 2020). However, there are still many unanswered questions related to the connectivity of different parts of the ecosystem. For instance, while it is clear that vegetation changes in a catchment can impact on acidity, nutrient loading or transparency of freshwater habitats such as lakes and streams (e.g. Neal *et al.* 1992; Drinan *et al.* 2013), it is currently unclear to what extent changes in the vegetation surrounding a lake can impact on the invertebrate community of a lake ecosystem. Impacts of changes in terrestrial vegetation on the invertebrate community of a lake could be relatively direct, through e.g. changing the quality and quantity of food availability. The impacts could also be more indirect, e.g. with changes in vegetation leading to changes in lake water turbidity, which could subsequently impact on the submerged macrophyte community, which forms an important habitat for many chironomid species. A better understanding of such impacts is of vital importance to landscape management, as ongoing climate and land use change is likely to lead to increased pressure on lake ecosystems (Keatley *et al.* 2011).

In this study, I apply chronological, sedimentological and palaeoecological techniques to a lake sediment record from lake Flocktjärn (northeast Sweden) to (i) reconstruct Holocene upland vegetation change; (ii) reconstruct chironomid fauna dynamics across the Holocene; (iii) quantitatively reconstruct past temperature change; and (iv) explore the interaction between changes in upland vegetation and the chironomid fauna of the lake.

Material and methods

Site description and fieldwork

Flocktjärn (64°42'29" N, 20°50'13" E, elevation: 121 m a.s.l.) is a small and shallow lake located ~10 km southwest of the town of Skellefteå (Västerbotten county, Sweden; Fig. 1). Following the retreat of the Scandinavian Ice Sheet at the end of the Last Glacial, the region became ice-free at around *c.* 10500 cal. a BP (Berglund 2004; Lindén *et al.* 2006). Regional shoreline displacement curves suggest that relative sea levels were up to 210 m a.s.l. directly following deglaciation (Lindén *et al.* 2006), implying that the area around lake Flocktjärn was inundated by the sea. The region subsequently became isolated from the sea as a result of isostatic uplift possibly from 9000 cal. a BP onward (Berglund 2004; Lindén *et al.* 2006). The modern-day lake consists of two interconnected basins – a shallower basin in the northern part of the lake (maximum water depth = 2.7 m), and a larger and slightly deeper basin in the southern part of the lake (maximum water depth = 5.2 m). The vegetation in the catchment is mainly boreal forest with *Pinus sylvestris*, *Picea abies* and *Betula* spp. as the main arboreal taxa. The lake is bordered by forests on its western and southern sides and grass meadows are found on the northern and eastern sides of the lake. Relatively extensive marshy areas are found to the north of the lake and could have been formed during phases of higher lake-levels, potentially associated with past changes in hydroclimate such as those associated with the 2.8 ka event (e.g. van Geel *et al.* 1996). Two houses and a gravel road are the only permanent anthropogenic features in the direct vicinity of the lake. At the time of coring (May 2014), the lake measured ~250 x 400 metres and had a pH of 5.4, electric conductivity of 24.2 µS cm^{-1} and dissolved oxygen levels of 48.4% near the bottom of the lake at the time of measurement.

A series of sediment records was obtained along a depth transect across the lake. This study focusses on the sediment record obtained from the centre of the deepest basin of the lake. The upper part of the record (0-26 cm sediment depth) was recovered using a HON/Kajak gravity corer (Renberg 1991) with a diameter of 6.2 cm, and was subsampled in 1-cm increments in the field. Overlapping 1-m-long increments were obtained using a piston corer deployed from a floating platform, and the core segments were subsequently wrapped and transported to the laboratory. Coring was halted when compact sands were reached. A composite sediment record was constructed using the loss-on-ignition profiles of the cores, and depths are reported relative to the sediment/water-interface.

Chronology

Ten samples distributed over the entire sediment record were selected for AMS ^{14}C dating (Table 1) to obtain an accurate chronostratigraphical framework for the palaeoecological data. 1-cm-thick subsamples were deflocculated in warm water and sieved over a 160 µm mesh. Organic material reflecting atmospheric ^{14}C concentrations (such as seeds and fruits from terrestrial plants) was subsequently hand-picked from the residues. As some subsamples were poor in identifiable macroremains, additional core material from adjacent subsamples was combined with the original sample in order to achieve an amount sufficient for radiocarbon dating.

An age-depth model was constructed for the core using the p-sequence approach as included in the OxCAL software v4.4 (Bronk Ramsey 2009) and the IntCAL20 calibration curve

(Reimer *et al.* 2020). In this study, calibrated ages are reported in cal. a BP with reference to the age-depth model presented in Fig. 2, with ages rounded to the nearest decade.

Laboratory analyses

The sediment cores were subsampled at 5 to 10 cm intervals, resulting in 46 1-cm-thick subsamples. 6 weighed samples (2-3 g wet weight) from the unconsolidated gravity core and 40 volumetric samples (1.4c m^3 each) from the more consolidated piston cores were used for loss-on-ignition analysis. The samples were dried in a 105 °C oven for 24 hours before being placed in a furnace at 550 °C for 4 h. Loss-on-ignition was calculated by comparing the dry weight of the samples before and after combustion at 550 °C following Heiri *et al.* (2001).

Volumetric samples of 0.7 cm^3 (upper sample = 2.2 cm^3 as it was unconsolidated material) were prepared for pollen analysis following standard techniques (Faegri & Iversen 1989; Moore *et al.* 1991). A *Lycopodium*-tablet was added to each pollen sample to enable the calculation of pollen concentrations (Stockmarr 1971). Pollen, fern and fungal spores, as well as other non-pollen palynomorphs (NPPs), were identified using a light microscope with 400x magnification using keys and illustrations by Van Geel (1978), Moore *et al.* (1991), Seppä (1996) and Beug (2004). The pollen sum in this study includes trees and upland herbs and varied between 524 and 761 pollen grains per sample, with the exception of the lowermost two samples, which did not yield any pollen and were subsequently excluded from further analyses. Abundances of all pollen, spore and NPP taxa, including those not included in the pollen sum (e.g. aquatic plants) are presented as a percentage relative to the pollen sum.

Samples of 0.8-11.7 g wet weight were used for chironomid analysis. The samples were treated with warm KOH for at least 15 mins and subsequently rinsed over a 100 µm mesh. Chironomid head capsules (hcs) and other zoological macroremains were hand-picked from the residues and mounted on permanent slides using Euparal mounting medium. Identification of chironomid hcs was achieved using a light microscope at 100x and 400x magnification following the taxonomy of Brooks *et al.* (2007). The sum of identified chironomid hcs ranges between 55.5 and 130 hcs per sample, except for the lowermost two samples that did not yield any head capsules.

Palaeoecological diagrams (pollen, chironomids and zoological remains) were plotted using C2 software (Juggins 2007).

Numerical analyses

Prior to numerical analysis, the chironomid dataset was converted to match the taxonomy of the merged Norwegian/Swiss chironomid-climate calibration dataset (Heiri *et al.* 2011). Specimens that could not be identified beyond subfamily or tribe level due to missing mouth parts were excluded from the revised dataset resulting in slightly reduced count sums (minimum = 53 hcs). Principal Component Analysis (PCA) was used to summarise the main trends in the chironomid data.

Zonation of the pollen and chironomid abundance diagrams was derived using the CONISS clustering algorithm (Grimm 1987) where statistical significance of the zones was determined using a Broken Stick model (Bennett 1996). Additional subdivision of the main pollen diagram was based on visual inspection of the downcore record and applied to enable easier interpretation of the main trends in the data.

Mean July air temperatures were reconstructed from the subfossil chironomid dataset using a chironomid–climate calibration data set that includes lakes from Switzerland, Norway and Svalbard (Heiri *et al.* 2011) and spans a mean July air temperature gradient of 3.5–18.4 °C. The calibration dataset contains a total of 274 lakes, where 19 outliers were omitted from the final model after screening of the dataset. A 2-component weighted-averaging partial least squares (WA-PLS) model was selected for reconstruction purposes as this model combined the strongest predictive power with a cross-validated bootstrapped r^2 value of 0.87 between observed mean July air temperature values and those inferred from the chironomid assemblages, a maximum bias of 0.96 °C and a root mean square error of prediction (RMSEP) of 1.40 °C.

A range of methods was used to test the reliability of the chironomid-based temperature reconstruction (Birks *et al.* 1990; Engels *et al.* 2010). The percentage abundance of the identified subfossil chironomids that are absent from or rare in the calibration dataset was calculated for each fossil sample. A taxon was considered rare if it had a Hill's N2 (Hill 1973) below 5 in the calibration data set (Birks *et al.* 1990). Subfossil samples were compared with calibration dataset samples to identify subfossil assemblages with "no close" and "no good" analogues using the modern analogue technique (MAT). Cut-levels of the 5th and 10th percentiles of all squared-chord distances in the modern calibration data were used to determine 'no close' and 'no good' analogues and were compared to the distance between an individual subfossil assemblage and its nearest modern analogue (Birks *et al.* 1990). A so-called goodness-of-fit test was performed using canonical correspondence analysis (CCA) (ter Braak 1986) with July air temperature as the sole constraining parameter with the subfossil samples added passively in the analysis. Residual distances of the subfossil samples to the first CCA axis were compared with the residual distances of all the modern samples to the first CCA axis. Thresholds of the 90th and 95th percentile of residual distances of modern calibration dataset samples to axis 1 were used to identify subfossil samples with a "poor" or "very poor" fit with temperature (Birks *et al.* 1990).

I assessed temporal trends in chironomid alpha diversity, here defined as the taxon richness of an assemblage at one point in time (Engels *et al.* 2020), using rarefaction analysis (e.g. Birks & Line 1992). Rarefaction simulates a random selection without replacement, estimating the taxon richness for each sample using a fixed count size. I first ran rarefaction analysis using the minimum head capsule count in the fossil dataset (n = 53) as the cut-value. As results of rarefaction analyses can be quantitatively compared between samples and data sets with different counts if an identical cut-value is used, I re-ran the analysis using the cut-value to 40 head capsules to enable a quantitative comparison between the results presented here and those by Engels *et al.* (2020). Prior to rarefaction analysis, counts were rounded to integers, where values of 0.5 were rounded up.

In order to test possible associations between changes in upland vegetation and variability in the chironomid record I ran a series of constrained multi-variate analyses. The choice of the type of analysis (linear versus unimodal) was based on the gradient length of the first axis of a Detrended Correspondence Analysis (DCA; Hill & Gauch 1980). DCA using the percent-abundance chironomid dataset showed the gradient length for DCA-axis1 was 3.75 standard deviation units, suggesting unimodal methods were most appropriate for subsequent analyses (Birks 1998). DCA has the advantage of scaling sample scores in SD or compositional turnover units, and the differences in DCA-scores on DCA-axis1 between subsequent samples of a downcore record have been used as an approximation of changes in beta-diversity (Smol *et al.* 2005; Engels *et al.* 2020).

Canonical Correspondence Analysis (CCAs; ter Braak 1986) was used to analyse the effects of vegetation change on the variability in the chironomid record. I summarised the main trends in the pollen record by performing a Principal Component Analysis (PCA) on a subset of the data including all taxa included in the pollen sum. I used the scores of the fossil pollen samples on PCA -axis1 and -axis2 as the sole explanatory variables in two CCA runs to determine the so-called marginal effects of vegetation change on the chironomid fauna of the lake (Lepš & Šmilauer 2003). To specifically test the marginal effect of the arrival of spruce on the variability in the chironomid record I ran a third CCA using the concentration curve of *Picea* as the explanatory variable.

Second, as I observed that the initial part of the chironomid record was mainly influenced by local processes, I repeated the set of constrained analyses using a truncated chironomid dataset. This truncated dataset only included the chironomid samples preserved after the landscape around the lake had stabilised following deglaciation and isostatic rebound, i.e. chironomid zones FL-C2 and -C3 (see below). A DCA on the truncated chironomid dataset showed that DCA-axis1 had a length of 1.97 SD units, and I subsequently used Redundancy Analysis (RDA; ter Braak & Looman 1994) to test the effects of upland vegetation change on the chironomid dataset.

Finally, visual data exploration indicated the existence of non-linear but monotonic relationships between vegetation change (approximated through PCA-axis1 scores) and chironomid diversity, and between vegetation change and the chironomid-inferred T_{jul} record. I therefore calculated Spearman rank-order correlation coefficients to establish the strength of the association between vegetation change and changes in the chironomid-derived records.

WA-PLS was carried out in C2 (Juggins 2007), RDA and CCA were performed using the analogue package (Simpson 2020), CONISS and MAT were performed using the rioja package (Juggins 2017), BSTICK, Rarefaction analysis and DCA were carried out using the vegan package (Oksanen *et al.* 2019) as included in R. PCA was performed using the prcomp function as included in R studio version 1.1.456 (R Core Team 2018). The R script used in this study can be found in Data S1 and all original data is provided in Table S2.

Results and interpretation

Core description and age-depth model

The lowermost part of the sediment record (378-377 cm) consists of grey silty sand with lots of mica. These sediments did not include any botanical or zoological remains, and had an LOI of 0.4% (Fig. 2). Between 377 and 349 cm, a grey silty clay with LOI values of 0.7-3.1% is found. A black organic band with roots and some macroremains (*Betula* seeds) is found at 349-348 cm depth, after which a sediment unit of grey clays transitioning to light brown, organic-rich clays is found between 348 and 328 cm depth. LOI values increase from values of 3% to values of ~11% in this part of the record. From 328 cm upward, the sediments of the Flocktjärn record exist of brown detrital gyttja, with some horizontal banding visible between 328 and 312 cm depth. The LOI record shows values that steadily increase from ~12% at 312 cm depth to values that fluctuate around 30% from 150 cm depth upward.

The age/depth model for the Flocktjärn record suggests lacustrine sedimentation started around 8230 cal. a BP (Fig. 2). It shows relatively high sedimentation rates prior to *c*. 8000 cal. a BP, although dating uncertainties are high in this lowermost part of the record as no radiocarbon dates are available below 348.5 cm core depth. A peak in sedimentation rates can be observed between

6600-6500 cal. a BP followed by relatively high, near linear sedimentation rates observed between *c.* 8000 and 5000 cal. a BP. Between 5000 cal. a BP and the present sedimentation rates are lower than in the preceding period, showing slightly increasing sedimentation rates toward the top of the record.

Pollen record

The pollen diagram is divided into two statistically significant zones where pollen zone FL-P1 is visually subdivided into three subzones (FL-P1a to FL-P1c) to enable interpretation. *Betula* and *Pinus* are the two most abundant tree taxa and are continuously present throughout the core (Figs. 3, S1).

Zone FL-P1a (370-347 cm depth; *c.* 8230-7700 cal. a BP) is characterised by relatively high abundances of *Alnus* (14-40%). FL-P1a furthermore shows relatively high abundances of Poaceae, *Lycopodium annotinum* and monolete spores, and low pollen concentrations. There is a strong peak in HdV-128B algal remains during FL-P1a. A decrease in *Alnus* abundance is observed at the transition to subzone FL-P1b (370 cm depth, *c.* 7700 cal. a BP), where HdV-128B disappears and *Botryococcus* increases in abundance. A minor increase in the abundance of *Ulmus* is seen at the onset of FL-P1c at 243 cm depth (*c.* 6000 cal. a BP), reaching maximum values of 8% before declining again toward the top of the subzone. *Pinus* starts to increase to values over 40% toward the top of subzone FL-P1c, whereas *Betula* abundances remain constant at ~50-60%.

A major change is observed at the onset of FL-B2 at 123 cm depth (*c.* 2930 cal. a BP), when *Picea* gradually increases from percentages below 2% to values over 35%. Whilst *Pinus* percentage-abundances and concentrations do not change across the transition into FL-B2, *Betula* shows a drop in percentage-abundances (from 50-60% to ~30%) as well as in concentrations around *c.* 2930 cal. a BP.

Sample scores on PCA-axis1 gradually increase throughout FL-P1, with a relatively high increase in scores observed at the onset of FL-P2 (Fig. 3). Sample scores on PCA-axis2 shows higher variability, with a sharp drop in sample scores around the transition from subzone FL-P1a to subzone FL-P1b, and minor changes across the other zonal boundaries.

Chironomid record

Following matching of the subfossil taxonomy to that of the combined Norwegian-Swiss calibration dataset, a total of 74 chironomid taxa were encountered in the Flocktjärn sediment record. Additionally, 12 taxa of zoological macroremains were encountered and identified in the chironomids samples. Three statistically significant zones were identified in the chironomid diagram.

The chironomid assemblages of FL-C1 (370-347 cm, *c.* 8230-7700 cal. a BP) are characterised by high abundances of *Heterotrissocladius grimshawi*-type, *Micropsectra insignilobus*-type, *Orthocladius* type S and *Paratanytarsus austriacus*-type (Fig. 4). The concentrations of chironomid head capsules are very low in this part of the record, and no macroremains of other zoological taxa are encountered (Fig. 5). The scores of the fossil samples on DCA-axis1 are high, whereas the taxonomic richness shows the lowest values of the entire record (Fig. 6). A major reorganisation of the chironomid fauna is observed at the onset of FL-C2 (437-204 cm, *c.* 7700-5260 cal. a BP). All taxa that were abundant during zone FL-C1 decline in abundance or disappear from the fauna, and chironomid assemblages characterised by high abundances of *Constempellina*, *Microtendipes pedellus*-type, *Tanytarsus lugens*-type and *Tanytarsus mendax*-type are observed during FL-C2 (Fig. 4). Chironomid concentrations show a slight increase at the onset of FL-C2 but then decrease again to lower values of ~10-20 hc g^{-1} (Fig. 5). A diverse range of macrofossils from other zoological taxa such as Ceratopogonidae head capsules, *Daphnia* ephippia and Ephemeroptera remains are encountered during zone FL-C2 (Fig. 5). The scores of the fossil samples on DCA-axis1 show a sharp decrease across the FL-C1/C2 zonal transition, and taxonomic richness values reach maximum abundances during FL-C2 (Fig. 6). The chironomid diagram shows more gradual changes across the onset of FL-C3 (204 – 0 cm, *c.* 5260 cal. a BP to the present). *Constempellina* disappears from the chironomid assemblages and *Polypedilum nubeculosum*-type, *Stempellinella/Zavrelia* and

Stempellina decrease in abundance. *Heterotanytarsus* appears for the first time at the onset of FL-C3, whereas *Sergentia coracina*-type and *Zalutschia zalutschicola*, already present in the fossil assemblages, increase in abundance (Fig. 4). Chironomid concentrations increase strongly after the onset of FL-C3, reaching maximum values of ~100 hc g^{-1}. Similarly, concentrations of other zoological macroremains such as Ceratopogonidae, *Fredericella* and oribatid mites increase in FL-C3 too (Fig. 5). The scores of the fossil samples on DCA-axis1 show no changes associated with the onset of FL-C3, whereas the taxonomic richness shows a gradual decrease from maximum values of 24 taxa at 259 cm depth to minimum values of 13-15 taxa in the topmost samples (Fig. 6).

Chironomid-inferred temperature record

Chironomid-inferred T_{jul} estimates range between 5.8 and 8.9 °C during FL-C1, increasing sharply to values of 13.5-14.8 °C during FL-C2. A small decrease of temperatures of ~2 °C to values of 12.2 °C is seen at the onset of zone FL-C3, although this is not outside of the uncertainty estimates of the reconstruction (Fig. 6). Chironomid-inferred T_{jul} values range between 11.5 and 13.4 °C for FL-C3.

The percent-abundance of taxa that are either absent from or rare in the modern calibration set does not exceed 2% in any of the fossil samples (Fig. 6). Most fossil samples have no close or no good analogues in the calibration dataset. Fossil samples show high squared-chord distances to their nearest modern analogue during FL-C1, suggesting that the quantitative temperature inferences for this part of the record should be treated with caution. For each zone, some samples have a good fit-to-temperature, whereas others have a poor or a very poor fit to T_{jul}.

Numerical tests

Each of the explanatory variables explains a statistically significant amount of the total inertia in the chironomid dataset (Table 2; $p < 0.05$). PCA-axis2 is the variable that is most strongly related to variation in the chironomid abundances, explaining 13.3% of the variance. PCA-axis2 only explains 2.7% of the variance in the truncated chironomid dataset (including the samples younger than 7700 cal. a BP only), whereas PCA-axis1 scores and the *Picea* concentration curve both explain a statistically significant amount of the total inertia of the truncated chironomid dataset.

The comparison of changes in upland vegetation (estimated through PCA-axis1 scores of the pollen sum taxa) against changes in chironomid diversity shows a Spearman's rank-order coefficient of correlation (rho) of -0.34 (p = 0.989), indicating that no statistically significant association exists between these parameters. Similarly, when the changes in the pollen record are compared to changes in the T_{jul} record no statistically significant association (rho = – 0.39, p = 0.995) is observed.

Discussion

Lake ecosystem development

Regional shoreline displacement reconstructions show a highest coastline approximately 210 m above the present sea level, formed directly after deglaciation at *c*. 10500 cal. a BP (Berglund 2004; Lindén *et al.* 2006). The Early Holocene then shows a period of rapid isostatic rebound with an exponential decline between 10500 and *c*. 9500 cal. a BP followed by a period characterised by constant uplift rates until *c*. 5000 cal. a BP (Lindén *et al.* 2006). As lake Flocktjärn is situated at 121m a.s.l., the regional shoreline curve suggests it could have become isolated from the sea somewhere between 9000 and 8000 cal. a BP. This is in line with the estimated onset of lacustrine sedimentation at lake Flocktjärn at 8230 cal. a BP as shown in this study (Fig. 2).

All chironomid taxa that are abundantly present prior to 7700 cal. a BP are indicative of oligotrophic conditions, profundal habitats and cold temperatures (e.g. Brooks *et al.* 2007). Additionally, low chironomid hc concentrations and the absence of other zoological macroremains suggest low organic productivity in the lake. Combined, this could be taken to indicate that these sediments were deposited during (sub-) arctic conditions. However, other Scandinavian records indicate that at around 8000 cal. a BP Sweden was experiencing temperatures as high as or higher than at present (e.g. Seppä *et al.* 2009b; Väliranta *et al*. 2015). There could be several explanations for the mismatch between the Flocktjärn results and those derived from elsewhere. First, the combination of low LOI values, low pollen concentrations and low chironomid concentrations suggests low production rates in and around the lake. Such conditions could have occurred in a landscape that recently became isolated from the sea following isostatic rebound (Lindén *et al.* 2006). The sparse vegetation that would be typical for such an environment combined with the undeveloped soil profile would mean that relatively high amounts of material were available in the catchment for erosion. Transport of these materials to the lake would have led to a high turbidity, an absence of aquatic macrophytes and low algal production rates, favouring chironomid taxa such as *H. grimshawi*-type that are adapted to such harsh conditions (e.g. Walker & Mathewes 1987). This suggests that the zoological assemblages from FL-C1 would reflect the local environmental processes, and not ambient temperatures. In such a scenario, the chironomid-inferred T_{jul} values for FL-C1 are thought to be unreliable, which is in line with the numerical results presented in Fig. 6. Alternatively, the sediments of FL-C1 could have been deposited during the colder interval known as the 8.2-event (e.g. Wiersma & Renssen 2006). However, the 8.2-event typically showed a temperature decrease of ~1-3 °C across most of the Northern Hemisphere, including Scandinavia (e.g. Seppä *et al.* 2009b; Matero *et al.* 2017), and the reconstructed difference between T_{jul} estimates for FL-C1 and the subsequent zone of ~6-7 °C is significantly larger than the amplitude of change observed elsewhere. A decrease of 1-3 °C would not have been large enough to explain the absence of aquatic macrophytes or the absence of chironomid taxa that prefer intermediate temperatures in favour of a fauna that consists of cold-stenothermic taxa only (Brooks *et al.* 2007). As such, I suggest that the most likely scenario is that the sediments of FL-C1 were deposited directly after isolation from the sea following isostatic rebound, and that the lake ecosystem at that time was strongly impacted by local processes such as sediment influx and turbidity.

At 7700 cal. a BP, cold-indicating taxa are replaced by a diverse fauna consisting of a mix of intermediate- to warm-indicating taxa that are typical inhabitants of the littoral of lakes, and taxa that might indicate sublittoral to profundal habitats (e.g. Engels & Cwynar 2011). Whereas some taxa present during FL-C2 (e.g. *T. lugens*-type) typically occur in oligotrophic lakes, many of the taxa present in lake Flocktjärn between 7700-5260 cal. a BP inhabit meso- to eutrophic lakes (e.g. *Stempellinella/Zavrelia, P. nubeculosum*-type; Brooks *et al.* 2007), in line with the increased abundance of *Botryococcus* remains which also suggests meso- to eutrophic lake water conditions. The taxonomic chironomid diversity of the lake is relatively high and is in line with diversity values found for lakes at similar latitudes across the Northern Hemisphere (Engels *et al.* 2020). The combined evidence therefore suggests that the chironomid fauna of lake Flocktjärn was in equilibrium with its environment and indicates the presence of a meso- to eutrophic lake of intermediate depth.

The chironomid fauna of lake Flocktjärn shows gradual changes around 5260 cal. a BP, with increasing abundances of taxa indicating oligotrophic to mesotrophic conditions and of cold to intermediate temperatures (Brooks *et al.* 2007) and a decrease in chironomid diversity, potentially reflecting a decrease in ambient temperatures. The decrease in deep-water taxon *T. lugens*-type (Engels & Cwynar 2011) could indicate a lowering in lake levels relative to the preceding zone, limiting the availability of profundal habitats.

Comparison of the Flocktjärn T_{jul} *record to other regional climate records*

Based on the reconstruction diagnostics and the identification of processes driving the composition of the chironomid fauna at lake Flocktjärn I suggest that only the part of the chironomid-inferred T_{jul} record between 7700 cal. a BP and the present can be reliably compared to other records from the region.

Kaufman *et al.* (2020) provide an overview of Holocene climate records with quantitative temperature reconstructions, a robust chronological framework and a relatively high sampling resolution over a large part of the Holocene. Whilst their Temperature-12K database contains 10 records for southern and southcentral Sweden (Kaufman *et al.* 2020), it shows that no palaeotemperature records are available for the Västerbotten region, or more generally, for northeast Sweden. A chironomid-inferred T_{jul} record derived from lake Gilltjärnen (Antonsson *et al.*

2006) in south Sweden shows rapidly increasing T_{jul} values from the start of the record to *c.* 7500 cal. a BP. In contrast with the local pollen-inferred temperature record, the chironomid-inferred T_{jul} curve suggests gradually increasing temperatures from 7500 cal. a BP onward to the present. However, Antonsson *et al.* (2006) suggest that acidification of the lake was probably a stronger driver of the local chironomid fauna than ambient air temperatures. The pollen-inferred mean annual temperature record for lake Gilltjärnen shows maximum reconstructed temperatures between *c.* 7000 and 5000 cal. a BP, in line with results derived for lake Flocktjärn. Similarly, Antonsson & Seppä (2007) present a pollen-based mean annual temperature reconstruction for lake Trehörningen and show maximum reconstructed values between 8000-7000 cal. a BP followed by gradually decreasing temperatures up to the present. Seppä *et al.* (2005) suggest that for lake Flarken the Holocene Thermal Maximum was characterised by annual temperatures that were ~2.5 °C higher than at present, which is in line with but slightly higher than the amplitude of 1.8 °C reconstructed for Flocktjärn, derived from comparing the maximum reconstructed temperature around 6230 cal. a BP to the chironomid-inferred T_{jul} value for the top-most sample. A pollen-inferred T_{jul} record from Svanåvatnet (northern Norway; Bjune & Birks 2008) shows highest values of ~14 °C in the Early Holocene, followed by a gradual cooling throughout the Middle and Late Holocene to temperatures of ~11 °C, showing an amplitude of temperature change that again is slightly larger than that observed for Flocktjärn.

Renssen *et al.* (2009) present the results of a set of transient climate model simulations used to study timing and amplitude of the Holocene Thermal Maximum in the Northern Hemisphere. Their model simulations suggest peak temperatures between 8000 and 5000 cal. a BP, with simulated temperatures of ~0.8 °C above current temperatures (Renssen *et al.* 2009). Summarising, both the trends and the amplitude of change observed in the temperature records for more southerly sites match well with the Flocktjärn chironomid-inferred T_{jul} record. Similarly, the timing of the HTM between 8000 and 5000 cal. a BP as determined using a combination of climate model simulations and proxy-evidence matches well with the T_{jul} record from lake Flocktjärn. Whereas

Berntsson *et al.* (2015) find evidence of increased precipitation in northern Sweden associated with the 2.8 ka event (Van Geel *et al.* 1996; Engels *et al.* 2016), no evidence of hydroclimate change either around 2.8 cal. a BP or later in the Holocene is seen in the Flocktjärn record.

Holocene vegetation development at lake Flocktjärn

The dominance of light-demanding pioneer taxa such as birch, ferns and clubmoss, together with the low pollen concentrations, indicates openness of the forest shortly after deglaciation and isolation from the sea (*c.* 8230-7700 cal. a BP). Whilst deglaciation happened at different times in Scandinavia, many lake records similarly show an initial phase of vegetation development with indicators of relative openness (e.g. Bigler *et al.* 2002; Segerström & von Stedingk 2003; Giesecke 2005). High abundances of *Alnus* indicate it most likely established locally between 8230-7700 cal. a BP. The relatively high abundances of *Humulus lupulus* could reflect the occurrence of wild hop growing in *Alnus* stands close to the lake (cf. Segerström 1990). *Alnus* also shows maximum abundances in the pollen record of Svartkälstjärn (close to lake Flocktjärn; Fig. 1) during the Early Holocene (Barnekow *et al.* 2008). Thermophilous arboreal taxa such as *Ulmus* and *Tilia* show only single occurrences prior to 7700 cal. a BP in both the Flocktjärn and the Svartkälstjärn records, potentially reflecting long-distance transport.

The transition to *Betula*-dominated pollen assemblages from 7700 and 7000 cal. a BP onward at Flocktjärn and Svartkälstjärn, respectively, could reflect the regional establishment of denser boreal forest. *Tilia* is present in very low percent-abundances between 7700 and 6000 cal. a BP, and is otherwise virtually absent from the Flocktjärn record. Similarly, many of the other thermophilous taxa (e.g. *Ulmus, Quercus*) occur in single occurrences or low abundances only, still likely reflecting long distance transport, in line with results for Svartkälstjärn (Barnekow *et al.* 2008). As temperatures across large parts of Scandinavia are already high enough to allow the establishment of thermophilous taxa such as *Quercus*, *Tilia* and *Ulmus* (Renssen *et al.* 2009; Väliranta *et al.* 2015), it is likely that migration processes together with edaphic factors are among the main controls on early Middle Holocene distribution patterns of thermophilous arboreal taxa.

Ulmus shows maximum abundances at 6000-2930 cal. a BP at Flocktjärn, 6300 -5000 cal. a BP at Kässjon (Fig. 1; Segerström 1990), and 7500-3500 cal. a BP at Svartkälstjärn (Barnekow *et al.* 2008). This suggest *Ulmus* was established throughout the Västerbotten region between *c.* 6000 and 3000 cal. a BP. In contrast to the Västerbotten region, more southern sites in Sweden (Giesecke 2005; Antonsson & Seppä 2007), in western Norway (Birks & Birks 2013) and in southern Finland (Heikkilä & Seppä 2003) show earlier maximum abundances in thermophilous taxa such as *Ulmus*. In southern Sweden, decreasing abundances in thermophilous taxa from *c.* 6000 cal. a BP onward (Giesecke 2005; Antonsson & Seppä 2007) potentially reflect decreasing temperatures at the end of the Holocene Thermal Maximum (Renssen *et al.* 2009). Hammarlund *et al.* (2004) illustrate the impact of increasing effective moisture and declining growing season length on the Late Holocene boreal forest of north-central Sweden. These environmental factors could additionally have impacted the vegetation around Flocktjärn. More northern locations in Sweden (e.g. Barnekow 1999; Bigler *et al.* 2002,), Norway (Bjune *et al.* 2004; Birks *et al.* 2012) and Finland (Väliranta *et al.* 2011; Salonen *et al.* 2013) do not register the local presence of thermophilous taxa, suggesting these taxa were probably at their northernmost distribution limits in the Västerbotten area.

A strong increase in *Picea* at 2930 cal. a BP is perhaps the most notable change in the Flocktjärn pollen record, and is in line with increases in the abundance of *Picea* at Kassjön at 3100 varve a BP (Segerström 1990) and at 2700 cal. a BP at Svartkälstjärn (Barnekow *et al.* 2008). The immigration of spruce into Fennoscandia has long been a topic of debate. Early studies focussed on the role of climate change as a driver of *Picea* immigration (e.g. Tallantire 1972, 1977; Bradshaw *et al.* 2000), whereas more recent studies further discuss the role of interaction between *Picea abies* and the resident vegetation through competitive replacement processes (Giesecke & Bennett 2004; Antonsson & Seppä 2007; Barnekow *et al.* 2008). Ultimately, the invasion of *Picea* led to a major ecosystem change from a mixed conifer-deciduous forest to the modern boreal conifer forest (Seppä *et al.* 2009a) in large parts of Scandinavia, including the Flocktjärn catchment. The Flocktjärn record shows hardly any evidence for human impact on the vegetation, with e.g. only few Secale-type grains recorded in the topmost samples only.

Influence of Holocene forest dynamics on chironomid fauna of a boreal lake

Terrestrial vegetation explains a statistically significant amount of the total inertia in the chironomid dataset ($p < 0.05$) regardless of how the changes in vegetation are approximated (Table 2). Pollen PCA-axis2 scores show a high amount of variability during the first part of the record (Fig. 7), and as such most likely at least partially reflect vegetation response to local processes such as soil development following isolation from the sea due to isostatic uplift. Similarly, the chironomid data suggested that the lowermost part of the record shows assemblages that reflect processes such as increased sediment influx and landscape instability. This suggests that the terrestrial vegetation as well as the chironomid fauna are influenced by local processes. Around 7700 cal. a BP, vegetation development in the catchment as seen through changes in assemblage composition as well as an increase in pollen concentrations (Fig. 3) could have stabilised the soils, reducing sediment input into the lake, thus potentially impacting on the transparency of the lake water, and ultimately, on the aquatic macrophyte flora as well as the chironomid fauna of Lake Flocktjärn.

When the effects of local processes between 8230-7700 cal. a BP are accounted for by leaving them out of the analysis, vegetation still accounts for a significant amount of the total inertia in the chironomid dataset, with PCA-axis1 and the *Picea* concentration curve explaining statistically significant amounts of the total inertia (Table 2). It should be noted that these parameters are not independent, as *Picea* counts are used to both calculate the *Picea* concentrations as well as the pollen sum, and as such also forms part of the pollen-PCA calculations.

First, it is possible that an external driver such as climate change impacted on both parts of the ecosystem, thus explaining the observed relationship between vegetation and chironomid fauna dynamics. This would be in line with results by Antonsson *et al.* (2006) who show that the chironomid assemblages of lake Gilltjärnen reorganise at *c.* 10200 cal. a BP, around the same time as the sudden expansion of *Alnus* is observed. Antonsson *et al.* (2006) suggest that both *Alnus* and the chironomid fauna of the lake responded to climate as the main driver. Second, it is possible that terrestrial vegetation dynamics directly impacted on the chironomid fauna of lake Flocktjärn. After deglaciation and isostatic uplift, the combined effects of soil and vegetation development most likely led to groundwater flow and overland run-off that gradually became more acidic and nutrient-poor. This could have directly impacted on the lake water quality, and, as a result, on the invertebrate fauna of the lake. However, the chironomid assemblages from 7700 cal. a BP onward are mainly composed of taxa that are indicative of meso- to eutrophic conditions (Fig. 4). The establishment of *Picea* is argued to have the potential to affect lake water quality. For instance, Barnekow *et al*. (2008) suggest that the arrival of *Picea* could have affected aquatic nutrient cycling at lake Svartkälstjärn through the alteration of the soil microbial ecosystem. Antonsson *et al*. (2006) argue that the expansion of spruce at lake Gilltjärnen led to falling pH and a potential increase of the total organic carbon content of the lake water, whereas Korsman *et al*. (1994) suggested that the immigration of *Picea* did not lead to lake water acidification in a set of eight boreal lakes. It is therefore not clear what the effects of the arrival of spruce on lake water quality are, and if the decline in *Betula* and the increase in *Picea* (Fig. 3) could have directly driven changes in the chironomid fauna of lake Flocktjärn. Shumilovskikh *et al.* (2015) observed that the nutrient cycles of ombrotrophic peat bogs can be altered through changes in the amount and source of the pollen that is deposited onto the bogs. Speculatively, nutrient input into lake Flocktjärn could have been altered through the establishment of *Picea* in the catchment. However, whilst *Picea* pollen is relatively large, Fig. 3 shows that overall there is a decrease in the amount of pollen that is deposited in the lake sediments following the establishment of *Picea*. Additionally, the chironomid record (Fig. 4) does not show any major changes between taxa indicative of mesotrophic conditions and those favouring eutrophic conditions around this time. Antonsson *et al.* (2006) additionally discuss the effects of peatland expansion in the lake catchment on lake water acidification. Whilst some peat formation occurs in the areas directly surrounding lake Flocktjärn, the palynological record does not suggest distinct phases of peat formation that could have driven changes in the chironomid fauna similar to those observed by Antonsson *et al.* (2006). Finally, it is possible that no relationship exists between changes in vegetation and changes in the chironomid fauna. It could be the case that the high amount of inertia in the chironomid dataset explained by vegetation is the result of the limited amount of turnover seen in the chironomid record combined with the large amplitude of shift in the *Picea* curve (and by extension in the pollen PCA-axis1 scores). It could also be the case that the observed changes in both palaeoecological records happened to coincide in time as a matter of chance.

Conclusions

Both the terrestrial vegetation and the chironomid fauna of lake Flocktjärn were strongly influenced by local processes prior to 7700 cal. a BP. The chironomid fauna indicates the presence of a meso- to eutrophic lake of intermediate depth between 7700 and 5260 cal. a BP, and chironomid-inferred T_{jul} values fluctuate between 13.5 and 14.8 °C during this time. An expansion of *Ulmus* occurred from 6000 cal. a BP onward, in line with results from nearby locations. The chironomid record indicates a decrease in temperatures of ~2 °C at the end of the Holocene Thermal Maximum at 5260 cal. a BP, and the assemblages change to a fauna more strongly dominated by oligo- to mesotrophic taxa. Around 2930 cal. a BP, *Picea* establishes itself in the vicinity of the lake. Numerical comparison between vegetation change and chironomid dynamics shows that vegetation changes explain a statistically significant proportion of the variance in the chironomid dataset, even when the influence of local processes, assumed to equally impact terrestrial and aquatic ecosystems, is accounted for. This study fills an existing gap in the literature describing quantitative climate records from Scandinavia, and is the first to show a direct relationship between forest dynamics and changes in the chironomid fauna of a boreal lake.

Acknowledgements. I would like to thank Derrick de Ruiter and Erwin Choy for assistance in the field, Annemarie Philip for preparation of the pollen slides, and Bas Van Geel and Heikki Seppä for advice on pollen and spore identification. I am grateful to Christine Lane for assistance with the age-depth modelling, and to Oliver Heiri and co-workers for making the Norwegian/Swiss chironomid-climate calibration dataset publicly available. I would like to thank Bas Van Geel and Jan Sevink for constructive comments that helped to improve an earlier draft of this manuscript. Prof. B. Wagner and an anonymous reviewer are thanked for their constructive feedback and suggestions that helped to improve this manuscript. The map for Fig. 1 was created using the “Creating simple location maps in R” blog post by Benjamin Bell, and numerical results presented in Fig. 6 are produced using the blog posts on quantitative palaeoecology by Richard Telford – thanks go out to both of them for making these scripts publicly available. The research of SE was financed by the Netherlands Organisation for Scientific Research (NWO, project 863.11.009)

Data availability. All data presented in this paper are included in the Supporting Information; the data will also be made available on the NOAA webpage.

References

Antonsson, K. & Seppä, H. 2007: Holocene temperatures in Bohuslän, southwest Sweden: a quantitative reconstruction from fossil pollen data. *Boreas 36,* 400-410.

Antonsson, K., Brooks, S. J., Seppä, H., Telford, R. J. & Birks, H. J. B. 2006: Quantitative palaeotemperature records inferred from fossil pollen and chironomid assemblages from Lake Gilltjärnen, northern central Sweden. *Journal of Quaternary Science 21,* 831-841.

Axford, Y., Briner, J. P., Francis, D. R., Miller, G. H., Walker, I. R. & Wolfe, A. P. 2009: Chironomids record terrestrial temperature changes throughout Arctic interglacials of the past 200,000 yr. *Geological Society of America Bulletin 123,* 1275–1287.

Barnekow, L. 1999: Holocene tree-line dynamics and inferred climatic changes in the Abisko area, northern Sweden, based on macrofossil and pollen records. *The Holocene 9,* 253-265.

Barnekow, L., Bragée, P., Hammarlund, D. & St Amour, N. 2008: Boreal forest dynamics in north-eastern Sweden during the last 10,000 years based on pollen analysis. *Vegetation History and Archaeobotany 17,* 687-700.

Bennett, K. D. 1996: Determination of the number of zones in a biostratigraphical sequence. *New Phytologist 132,* 155–170.

Berglund, M. 2004: Holocene shore displacement and chronology in Ångermanland, eastern Sweden, the Scandinavian glacio-isostatic uplift centre. *Boreas 33*, 48-60.

Berntsson, A., Jansson, K. N., Kylander, M. E., de Vleeschouwer, F. & Bertrand, S. 2015: Late Holocene high precipitation events recorded in lake sediments and catchment geomorphology, Lake Vuoksjávrátje, NW Sweden. *Boreas 44*, 676-692.

Beug, H. 2004: *Leitfaden der Pollenbestimmung für Mitteleuropa und angrenzende Gebiete.* 542 pp. Verlag Dr. Friedrich Pfeil, Munich.

Bigler, C., Larocque, I., Peglar, S. M., Birks, H. J. B. & Hall, R. I. 2002: Quantitative multiproxy assessment of long-term patterns of Holocene environmental change from a small lake near Abisko, northern Sweden. *The Holocene 12,* 481-496.

Birks, H. J. B. 1998: Numerical tools in palaeolimnology—progress, potentialities, and problems. *Journal of Paleolimnology 20,* 307–332.

Birks, H. H. & Birks, H. J. B. 2008: Biological responses to rapid climate change at the Younger Dryas-Holocene transition at Kråkenes, Western Norway. *The Holocene 18,* 19-30.

Birks, H. H. & Birks, H. J. B. 2013: Vegetation responses to late-glacial climate changes in western Norway. *Preslia 85*, 215–237.

Birks, H. J. B. & Line, J. M. 1992: The use of rarefaction analysis for estimating palynological richness from Quaternary pollen-analytical data. *The Holocene 2,* 1–10.

Birks, H. J. B., Line, J. M., Juggins, S., Stevenson, A. C. & ter Braak, C. J. F. 1990: Diatoms and pH reconstruction. *Philosophical Transactions of the Royal Society of London Series B 327,* 263–278.

Birks, H. J. B., Heiri, O., Seppä, H. & Bjune, A. E. 2010: Strengths and Weaknesses of Quantitative Climate Reconstructions Based on Late-Quaternary Biological Proxies. *The Open Ecology Journal 3,* 68-110.

Birks, H. H., Jones, V. J., Brooks, S. J., Birks H. J. B., Telford, R. J., Juggins, S. & Peglar, S. M. 2012: From cold to cool in northernmost Norway: Lateglacial and early Holocene multi-proxy environmental and climate reconstructions from Jansvatnet, Hammerfest. *Quaternary Science Reviews 33*, 100-120.

Bjune, A. E. & Birks, H. J. B. 2008: Holocene vegetation dynamics and inferred climate changes at Svanåvatnet, Mo i Rana, northern Norway. *Boreas 37*, 146-156.

Bjune, A. E., Birks, H. J. B. & Seppä, H. 2004: Holocene vegetation and climate history on a continental–oceanic transect in northern Fennoscandia based on pollen and plant macrofossils. *Boreas 33*, 211-223.

Bradshaw, R. H. W., Holmqvist, B. H., Cowling, S. A. & Sykes, M. T. 2000: The effects of climate change on the distribution and management of Picea abies in southern Scandinavia. *Canadian Journal of Forest Research 30,* 1992-1998.

Bronk Ramsey, C. 2009: Bayesian analysis of radiocarbon dates. *Radiocarbon 51,* 337–360.

Brooks, S. J. 2006: Fossil midges (Diptera: Chironomidae) as palaeoclimatic indicators for the Eurasian region. *Quaternary Science Reviews 25,* 1894–1910.

Brooks, S. J. & Birks, H. J. B. 2001: Chironomid-inferred air temperatures from Late-glacial and Holocene sites in north–west Europe: progress and problems. *Quaternary Science Reviews 20,* 1723–1741.

Brooks, S. J. & Langdon, P. G. 2014: Summer temperature gradients in northwest Europe during the Lateglacial to early Holocene transition (15-8 ka BP) inferred from chironomid assemblages. *Quaternary International 341,* 80-90.

Brooks, S. J., Bennion, H. & Birks, H. J. B. 2001: Tracing lake trophic history with a chironomid-total phosphorus inference model. *Freshwater Biology 46,* 513-533.

Brooks, S. J., Langdon, P. G. & Heiri, O. 2007: *The Identification and Use of Palaearctic Chironomidae Larvae in Palaeoecology (Quaternary Research Association Technical Guide No. 10)*. 276 pp. Quaternary Research Association, London.

Brooks, S. J., Axford, Y., Heiri, O., Langdon, P. G. & Larocque-Tobler, I. 2012: Chironomids can be reliable proxies for Holocene temperatures. A comment on Velle *et al.* (2010). *The Holocene 22,* 1495-1500.

Drinan, T. J., Graham, C. T., O'Halloran, J. & Harrison, S. C. C. 2013: The impact of catchment conifer plantation forestry on the hydrochemistry of peatland lakes. *Science of the Total Environment 443,* 608-620.

Dudgeon, D., Arthinton, A. H., Gessner, M. O., Kawabata, Z.-I., Knowler, D.J., Lévêque, C., Naiman, R. J., Prieur-Richard, A.-H., Soto, D., Stiassny, S. L. J. & Sullivan, C. A. 2006: Freshwater biodiversity: importance, threats, status and conservation challenges. *Biological Reviews 81,* 163-182.

Eggermont, H. & Heiri, O. 2012: The chironomid-temperature relationship: expression in nature and palaeoenvironmental implications. *Biological reviews 87,* 430-456.

Engels, S. & Cwynar, L. C. 2011: Changes in fossil chironomid remains along a depth gradient: evidence for common faunal breakpoints within lakes. *Hydrobiologia 665,* 15-38.

Engels, S., Bohncke, S. J. P., Bos, J. A. A., Brooks, S. J., Heiri, O. & Helmens, K. F. 2008: Chironomid-based palaeotemperature estimates for northeast Finland during Oxygen Isotope Stage 3. *Journal of Paleolimnology 40,* 49-61.

Engels, S., Helmens, K. F., Väliranta, M., Brooks, S. J. & Birks, H. J. B. 2010: Early Weichselian (MIS 5d and 5c) temperatures and environmental changes in northern Fennoscandia as recorded by chironomids and macroremains at Sokli, northeast Finland. *Boreas 39,* 689-704.

Engels, S., Cwynar, L. C., Shuman, B. N. & Rees, A. B. H. 2012: Chironomid-based water depth reconstructions: an independent evaluation of site-specific and local inference models. *Journal of Paleolimnology 48,* 693-709.

Engels, S., Self, A. E., Luoto, T. P., Brooks, S. J. & Helmens, K. F. 2014: A comparison of three Eurasian chironomid–climate calibration datasets on a W–E continentality gradient and the implications for quantitative temperature reconstructions. *Journal of Paleolimnology 51,* 529–547.

Engels, S., Bakker, M. A. J., Bohncke, S. J. P., Cerli, C., Hoek, W. Z., Jansen, B., Peters, T., Renssen, H., Sachse, D., van Aken, J. M., van den Bos, V., van Geel, B., van Oostrom, R., Winkels, T. & Wolma, M. 2016: Centennial-scale lake-level lowstand at Lake Uddelermeer (The Netherlands) indicates changes in moisture source region prior to the 2.8-kyr event. *The Holocene 26,* 1075-1091.

Engels, S., Medeiros, A. S., Axford, Y., Brooks, S. J., Heiri, O., Luoto, T. P., Nazarova, L., Porinchu, D. F., Quinlan, R. & Self, A. E. 2020: Temperature change as a driver of spatial patterns and long-term trends in chironomid (Insecta: Diptera) diversity. *Global Change Biology 26,* 1155-1169.

Faegri, K. & Iversen, J. 1989: *Textbook of Pollen Analysis*. 328 pp. John Wiley & Sons, Chichester.

Giesecke, T. 2005: Holocene dynamics of the southern boreal forest in Sweden. *The Holocene 15,* 858-872.

Giesecke, T. & Bennett, K. D. 2004: The Holocene spread of *Picea abies* (L.) Karst. in Fennoscandia and adjacent areas. *Journal of Biogeography 31*, 1523–1548.

Grimm, E. C. 1987: CONISS: a FORTRAN 77 program for stratigraphically constrained cluster analysis by the method of incremental sum of squares. *Computers and Geosciences 13,* 13-35.

Hallmann, C. A., Sorg, M., Jongejans, E., Siepel, H., Hofland, N., Schwan, H., Stenmans, W., Müller, A., Sumser, H., Hörren, T., Goulson, D. & de Kroon, H. 2017: More than 75 percent decline over 27 years in total flying insect biomass in protected areas. *PLOS One 12,* e0185809, doi:10.1371/journal.pone.0185809.

Hammarlund, D., Velle, G., Wolfe, B. B., Edwards, T. W. D., Barnekow, L., Bergman, J., Holmgren, S., Lamme, S., Snowball, I., Wohlfarth, B. & Possnert, G. 2004: Palaeolimnological and sedimentary responses to Holocene forest retreat in the Scandes Mountains, west-Central Sweden. *The Holocene 14*, 862-876.

Heikkilä, M. & Seppä, H. 2003: A 11,000 yr palaeotemperature reconstruction from the southern boreal zone in Finland. *Quaternary Science Reviews 22*, 541–554.

Heiri, O., Lotter, A. F. & Lemcke, G. 2001: Loss on ignition as a method for estimating organic and carbonate content in sediments: reproducibility and comparability of results. *Journal of Paleolimnology 25,* 101–110.

Heiri, O., Brooks, S. J., Birks, H. J. B. & Lotter, A. F. 2011: A 274-lake calibration data-set and inference model for chironomid-based summer air temperature reconstruction in Europe. *Quaternary Science Reviews 30,* 3445-3456.

Heiri, O., Brooks, S. J., Renssen, H., Bedford, A., Hazekamp, M., Ilyashuk, B., Jeffers, E. S., Lang, B., Kirilova, E., Kuiper, S., Millet, L., Samartin, S., Toth, M., Verbruggen, F., Watson, J. E., van Asch, N., Lammertsma, E., Amon, L., Birks, H. H., Birks, H. J. B., Mortenson, M. F., Hoek, W. Z., Magyari, E., Munoz Sobrino, C., Seppä, H., Tinner, W., Tonkov, S., Veski, S. & Lotter, A. F. 2014: Validation of climate model-inferred regional temperature change for late-glacial Europe. *Nature Communications 5,* 4914, doi:10.1038/ncomms5914.

Hill, M. O. 1973: Diversity and evenness: a unifying notation and its consequences. *Ecology 54,* 427–432.

Hill, M. O. & Gauch, H.G. 1980: Detrended correspondence analysis: an improved ordination technique. *Vegetatio 42,* 47–58.

Hölker, F., Vanni, M. J., Kuiper, J. J., Meile, C., Grossart, H.-P., Stief, P., Adrian, R., Lorke, A., Dellwig, O., Brand, A., Hupfer, M., Mooij, W. M., Nützmann, G. & Lewandowski, J. 2015: Tube-dwelling invertebrates: tiny ecosystem engineers have large effects in lake ecosystems. *Ecological Monographs 85,* 333-351.

Juggins, S. 2007: *C2 User Guide. Software for Ecological and Palaeoecological Data Analysis and Visualisation, version 1.5.* University of Newcastle, Newcastle upon Tyne.

Juggins, S. 2017: *rioja: Analysis of Quaternary Science Data, R package version (0.9-21).* http://cran.r-project.org/package=rioja

Kaufman, D. and 92 others 2020: A global database of Holocene paleo-temperature records. *Nature Scientific Data 7,* 115, doi:10.1038/s41597-020-0445-3.

Keatley, B. E., Bennett, E. M., MacDonald, G. K., Taranu, Z. E. & Gregory-Eaves, I. 2011: Land-Use Legacies Are Important Determinants of Lake Eutrophication in the Anthropocene. *PloS One 6,* e15913, doi:10.1371/journal.pone.0015913.

Korsman, T., Renberg, I. & Anderson, N. J. 1994: A palaeolimnological test of the influence of Norway spruce (Picea abies) immigration on lake-water acidity. *The Holocene 4*, 132–140.

Laug, A., Schwarz, A., Lauterbach, S., Engels, S. & Schwalb, A. 2020: Ecosystem Reactions to two Mid-Holocene Tipping Points in the Central Asian Lake Son Kol. *The Holocene 30,* 1410-1419.

Lepš, J. & Šmilauer, P. 2003: *Multivariate Analysis of Ecological Data using CANOCO.* 296 pp. University Press, Cambridge.

Lindén, M., Möller, P., Björk, S. & Sandgren, P. 2006: Holocene shore displacement and deglaciation chronology in Norrbotten, Sweden. *Boreas 35,* 1-22.

Matero, I. S. O., Gregoire, L. J., Ivanovic, R. J., Tindall, J. C. & Haywood, A. M. 2017: The 8.2 ka cooling event caused by Laurentide ice saddle collapse. *Earth and Planetary Science Letters 473,* 205-214.

Moore, P. D., Webb, J. A. & Collinson, M. E. 1991: *Pollen Analysis*. 216 pp. Blackwell, Malden.

Nazarova, L., Self, A. E., Brooks, S. J., van Hardenbroek, M., Herzschuh, U. & Diekmann, B. 2015: Northern Russian chironomid-based modern summer temperature data set and inference models. *Global and Planetary Change 134,* 10–25.

Neal, C., Reynolds, B., Smith, C. J., Hill, S., Neal, M., Conway, T., Ryland, G. P., Jeffrey, H., Robson, A. J. & Fisher, R. 1992: The impact of conifer harvesting on stream water pH, alkalinity and aluminium concentrations for the British uplands: an example for an acidic and acid sensitive catchment in mid-Wales. *Science of the Total Environment 126*, 75-87.

Nevalainen, L. & Luoto, T. P. 2017: Relationship between cladoceran (Crustacea) functional diversity and lake trophic gradients. *Functional Ecology 31*, 488-498.

Oksanen, J., Blanchet, F. G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., Minchin, P. R., O'Hara, R. B., Simpson, G. L., Solymos, P., Stevens, M. H. H., Szoecs, E. & Wagner, H. 2019: *vegan: Community Ecology Package. R package version 2.5-5*. https://CRAN.R-project.org/package=vegan.

Plikk, A., Engels, S., Luoto, T. P., Nazarova, L., Salonen, S. J. & Helmens, K. F. 2019: Chironomid-based temperature reconstruction for the Eemian Interglacial (MIS 5e) at Sokli, northeast Finland. *Journal of Paleolimnology 61,* 355-371.

Quinlan, R. & Smol, J. P. 2001: Chironomid-based inference models for estimating end-of-summer hypolimnetic oxygen from south-central Ontario shield lakes. *Freshwater Biology 46,* 1529–1551.

R Core Team 2018: *R: A language and environment for statistical computing.* https://www.R-project.org

Reimer, P. and 41 others 2020: The IntCal20 Northern Hemisphere radiocarbon age calibration curve (0–55 cal kBP). *Radiocarbon 62*, 725-757.

Renberg, I. 1991: The HON-Kajak sediment corer. *Journal of Paleolimnology 6,* 161–170.

Renssen, H., Seppä, H., Heiri, O., Roche, D. M., Goosse, H. & Fichefet, T. 2009: The spatial and temporal complexity of the Holocene thermal maximum. *Nature Geoscience 2,* 411–414.

Ripple, W. J., Wolf, C., Newsome, T. M., Galetti, M., Alamgir, M., Crist, E., Mahmoud, M. I. & Laurance, W. F. 2017: World scientists' warning to humanity: a second notice. *Bioscience 67,* 1026-1028.

Robroek, B. J. M., Jassey, V. E. J., Payne, R. J., Martí, M., Bragazza, L., Bleeker, A., Buttler, A., Caporn, S. J. M., Dise, N. B., Kattge, J., Zając, K., Svensson, B. H. & Verhoeven, J. T. A. 2017: Taxonomic and functional turnover are decoupled in European peat bogs. *Nature Communications 8,* 1161, doi:10.1038/s41467-017-01350-5.

Salonen, J. S., Helmens, K. F., Seppä, H. & Birks, H. J. B. 2013: Pollen-based palaeoclimate reconstructions over long glacial–interglacial timescales: Methodological tests based on the Holocene and MIS 5d–c deposits of Sokli, northern Finland. *Journal of Quaternary Science 28*, 271– 282.

Segerström, U. 1990: *The Natural Holocene Vegetation Development and the Introduction of Agriculture in Northern Norrland, Sweden*. 160 pp. University of Umeå, Umeå.

Segerström, U. & van Stedingk, H. 2003: Early-Holocene spruce, Picea abies (L.) Karst., in west central Sweden as revealed by pollen analysis. *The Holocene 13,* 897-906.

Seppä, H. 1996: Postglacial dynamics of vegetation and tree-lines in the far north of Fennoscandia. *Fennia 147*, 1-96.

Seppä, H., Hammarlund, D. & Antonsson, K. 2005: Low-frequency and high-frequency changes in temperature and effective humidity during the Holocene in south-central Sweden: implications for atmospheric and oceanic forcings of climate. *Climate Dynamics 25,* 285-297.

Seppä, H., Alenius, T., Bradshaw, R. H. W., Giesecke, T., Heikkilä, M. & Muukkonen, P. 2009a: Invasion of Norway spruce (*Picea abies*) and the rise of the boreal ecosystem in Fennoscandia. *Journal of Ecology 97*, 629-640.

Seppä, H., Bjune, A. E., Telford, R. J., Birks, H. J. B. & Veski, S. 2009b: Last nine-thousand years of temperature variability in Northern Europe. *Climate of the Past 5,* 523-535.

Shumilovskikh, L. S., Schlütz, F., Achterberg, I., Kvitkina, A., Bauerochse, S. & Leuschner, H. H. 2015: Pollen as nutrient source in Holocene ombrotrophic bogs. *Review of Palaeobotany and Palynology 221*, 171-178.

Simpson, G. 2020*: Analogue: Analogue and Weighted Averaging Methods for Palaeoecology. R package version (0.17-4).* https://cran.r-project.org/web/packages/analogue/analogue.pdf.

Smol, J. P., Wolfe, A. P., Birks, H. J. B., Douglas, M. S. V., Jones, V. J., Korhola, A., Pienitz, R., Rühland, K., Sorvari, S., Antoniades, D., Brooks, S. J., Fallu, M.-A., Hughes, M., Keatley, B. E., Laing, T. E., Michelutti, N., Nazarova, L., Nyman, M., Paterson, A. M., Perren, A. M., Quinlan, R., Rautio, M., Saulnier-Talbot, E., Siitonen, S., Solovieva, N. & Weckström, J. 2005: Climate-driven regime shifts in the biological communities of arctic lakes. *Proceedings of the National Academy of Sciences 102,* 4397-4402.

Steffen, W., Richardson, K., Rockström, J., Cornell, S. E., Fetzer, I., Bennett, E. M., Biggs, R., Carpenter, S. R., de Vries, W., de Wit, C. A., Folke, C., Gerten, D., Heinke, J., Mace, G. M., Persson, L. M., Ramanathan, V., Reyers, B. & Sörlin, S. 2015: Planetary boundaries: Guiding human development on a changing planet. *Science 347,* 1259855, doi:10.1126/science.1259855.

Stockmarr, J. 1971: Tablets with spores used in absolute pollen analysis. *Pollen et Spores 13,* 615–621.

Tallantire, P. A. 1972: The regional spread of spruce (Picea abies (L.) Karst.) within Fennoscandia: a reassessment. *Norwegian Journal of Botany 19,* 1-16.

Tallantire, P. A. 1977: A further contribution to the problem of the spread of spruce (Picea abies (L.) Karst.) in Fennoscandia. *Journal of Biogeography 4*, 219-227.

ter Braak, C. J. F. 1986: Canonical correspondence analysis: a new eigenvector method for multivariate direct gradient analysis. *Ecology 67,* 1167–1179.

ter Braak, C. J. F. & Looman, C. W. N. 1994: Biplots in reduced-rank regression. *Biometrical Journal 36,* 983–1003.

Väliranta, M., Weckström, J., Siitonen, S., Seppä, H., Alkio, J., Juutinen, S. & Tuittila, E.-S. 2011: Holocene aquatic ecosystem change in the boreal vegetation zone of northern Finland. *Journal of Paleolimnology* 45, 339-352.

Väliranta, M., Salonen, J. S., Heikkilä, M., Amon, L., Helmens, K. F., Klimaschewski, A., Kuhry, P., Kultti, S., Poska, A., Shala, S., Veski, S. & Birks, H. H. 2015: Plant macrofossil evidence for an early onset of the Holocene summer thermal maximum in northernmost Europe. *Nature Communications 6*, 6809, doi:10.1038/ncomms7809.

Van Geel, B. 1978: A palaeoecological study of Holocene peat bog sections in Germany and the Netherlands. *Review of Palaeobotany and Palynology 25,* 1–120.

Van Geel, B., Buurman, J., & Waterbolk, H. T. 1996: Archeological and palaeoecological indications of an abrupt climate change in The Netherlands, and evidence for climatological teleconnections around 2650 BP. *Journal of Quaternary Science 11,* 451–460.

Van Hardenbroek, M., Heiri, O., Grey, J., Bodelier, P. L. E., Verbruggen, F. & Lotter, A. F. 2010: Fossil chironomid $\delta^{13}C$ as a proxy for past methanogenic contribution to benthic food webs in lakes? *Journal of Paleolimnology 43,* 235-245.

Walker, I. R. & Mathewes, R. W. 1987: Chironomidae (Diptera) and Postglacial Climate at Marion Lake, British Columbia, Canada. *Quaternary Research 27,* 89-102.

Wiersma, A. P. & Renssen, H. 2006: Model–data comparison for the 8.2 ka BP event: confirmation of a forcing mechanism by catastrophic drainage of Laurentide Lakes. *Quaternary Science Reviews 25,* 63-88.

Willis, K. J. & Birks, H. B. J. 2006: What Is Natural? The Need for a Long-Term Perspective in Biodiversity Conservation. *Science 314,* 1261-1265.

Figures:

Fig. 1. A. Location of lake Flocktjärn (grey diamond) and other sites mentioned in the text (blue squares). See Table S1 for the names of the sites. B. Local map showing lake bathymetry (blue-grey, isolines showing 1-m depth intervals) and land use around the lake. Coordinates in the Swedish grid system (RT90) with units in metres. P = production forest; W = wetland including alder carr; G = grass meadow.

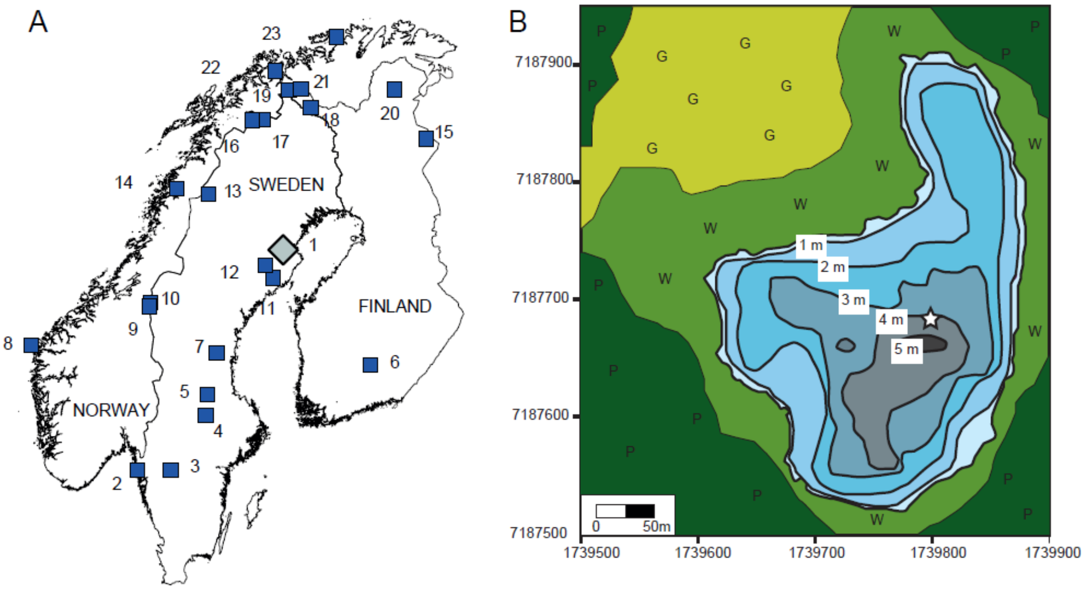


Fig. 2. A. Simplified core description, loss-on-ignition (%) and positions (depths) of the radiocarbon samples (Table 1). Rt = root material; mr= other visible macroremains. B. Age-depth model (grey) and probability distributions for the radiocarbon dates (black). C. Sedimentation rates (mm a^{-1}).

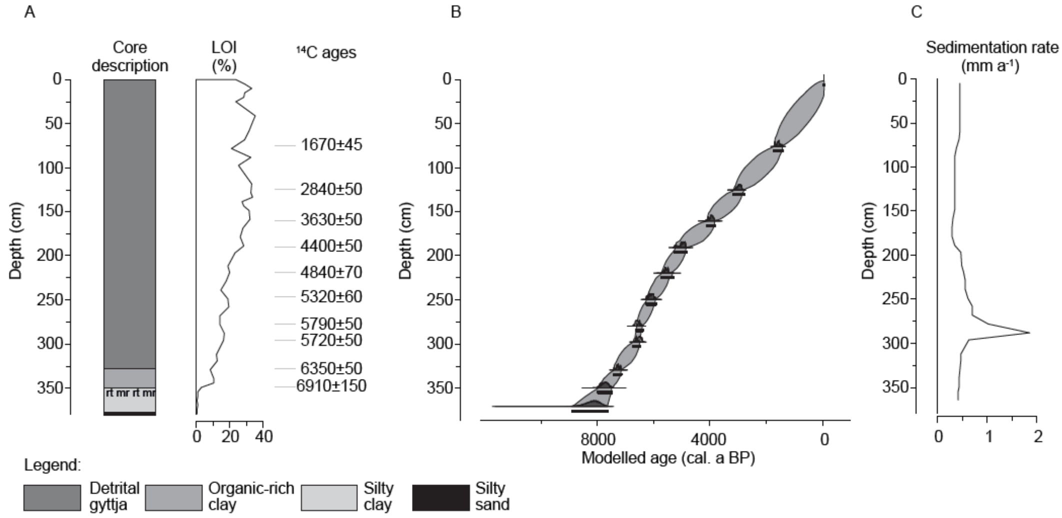


Fig. 3. Summary diagram of the Flocktjärn pollen record. A. Percentage curves of selected pollen, spore and algal taxa (%). B. Pollen concentration curves (pollen g^{-1}). C. Scores of the samples on the first two axes of a PCA on the pollen sum taxa. Data are plotted on a depth scale (cm) with a time scale (cal. a BP) plotted for reference. Note the different scale used for HDV-128B in A. Main zonation (solid grey line) based on CONISS analysis with zonal subdivisions (dashed grey line) based on important transitions in the pollen spectra.

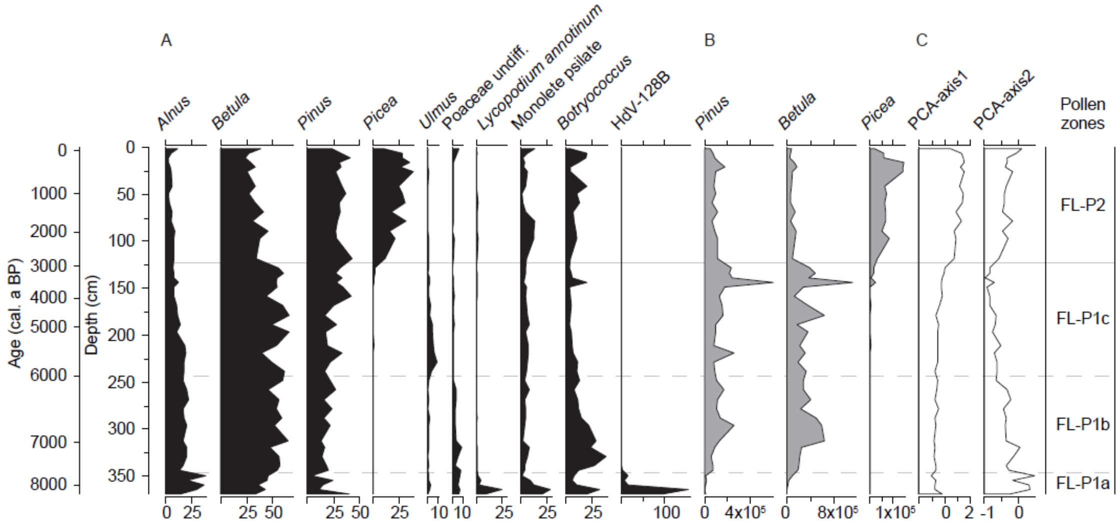


Fig. 4. Percent-abundance diagram showing selected chironomid taxa for Flocktjärn. Data are plotted on a depth scale (cm) with a time scale (cal. a BP) plotted for reference. Count sum per sample (number of hcs) and CONISS-based zonation plotted to the right.

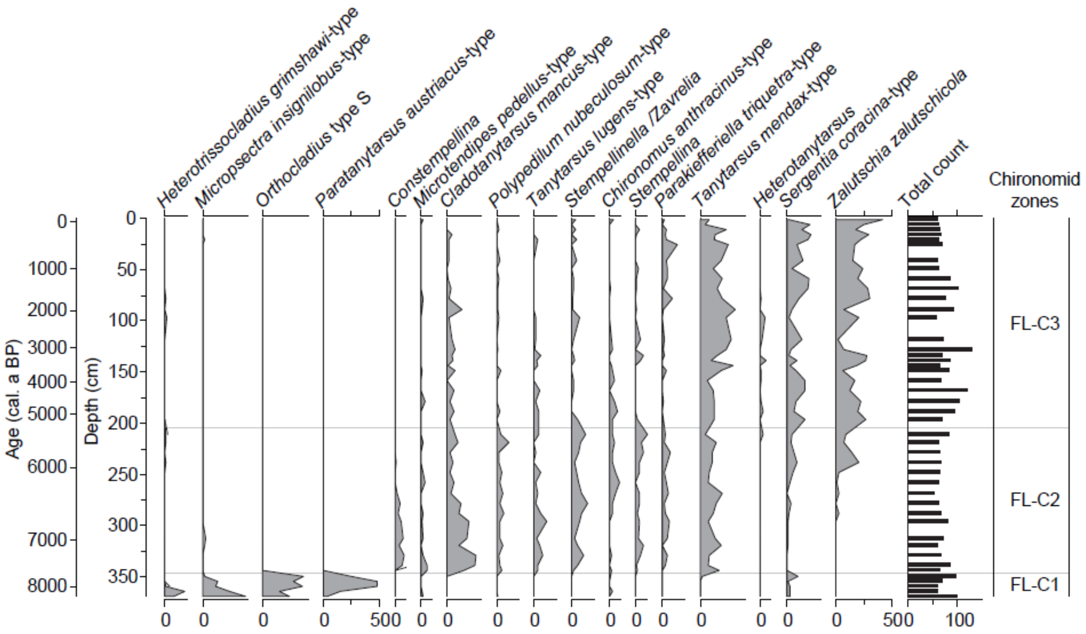


Fig. 5. Chironomid head capsule concentrations and concentrations of other zoological macrofossils encountered during chironomid analysis (number cm^{-3}). Note the different scalings used for the x-axes. Data are plotted on a depth scale (cm) with a time scale (cal. a BP) plotted for reference. Chironomid-based zonation plotted to the right.

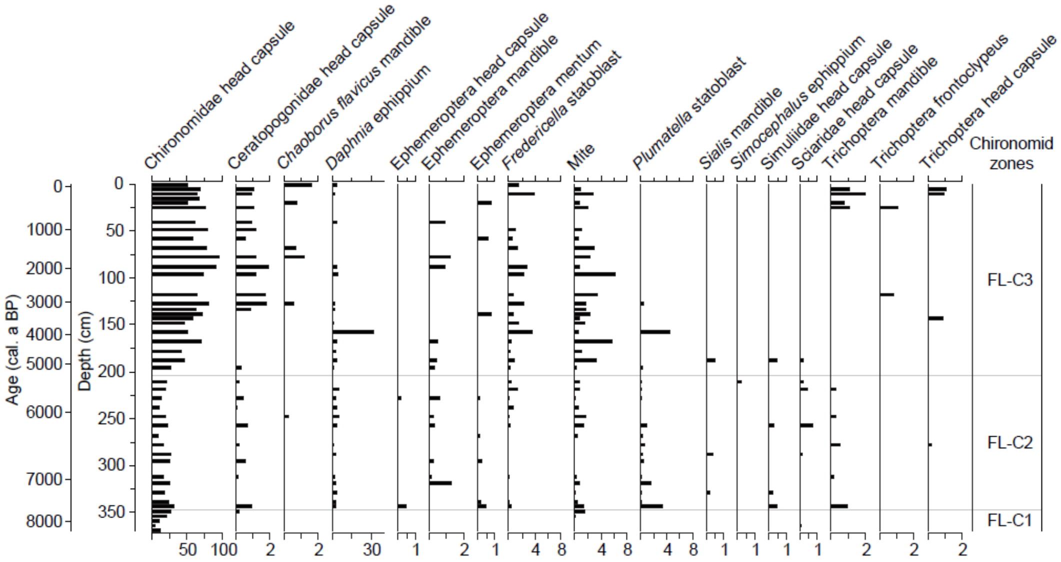


Fig. 6. A. Chironomid diversity trends with compositional turnover as scores of the fossil samples on the first axis of a detrended correspondence analysis (DCA) in Standard Deviation (SD) units and taxonomic richness estimated through rarefaction analysis with cut-values of 40 and 53 head capsules (dotted and solid line, respectively). B. Chironomid-inferred July air temperature (T_{jul}) record with reconstruction diagnostics: cumulative percent-abundance of fossil chironomids that are absent from the calibration dataset (%Absent); cumulative percent-abundance of fossil chironomids that are rare in the calibration dataset (%Rare); the distance to the nearest modern analogues (MAT) in the calibration dataset (squared-chord distance) with vertical lines showing no close (dotted) and no good (dashed) analogues; Goodness-of-fit (G-O-F) of the fossil samples to the first axis of a CCA constrained to temperature as squared residual length, with vertical lines indicating the 90th (poor, dotted) and 95th (very poor, dashed) percentiles of residual distances of the modern samples to CCA-axis1, respectively. Data are plotted on a depth scale (cm) with a time scale (cal. a BP) plotted for reference. Chironomid-based zonation plotted to the right.

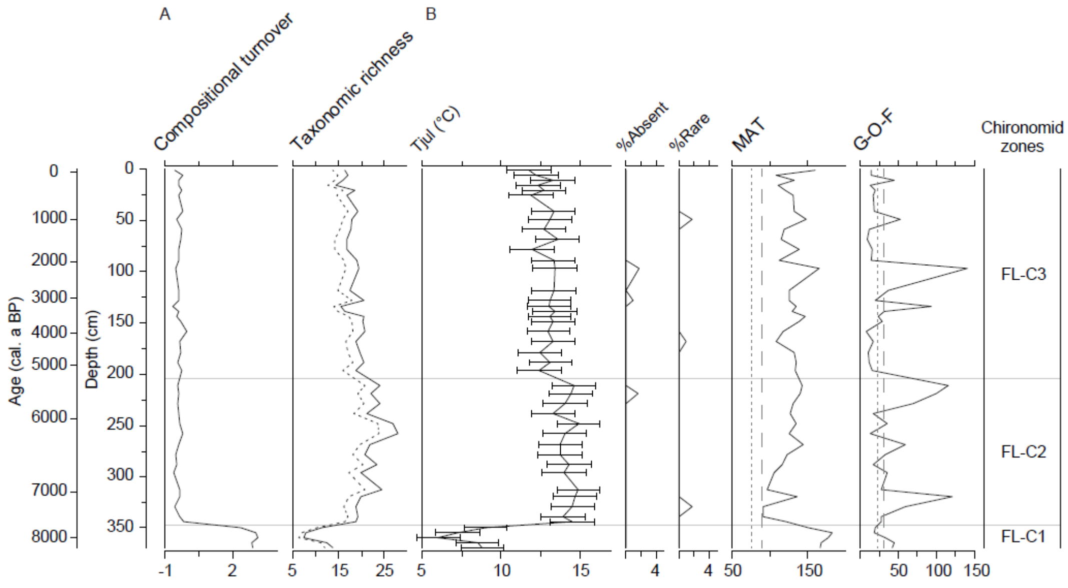


Fig. 7. Summary diagram of the main palaeoecological results for the Flocktjärn record. A. Pollen results: PCA-axis1 and -axis2 scores and *Picea* concentrations (pollen grains/g), with pollen-based zonation. B. Chironomid results: percent-abundance curves of selected taxa, PCA-axis1 and -axis2 scores, chironomid-inferred July air temperature (T_{jul}) and taxonomic richness curves, with chironomid-based zonation.

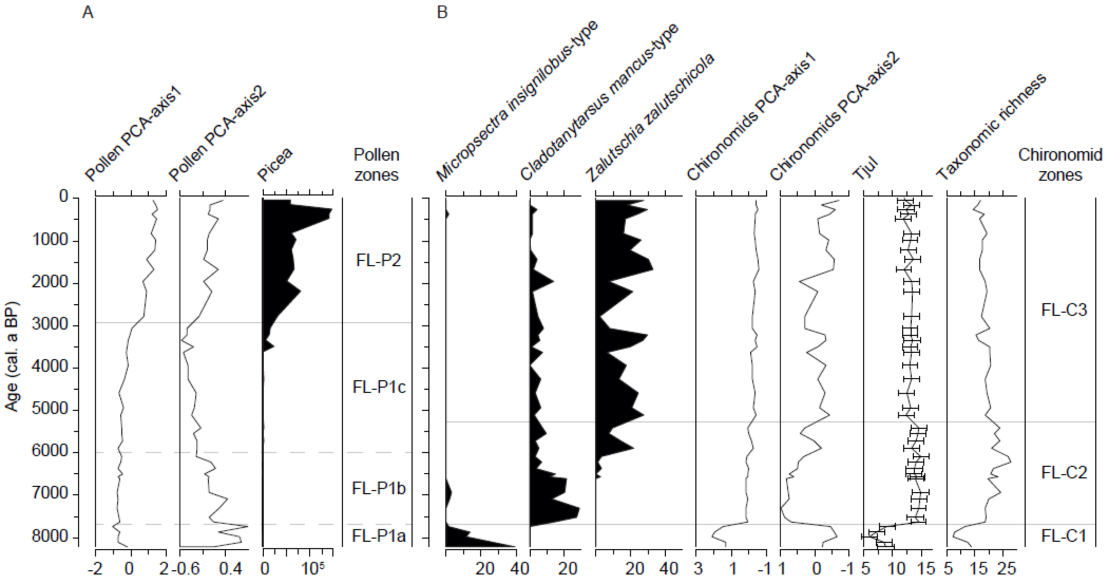
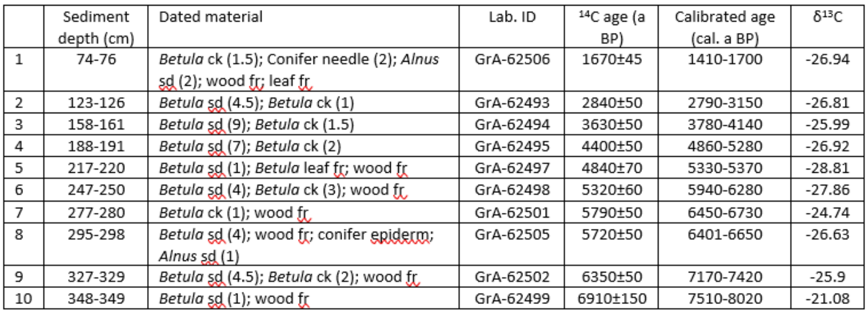


Table captions:

Table 1. AMS ^{14}C ages of dated terrestrial macroremains from the Flocktjärn record. GrA = Groningen Centre for Isotope Research; Ck: catkin scale; sd: seed; fr: fragment, with numbers in brackets indicating the number of remains included in the sample. Calibrated ages represent single-sample calibration using the IntCAL20 calibration curve (Reimer *et al.* 2020) and are presented as 95.4% probability intervals, with dates rounded to the nearest decade.

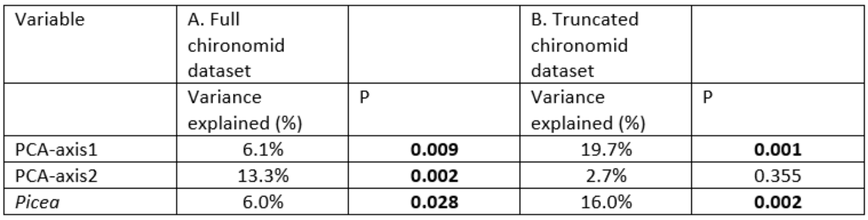


	Sediment depth (cm)	Dated material	Lab. ID	^{14}C age (a BP)	Calibrated age (cal. a BP)	δ^{13}C
1	74-76	*Betula* ck (1.5); Conifer needle (2); *Alnus* sd (2); wood fr; leaf fr	GrA-62506	1670±45	1410-1700	-26.94
2	123-126	*Betula* sd (4.5); *Betula* ck (1)	GrA-62493	2840±50	2790-3150	-26.81
3	158-161	*Betula* sd (9); *Betula* ck (1.5)	GrA-62494	3630±50	3780-4140	-25.99
4	188-191	*Betula* sd (7); *Betula* ck (2)	GrA-62495	4400±50	4860-5280	-26.92
5	217-220	*Betula* sd (1); *Betula* leaf fr; wood fr	GrA-62497	4840±70	5330-5370	-28.81
6	247-250	*Betula* sd (4); *Betula* ck (3); wood fr	GrA-62498	5320±60	5940-6280	-27.86
7	277-280	*Betula* ck (1); wood fr	GrA-62501	5790±50	6450-6730	-24.74
8	295-298	*Betula* sd (4); wood fr; conifer epiderm; *Alnus* sd (1)	GrA-62505	5720±50	6401-6650	-26.63
9	327-329	*Betula* sd (4.5); *Betula* ck (2); wood fr	GrA-62502	6350±50	7170-7420	-25.9
10	348-349	*Betula* sd (1); wood fr	GrA-62499	6910±150	7510-8020	-21.08

Table 2. Marginal effects of vegetation on the variability in the chironomid record of lake Flocktjärn.

A. Full chironomid dataset. B. Truncated chironomid dataset (including FL-C2 and -C3 only).

Statistically significant relationships ($p < 0.05$) are plotted in bold.



Variable	A. Full chironomid dataset		B. Truncated chironomid dataset	
	Variance explained (%)	P	Variance explained (%)	P
PCA-axis1	6.1%	**0.009**	19.7%	**0.001**
PCA-axis2	13.3%	**0.002**	2.7%	0.355
Picea	6.0%	**0.028**	16.0%	**0.002**

Supporting Information

Fig. S1: Complete Pollen diagram.

Data S1: Combined R script.

Table S1: Details on sites discussed in this paper.

Table S2: Original data and results of statistical analyses.