

# Prolonged interglacial warmth during the Last Glacial in northern Europe

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**BOREAS**



Helmens, K. F., Katrantsiotis, C., Kuosmanen, N., Luoto, T. P., Salonen, J. S. & Väiliranta, M. 2021 (April): Prolonged interglacial warmth during the Last Glacial in northern Europe. *Boreas*, Vol. 50, pp. 331–350. <https://doi.org/10.1111/bor.12495>. ISSN 0300-9483.

Few fossil-based environmental and climate records in northern Europe are dated to Marine Isotope Stage (MIS) 5a around 80 ka BP. We here present multiple environmental and climate proxies obtained from a lake sequence of MIS 5a age in the Sokli basin (northern Finland). Pollen/spores, plant macrofossils, NPPs (e.g. green algae), bryozoa, diatoms and chironomids allowed an exceptionally detailed reconstruction of aquatic and telmatic ecosystem successions related to the development of the Sokli Ice Lake and subsequent infilling of a relatively small and shallow lake confined to the Sokli basin. A regional vegetation development typical for the early half of an interglacial is recorded by the pollen, stomata and plant macrofossil data. Reconstructions of July temperatures based on pollen assemblages suffer from a large contribution of local pollen from the lake's littoral zone. Summer temperatures reaching present-day values, inferred for the upper part of the lake sequence, however, agree with the establishment of pine-dominated boreal forest indicated by the plant fossil data. Habitat preferences also influence the climate record based on chironomids. Nevertheless, the climate optima of the predominant intermediate- to warm-water chironomid taxa suggest July temperatures exceeding present-day values by up to several degrees, in line with climate inferences from a variety of aquatic and wetland plant indicator species. The disequilibrium between regional vegetation development and warm, insolation-forced summers is also reported for Early Holocene records from northern Fennoscandia. The MIS 5a sequence is the last remaining fossil-bearing deposit in the late Quaternary basin infill at Sokli to be studied using multi-proxy evidence. A unique detailed climate record for MIS 5 is now available for formerly glaciated northern Europe. Our studies indicate that interglacial conditions persisted into MIS 5a, in agreement with data for large parts of the European mainland, shortening the Last Glacial by some 50 ka to MIS 4-2.

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Long proxy climate records, a wide geographical spread of proxy climate data, and quantification of climate parameters are essential for the reconstruction of past climate variability, understanding of forcing/feedback mechanisms, and validation of climate model simulations. Long continuous records that pre-date the present interglacial period (Holocene, i.e. the last *c.* 11 ka) are particularly scarce from high northern latitudes due to glacial erosion. In Fennoscandia (northern Europe), late Quaternary (last 130 ka) environmental and climate conditions have been classically reconstructed through correlation of generally poorly dated bio/litho-stratigraphical fragments with the northwest European mainland climate stratigraphy and the deep-sea oxygen-isotope stratigraphy (e.g. Lundqvist 1992; Donner 1995). As clearly outlined in Donner (1996), the correlations on land were fraught with uncertainties, caused by e.g. the long distance of correlation and truncations of geological beds resulting in incomplete interstadial or interglacial sequences. The marine oxygen-isotope stratigraphy was used as a proxy for global ice volume changes (e.g. Kleman *et al.* 1997), even though this

record carries a composite signal of e.g. ice volume and ocean water temperature (Lisiecki & Raymo 2005). Furthermore, climate reconstructions were made mostly using pollen data and quantifications of climate parameters were rare.

We here present an environmental and climate record obtained from a lake deposit of Marine Isotope Stage (MIS) 5a age, centred around 82 ka BP (Lisiecki & Raymo 2005), found in the Sokli basin in the northern boreal forest of northeastern Finland. The MIS 5a lake sequence forms part of a unique long sedimentary sequence that spans the last 130 ka (Helmens *et al.* 2000, 2007a, b) and it is the last remaining fossil-bearing deposit at Sokli to be studied in detail. We use sediment characteristics (lithology, loss-on-ignition (LOI)), pollen and spores, non-pollen palynomorphs (NPPs), macrofossils of plants and zoological taxa, diatoms and chironomids (aquatic insects) to reconstruct in detail local successions in aquatic and telmatic ecosystems, the lake development, and developments in regional vegetation. Mean July air temperatures are quantified by means of plant indicator species identified in the pollen

and macrofossil analyses, and by applying the transfer function approach to pollen and chironomid assemblages. The climate inferences are validated against the local lake development.

We use the data obtained on the MIS 5a lake deposit from Sokli to further explore the interglacial character of MIS 5 as earlier discussed in Helmens (2014). The latter paper compares long terrestrial records from central and northern Europe with marine data. It proposes a subdivision of the last climate cycle into an early, overall mild interglacial half (MIS 5) and a late, overall cold glacial half (MIS 4-2), each with duration of *c.* 60 ka. This subdivision deviates from the northwest European mainland climate stratigraphy where the Last Glacial (Weichselian) lasts *c.* 100 ka, starting at the base of MIS 5d at *c.* 115 ka. It also sharply contrasts with earlier reconstructions in Fennoscandia, which suggested cold tundra conditions at Sokli, with sub-arctic birch woodland in areas presently covered by mixed boreal forest south of Sokli, during MIS 5c and MIS 5a (e.g. Donner 1995). The paper by Helmens (2014) used low-resolution pollen data from fragmented core sections to infer past environmental and climate conditions for MIS 5e and 5a at Sokli. The MIS 5e lake deposit has since been studied in detail, and the lake deposit of MIS 5a age is studied here, both using multiple proxies on new boreholes from the Sokli basin.

## Present environmental setting and stratigraphy

### Study site

The Sokli site is situated in the northern boreal forest of northeastern Finland (latitude 67°48'N, longitude 29°18'E, elevation ~220 m a.s.l.), on the main water divide that separates drainage into the Barents and White Seas to the east and the Baltic Sea to the southwest. The Sokli wetland (Sokliaapa; Fig. 1) is drained by the Sokli rivulet (Soklioja) that flows to the southwest into the Yli-Nuortti river. Bedrock in the region is Precambrian Shield with the exception of the immediate surroundings of the study site that is underlain by Palaeozoic carbonate-rich rocks of the Sokli Carbonatite Massif. Dispersed residual phosphorous deposits occur at the surface of the carbonatite, particularly in the western part of the massif on the slopes above Lake Loitsana (Talvitie *et al.* 1981).

Present climate at Sokli is cool boreal with mean July and February temperatures of 13 and -14 °C, respectively; mean annual precipitation amounts to 500–550 mm (Drebs *et al.* 2002). Lakes in the area are ice-covered between October and the end of May. Mires of the aapa-type (i.e. a patterned fen) with *Sphagnum* spp., *Rubus chamaemorus*, Ericales, *Betula nana*, *Salix* spp. and *Carex* spp. are extensively present in the region. Birch (*Betula pubescens* and *B. pendula*), pine (*Pinus sylvestris*) and spruce (*Picea abies*) are the dominant tree species in the regional forest. Spruce reaches its northern

limit some 100 km north of Sokli. Further north, pine forest predominates, succeeded northwards and upwards by birch-pine forest and then sub-arctic birch forest. The forest limit, which is situated some 300 km north of Sokli, is formed by the polycormic mountain birch *B. pubescens* subsp. *czerepanovii*, syn. *tortuosa*. The vegetation of the tundra region beyond the forest limit is low-arctic dwarf-shrub tundra dominated by *B. nana* and Ericales.

### Sediment preservation

The Sokli Carbonatite Massif consists of carbonate-rich rocks of magmatic derivations/descent (carbonatite) and a fenite halo. The latter developed by metasomatism of the crystalline rocks that surround the magma intrusions (Vartiainen 1980). The deeply weathered carbonatite manifests itself in the landscape as a circular depression, ~5 km in diameter, bordered by a hilly ring of fenites (Fig. 1). Drillings carried out in connection with carbonatite prospecting revealed a string of hollows, with sedimentary infillings up to 10–30 m thick, that follows a NE–SW trending fracture zone (Talvitie *et al.* 1981). A 30-m-thick sedimentary sequence that includes a series of thick organic-bearing units of late Quaternary age occurs in the centre of the massif where two fracture zones cross (Ilvonen 1973a, b; Johansson & Räsänen 1994; Helmens *et al.* 2000, 2007a). The latter depression is referred to as the Sokli basin (Helmens *et al.* 2000).

Sokli is located in the eastern part of a zone, which stretches over central Finnish Lapland, with a concentration of findings of pre-LGM sediments (Hirvas 1991). This sediment preservation is ascribed to low ice-flow velocities and/or frozen-bed conditions under the central part of the Fennoscandian Ice Sheet (e.g. Kleman *et al.* 1997). However, a closer look at the till-covered organic beds shows that these beds are generally only a few decimetres thick and often occur in a secondary position, i.e. the sediments are not found *in situ* but have been truncated and transported by the ice sheet (Hirvas 1991). This means that, although limited erosion in the ice-divide zone might have contributed to its preservation, the unique preservation in the Sokli basin of multiple, thick fossil-bearing deposits is most probably due to the non-typical bedrock conditions at Sokli. It is the combination of a steep hollow in the relatively soft carbonatite rocks combined with the presence of surrounding hills formed in hard fenite rocks that have provided shelter against glacial erosion. Another site with preservation of a long, 22-m-thick sediment sequence is Rautuvaara in western Finnish Lapland. Here, a series of individual till beds, interbedded with sorted glaciolacustrine sediment, but not including any organic-rich unit, can be followed over a distance of up to some 400 m on the eastern flank of the Alainen Rautuvaara hill. The sediments form part of an up to 40-m-thick valley-infill

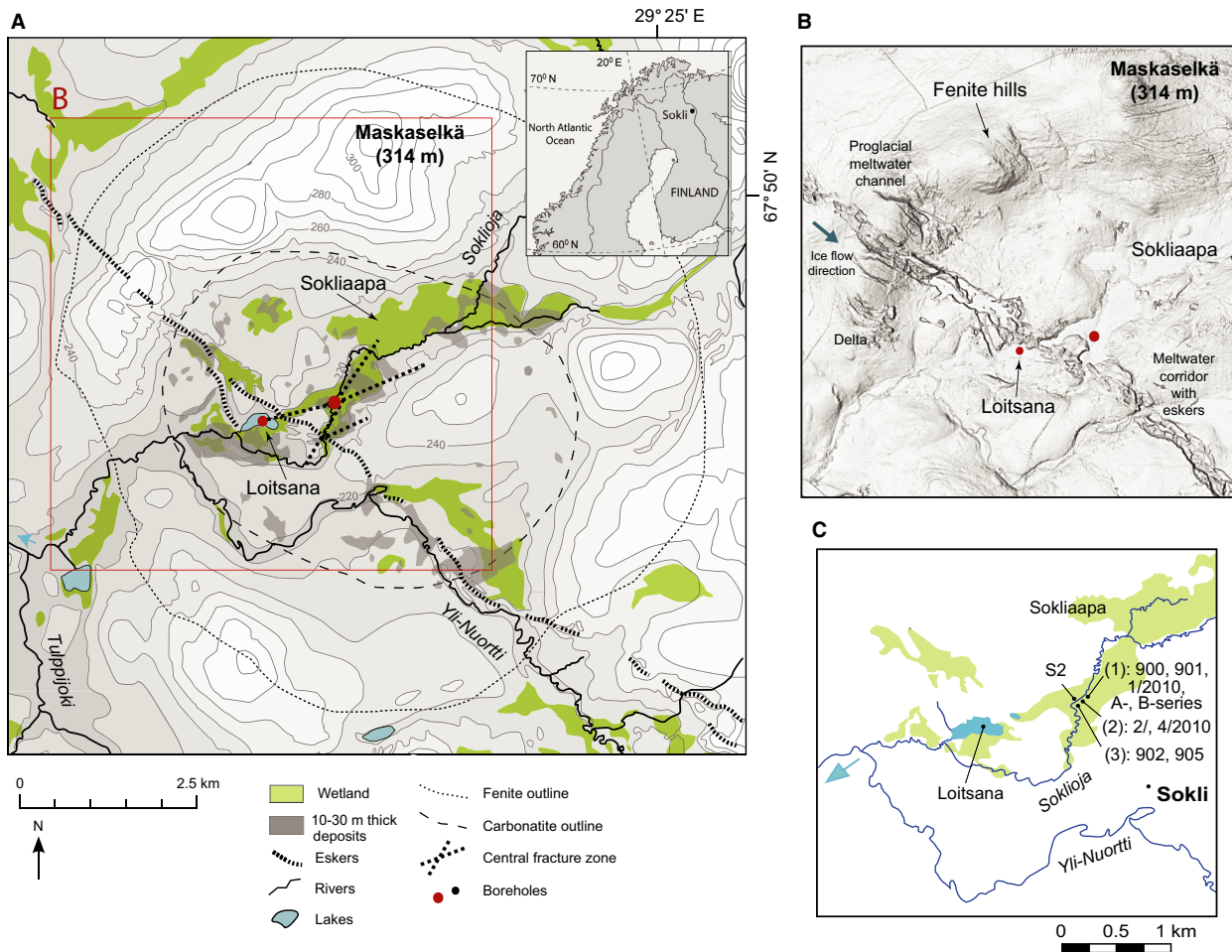


Fig. 1. A. The Sokli Carbonatite Massif and direct surroundings with locations of boreholes. B. Raw hill-shade map created from high-resolution (2 m) digital elevation data (Geological Survey of Finland CC BY 4.0 license; downloaded 2019/10). C. Locations of boreholes shown in detail. [Colour figure can be viewed at [www.boreas.dk](http://www.boreas.dk)]

consisting of glacial and fluvial deposits. The Rautuvaara section has earlier been considered as the stratotype for the northern Fennoscandian late Middle and Late Pleistocene (Hirvas 1991). However, recent dating by OSL indicates that the whole sediment succession was deposited during the Weichselian (Lunkka *et al.* 2014; Howett *et al.* 2015).

#### Late Quaternary stratigraphy

A series of boreholes has been collected from the Sokli basin since 1996 using percussion drilling from the frozen surface of the Sokli wetland (Fig. 2). Coring was performed at three different locations along a 200-m-long transect and, at each location, several cores were taken within a few metres distance from each other (Fig. 1C). Additionally, a 9-m-thick Holocene sediment sequence was collected from Lake Loitsana using a Russian peat-corer from the frozen lake surface. This lake, which occupies a depression associated with a NW–SE trending esker chain (Fig. 1A, B), is the only place

within the Sokli massif where open water conditions persist today.

The Sokli and Loitsana sediments have been dated by means of AMS  $^{14}\text{C}$  dating on macrofossils of terrestrial plants, TL and IRSL dating, and OSL dating on quartz using the SAR dose protocol (Helmens *et al.* 2000, 2007a, b, 2018; Alexanderson *et al.* 2008; Shala *et al.* 2014b; Fig. 2). The latter yielded large standard errors mainly due to small sample sizes, relatively poor luminescence characteristics, and uncertainties in dose-rate determinations. OSL ages on glacialfluvial and fluvial sediments are, however, in sequence and group according to stratigraphical units. Also, the youngest age determination agrees with  $^{14}\text{C}$  dates, and the oldest ages are in line with the TL and IRSL dates. Moreover, the absolute chronology is in agreement with earlier land–sea comparisons (Helmens *et al.* 2000, 2007a; Alexanderson *et al.* 2008).

An up to 9-m-thick, yellowish-brown diatom gyttja deposit, dated to MIS 5e, stretches as a marker

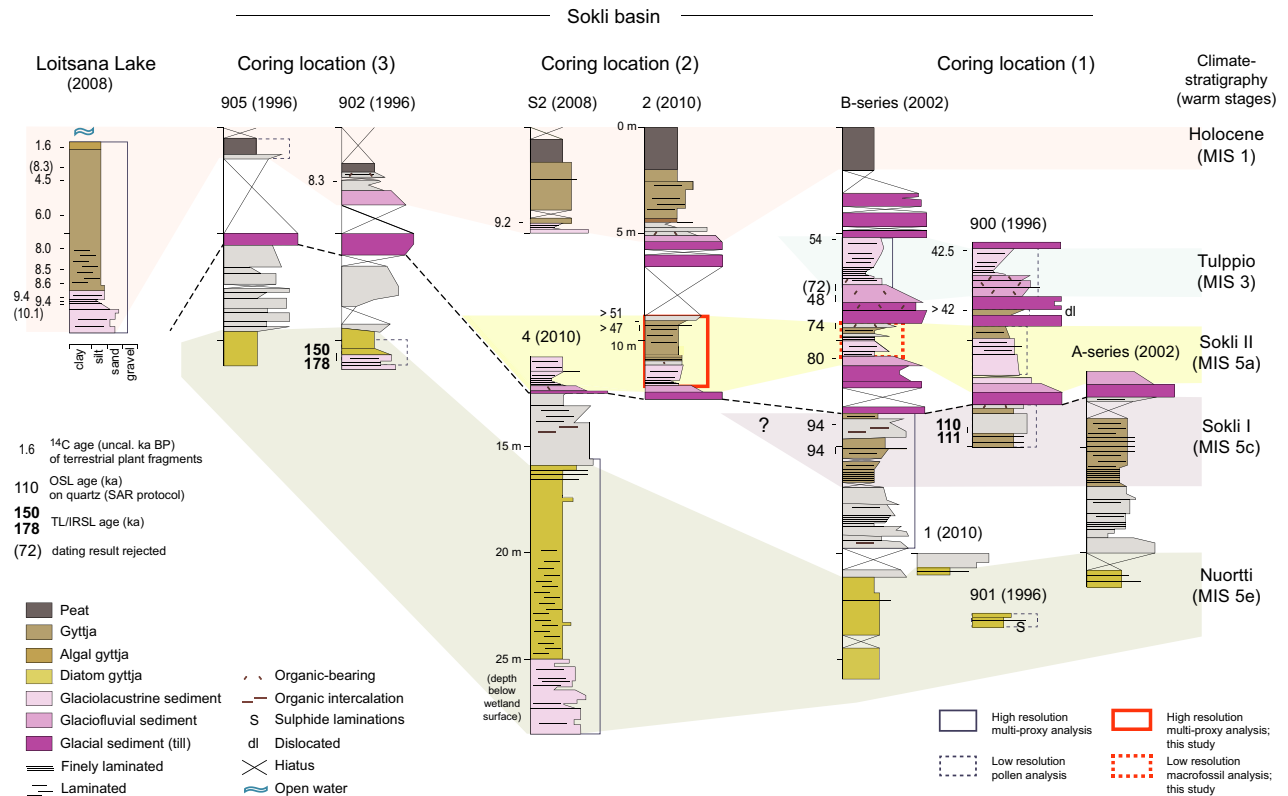


Fig. 2. Borehole lithologies and chronology, local climate stratigraphy (Helmens 2014), and types of analyses applied to the Sokli sediments. For location of boreholes see Fig. 1C. [Colour figure can be viewed at [www.boreas.dk](http://www.boreas.dk)]

horizon near the base of the Sokli basin infill (Fig. 2). The diatom gytija is underlain by minerogenic sediment of glaciolacustrine origin. According to prospecting by Ilvonen (1973a, b), the diatom gytija unit overlies till (MIS 6) that rests on weathered bedrock. The ice-divide zone was situated over the northernmost part of Finnish Lapland during the Penultimate Glacial (MIS 6; Johansson 1995), which would have allowed for more glacial erosion at Sokli at this time compared to the LGM (MIS 2).

The MIS 5e sediments, which were deposited in an initially deep and stratified lake, are overlain by a several metres thick, minerogenic fluvial deposit. Fossil remains in the upper, more fine-grained portion of the latter deposit of MIS 5d age, together with lithology, indicate a braided river pattern. The prolonged infilling of a small oxbow lake, and return to stream channel deposition, are subsequently recorded in an overlying, over 3-m-thick gytija deposit interbedded with sand and gravel, dated to MIS 5c.

The upper part of the Sokli sedimentary record consists of till interbedded with two more sorted sediment units dated to MIS 5a and early MIS 3. The glacial lake sediments of early MIS 5a age are overlain by up to ~2 m of gytija, and this lake sequence can be followed over a distance of at least 100 m (coring

locations 1 and 2). The glaciolacustrine sediments of early MIS 3 age are capped by till.

## Material and methods

### Lithology and chronology

The MIS 5a deposit occurs at depths of ~9–12 m below the surface of the Sokliaapa (Fig. 2). The underlying compact diamicton is clast supported in its lower part, whereas a sandy matrix dominates in the weakly stratified upper part. The diamicton is interpreted as basal till possibly overlain by ablation till (Helmens *et al.* 2000, 2007a). Subsequently, the sediment becomes more sorted and fines upward to sand. This glaciofluvial sediment is abruptly overlain by a laminated silt-clay deposit of glaciolacustrine origin (Helmens *et al.* 2018). The overlying gytija deposit is truncated by till in borehole 900, whereas in boreholes B-series and 2/2010, the gytija becomes increasingly interlayered with sand before turning to sand interbedded with thin organic laminae and then gravel at the top. The gytija deposit attains its greatest thickness (~2 m) in borehole 2/2010 that is studied here.

A detailed lithological column, with LOI to the right and absolute age determinations to the left, is

given in front of the diagrams in Fig. 3. The  $^{14}\text{C}$  dating results have been presented in Helmens *et al.* (2018) and the OSL ages (which were determined on the B-series borehole; Fig. 2) in Alexanderson *et al.* (2008). The chronology roughly corresponds with MIS 5a around 82 ka BP (Helmens *et al.* 2007a; Alexanderson *et al.* 2008).

#### Biotic proxy analyses

The MIS 5a deposit in borehole 2/2010 was sliced into ~10-cm- (minerogenic sediment) and ~5-cm-thick samples (gyttja; clayey sediment below 11.90 m). The majority of samples was analysed for pollen, spores and NPPs (i.e. the palynological analysis) and chironomids. A lower sample resolution was used in the macrofossil, diatom and LOI analyses. The multi-proxy analysis is similar to that applied to the sediments of MIS 5e and Holocene age in the Sokli basin and follows the methods described in Salonen *et al.* (2018; palynological analysis) and Shala *et al.* (2014a, b); other analyses). The coring operation is described in Pliikk *et al.* (2016). A minimum of 500 diatom valves, 50 chironomid head capsules and 400 terrestrial pollen/spore grains were identified per sample. Percentages of all microfossils encountered in the palynological analysis were calculated based on the sum of terrestrial plant taxa (trees, shrubs, dwarf shrubs, herbs, Pteridophytes). The sample sizes used in the macrofossil analysis varied between ~15 (gyttja) and 35 cm<sup>3</sup> (minerogenic sediment), and ~5 cm<sup>3</sup> of sediment per sample was analysed below 11.90 m.

A selection of diatom and chironomid taxa is given in Fig. 3A. Pollen, spores, NPPs and macrofossils of plants and zoological taxa (excluding insects) are presented in Fig. 3B and C, where Fig. 3B combines micro- and macrofossil remains of taxa that occur in aquatic and wetland environments and Fig. 3C combines fossil remains of terrestrial plant taxa. Zonation of the diagrams is based on visual examination of the entire data set including lithology, following earlier studies at Sokli (e.g. Helmens *et al.* 2012). A common zonation is applied to the diatom, chironomid and other aquatic and wetland taxa diagrams (Fig. 3A, B). This zonation consists of five local zones, I-1 and -2 and II-1, -2 and -3. The zonation in Fig. 3C (zones I, II, III-a and -b) follows the terrestrial vegetation development. In addition to this multi-proxy analysis that was performed on core 2/2010, a low-resolution macrofossil analysis was carried out on the MIS 5a deposit in the B-series borehole; results are given in Table 1. The previously obtained low-resolution pollen data for the MIS 5a deposit in the Sokli basin (Helmens *et al.* 2000, 2007a) come from borehole 900 (Fig. 2).

It is important to note that in Fennoscandia several plant taxa (e.g. Cyperaceae, *Betula nana*, Ericales) occur as important elements in both terrestrial and wetland

settings. Herbs for which a distinct wetland habitat could be inferred for at least parts of our record (e.g. Cyperaceae), as well as herbs in shore settings (e.g. *Rorippa*) or for which the habitat was undifferentiated (e.g. *Thalictrum*), are given in the lower diagram in Fig. 3C ('other herbs'). The macrofossils of e.g. *Carex*, *Salix*, *B. nana* and Ericales, however, which can be assumed to have an overall local wetland source, are shown in the aquatic/wetland diagram of Fig. 3B. It should also be stressed that pollen and spores of plants from nearby, local wetland or shore environments (i.e. azonal vegetation) are often over-represented in the palynological record and may obscure the regional (zonal) vegetation signal in the percentage diagram. Therefore, we begin our environmental reconstruction with an interpretation of the lake development and associated azonal vegetation types before reconstructing the regional vegetation history.

#### Climate reconstruction methods

*Plant indicator species.* – Minimum mean July air temperatures ( $T_{\text{Jul}}$ ) are reconstructed from the plant macro- and microfossil records using the approach introduced in Väiliranta *et al.* (2015). In this protocol, current plant species distribution data in Finland are linked to measured meteorological data over a  $T_{\text{Jul}}$  gradient from ~7.5 to 17 °C. This gradient spans over several bioclimatic zones from hemiboreal, via boreal to sub-arctic, and, therefore, many plant species reach their northern distribution limits within this gradient. Only in the northernmost part of the country, the plant distributions are constrained by altitude-related (orohemiarctic) factors. A unique modern species-specific spatial plant distribution data set (<http://www.luomus.fi/kasviatlas>) covers the whole of Finland and is subject to continuous botanical surveys. Long-term meteorological climate normal data are readily available. Thus, the plant distribution database can be used to correlate modern species distributions with climate.

Plant indicator species identified in the MIS 5a fossil record, together with their minimum  $T_{\text{Jul}}$  requirements in Finland, are listed in Table 2. These plant species require a specific minimum  $T_{\text{Jul}}$  in order to flower and reproduce and have a rather sharp northern distribution limit. For each species, we use an interpolated  $T_{\text{Jul}}$  over a 10×10 km grid cell, and we analysed several grid cells containing species occurrences along the current northern distribution boundary. A median and mean July temperature range, i.e. the lowest and highest temperature value along the species-specific distribution boundary in the grid cells, is given in Table 2 and Fig. 4B.

*Pollen-based climate reconstruction.* – The pollen-based climate reconstruction method, similar to the chironomid-based reconstruction discussed below, makes use of the transfer function approach (Birks *et al.* 2010). It uses

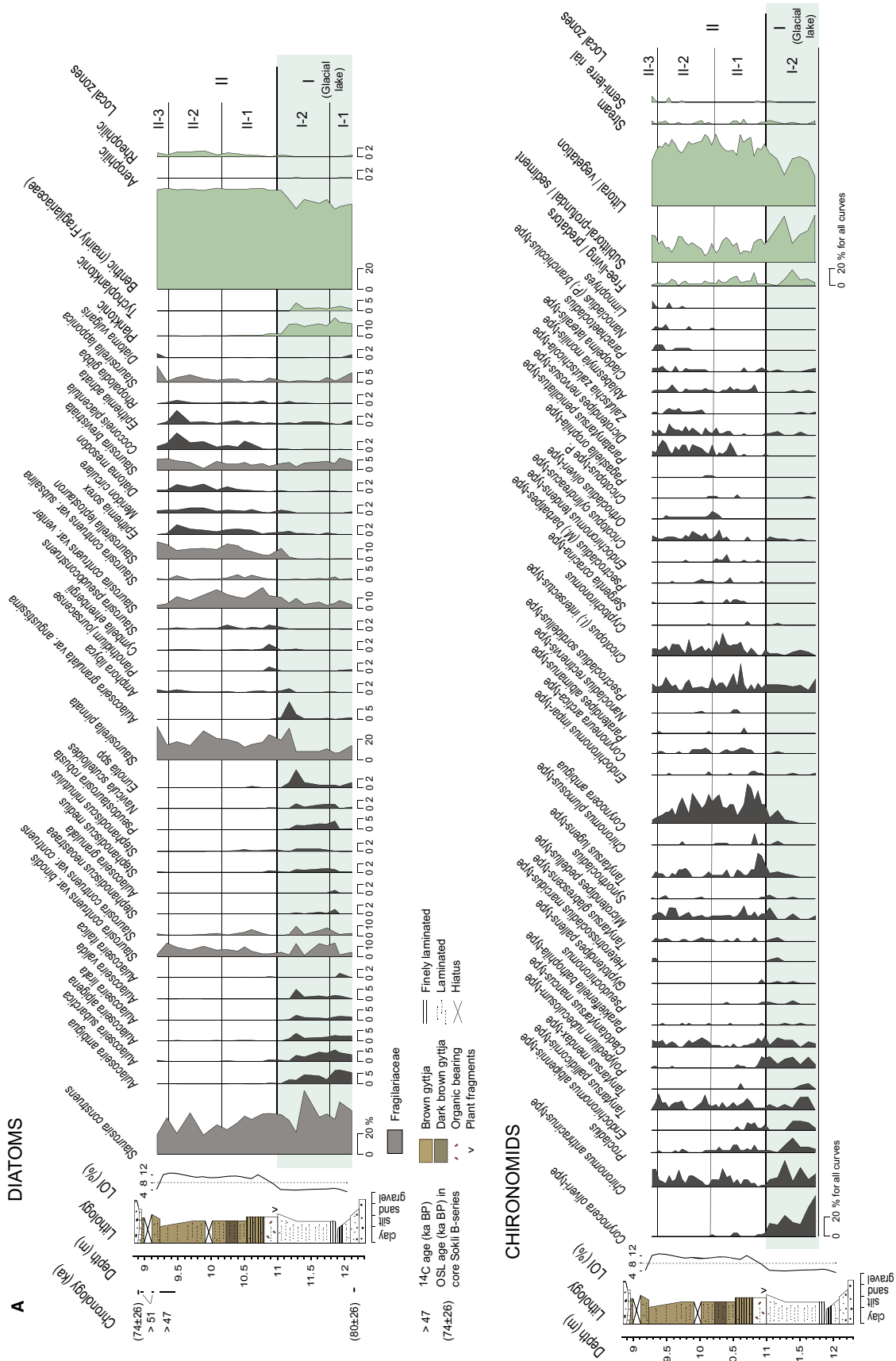
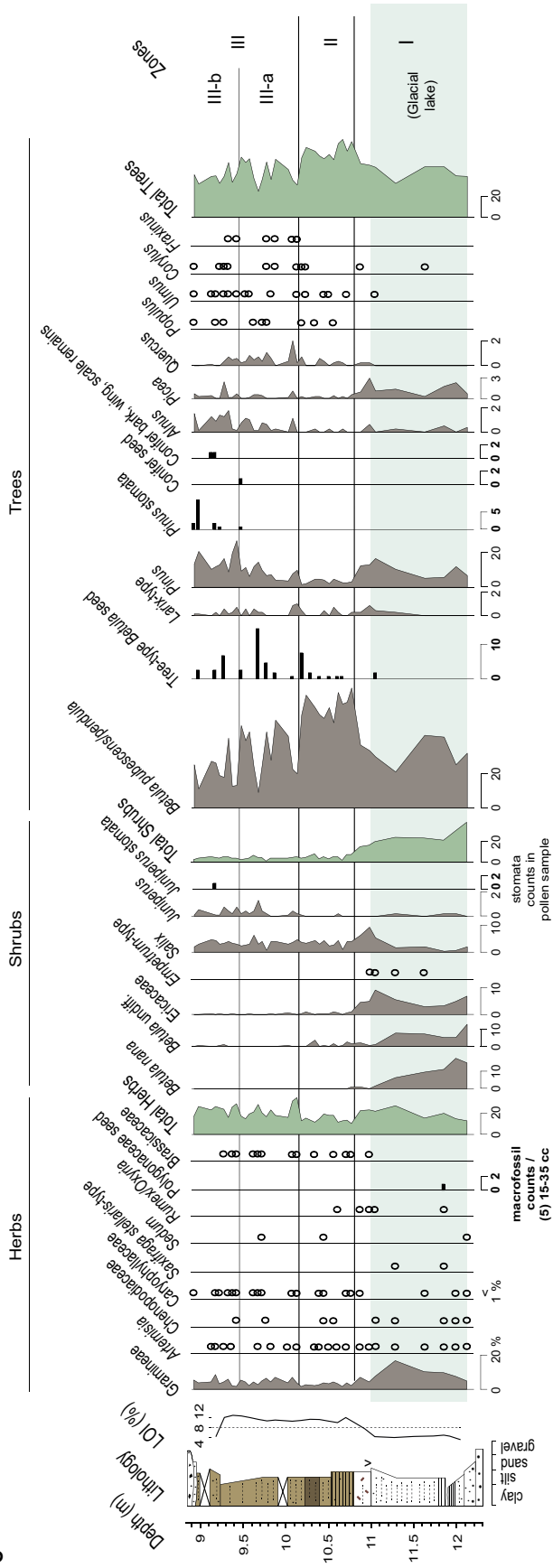


Fig. 3. Selections of fossil remains encountered in the MIS 5a deposit in borehole 2/2010. A. Diatom and chironomid taxa. B. Other aquatic and wetland taxa. C. Terrestrial plant taxa. Shown in (A) are diatom taxa with values > 1%, and selected taxa with values  $\geq 0.5\%$ , and chironomid taxa with  $\geq 2$  occurrence and  $\geq 2$  abundance and N2  $\geq 2$ . [Colour figure can be viewed at [www.boreas.dk](http://www.boreas.dk)]

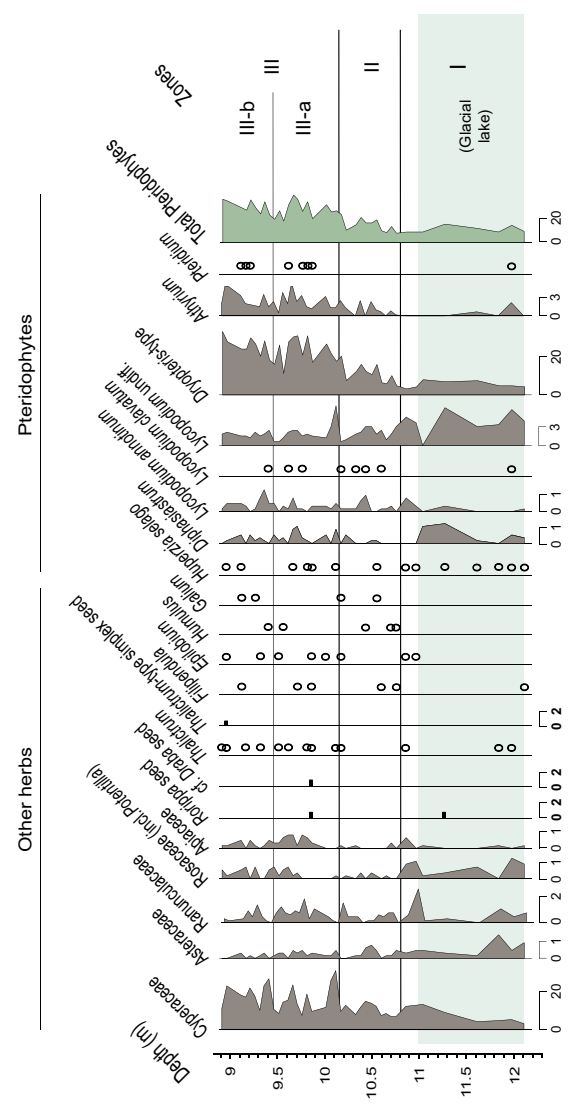


TERRESTRIAL PLANT TAXA

C



A-C



Diatom analysis: Christos Katrantsiotis  
 Chironomid analysis: Tomi Luoto  
 Plant microfossil analysis: Niina Kuosmanen  
 Macrofossil analysis: Minna Välranta

Table 1. Macrofossils encountered in the MIS 5a deposit in borehole B-series. Fossil remains are expressed as concentrations (amounts per 5–15 cm<sup>3</sup>) or as presence (+) to high abundances (+++).

Depth (m), lithology	Woody fragments	<i>Salix</i> bark, bud, leaf	Fungi sclerotia	Poaceae fruit	<i>Rorippa</i> seed	cf. <i>Ranunculus</i> seed	<i>Carex</i> seed	Organic bits	Mixed bryophyte remains	<i>Equisetum</i> remains	<i>Ranunculus</i> sect. <i>Batrachium</i> seed	Tree <i>Betula</i> seed, catkin scale	<i>Betula</i> seed	<i>Betula</i> bark, leaf remains
9.40 Organic-rich sand	+++	+	2	1			7		++		1	1		+
9.68 Gyttja							15	+++	++	+				
9.82 Minerogenic glacial lake sediment	++						2					1		+
10.41 Minerogenic glacial lake sediment	++	+	1	6	1	2	1					2		
10.60 Minerogenic glacial lake sediment	+++	++	3	5	10		6	++				1	2	+++
10.69 Minerogenic glacial lake sediment	+++	+												

Analyst: M. Väiranta.

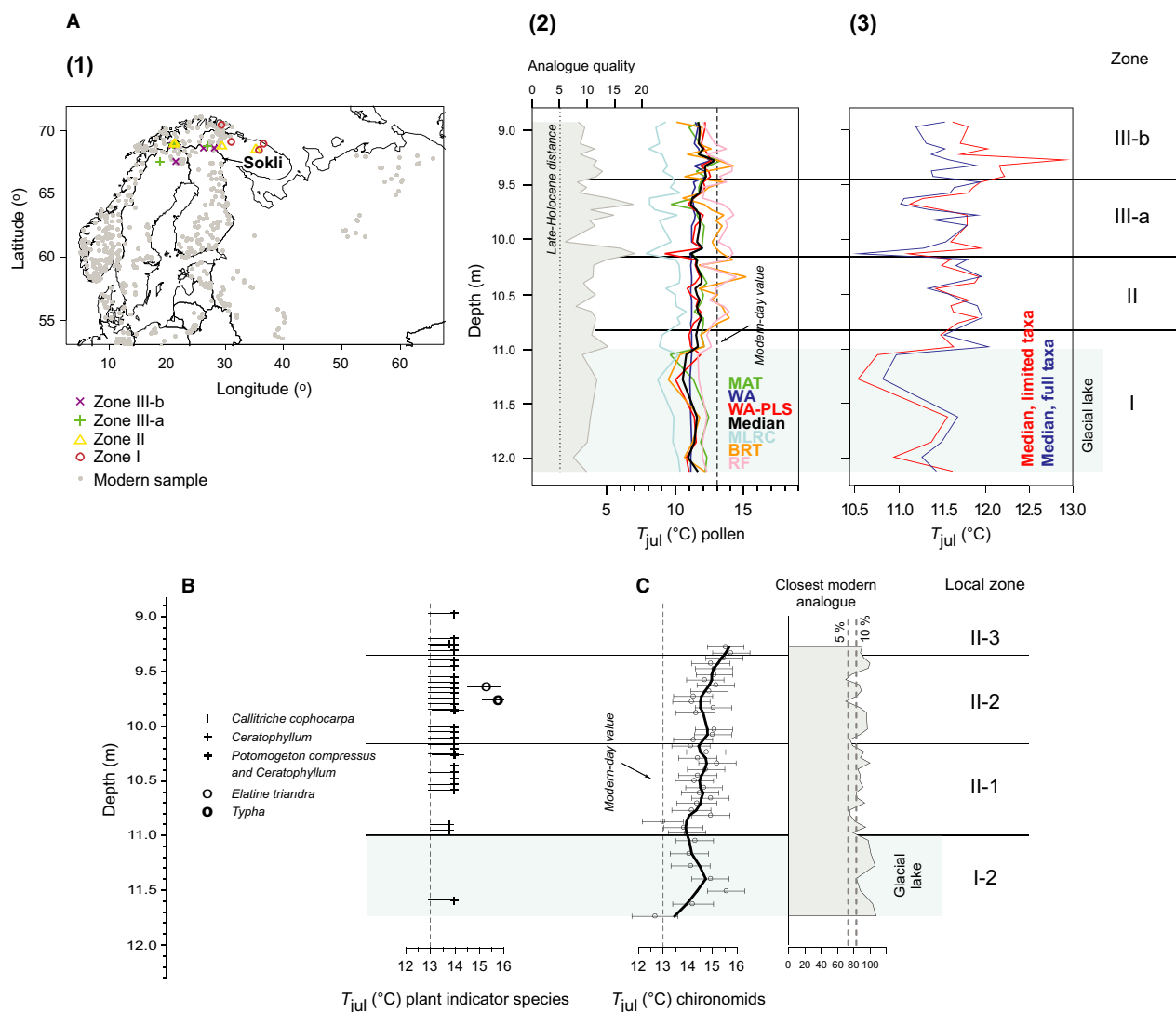
**Table 2.** List of plant indicator species identified in the MIS 5a macro- and microfossil records from borehole 2/2010 with related mean July air temperature ranges determining the species' current northernmost distribution limit in Finland.

Taxon	Median of July mean (°C)	July mean range (°C)
<i>Callitriche cophocarpa</i>	13.7	13.5–13.9
<i>Potamogeton compressus</i>	13.9	13.1–14.3
<i>Ceratophyllum</i>	13.9	12.9–14.1
<i>Elatine triandra</i>	15.2	14.5–15.9
<i>Typha</i>	15.7	15.1–16

a modern calibration set linked to current meteorological data. The calibration set consists of pollen/chironomid assemblages analysed in surface sediment from a series of lakes situated along a gradient that covers changes in the

parameter of interest, here  $T_{jul}$ . The established relationship is used in combination with the fossil data to model past changes in  $T_{jul}$ .

The pollen-based  $T_{jul}$  reconstruction method applied here generally follows Salonen *et al.* (2018). The latter presented a reconstruction based on the MIS 5e pollen sequence at Sokli. The climate reconstruction uses a modern calibration data set consisting of 807 European lakes, derived from the European Modern Pollen Database (Davis *et al.* 2013), with modern climate data extracted for each sample location. For further details about this calibration data set, see Salonen *et al.* (2019). We fitted pollen- $T_{jul}$  calibration models to the calibration data using six generally well-performing (in modern cross-validation experiments; Salonen *et al.* 2018, 2019) statistical approaches (weighted averaging (WA);



**Fig. 4.** Pollen- (A), plant indicator species- (B) and chironomid-based (C) climate reconstructions for MIS 5a at Sokli. Fossil pollen assemblages are compared with modern pollen assemblages encountered in the calibration-set lakes in (1). The chironomid-inferred temperatures values are given with a locally weighted scatterplot smoother (LOWESS, span = 0.20; Cleveland 1979) applied to the reconstructed values. [Colour figure can be viewed at [www.boreas.dk](http://www.boreas.dk)]

weighted averaging-partial least squares (WA-PLS); maximum likelihood response surfaces (MLRC); modern analogue technique (MAT); random forest (RF); boosted regression trees (BRT)). The median of the six-method ensemble was calculated to summarize the individual reconstructions. Furthermore, to assess the reliability of the palaeo-climate reconstructions beyond the cross-validated errors, we calculated the compositional distance (squared chord distance; Overpeck *et al.* 1985) to the closest-matching modern pollen assemblage for each fossil sample. Results are presented in Fig. 4A.

*Chironomid-based climate reconstruction.* – The chironomid-based  $T_{\text{Jul}}$  reconstruction was performed using the Finnish latitudinal (60–70°N) calibration model presented in Luoto (2009). The model is specifically designed for shallow (<7 m) boreal to sub-arctic sites. The calibration set has a temperature range of 11.3–17.1 °C and it includes 82 sites and 110 chironomid taxa. The model is constructed using the WA-PLS technique and has a jackknife cross-validated coefficient of determination ( $R^2_{\text{jack}}$ ) of 0.78 °C and a root mean squared error of prediction (RMSEP) of 0.72 °C. Estimated standard errors of prediction (eSEP), i.e. sample-specific errors in the reconstructions, were established using bootstrapping with 999 iterations. Closest modern analogues of the fossil samples in the calibration sets were assessed using the modern analogue technique (MAT) with squared chi-square distance as a dissimilarity coefficient and a 5-percentile threshold (minDC) for poor/good analogues. Results are presented in Fig. 4C.

## Environmental reconstruction

### *Successions in aquatic and telmatic ecosystems and lake development*

*Local zone I (depth interval 12.15–11.00 m).* – Local zone I corresponds to over 1 m of minerogenic sediment (organic content measured by LOI varies between 3 and 5%; Fig. 3) found at the base of the MIS 5a sequence. This sediment accumulated in the Sokli Ice Lake that developed during deglaciation between the retreating margin of the Fennoscandian Ice Sheet in the northwest and higher terrain to the southeast (Johansson 1995; Helmens *et al.* 2009; Shala *et al.* 2014a). A selection of fossil remains from the glacial lake sediment has been earlier presented, and compared with fossil assemblages found in similar sediment of early MIS 3 and Early Holocene age in the Sokli basin, in Helmens *et al.* (2018).

*Local zone I-1 (12.15–11.80 m).* – The lower, upward-fining sequence of sands and silts grading into rhythmically laminated silts and clays (local zone I-1) was deposited in a deep and expanding glacial lake and contains few macrofossils and fossil head capsules of chironomids. The cladoceran *Daphnia* (water-flea;

recorded by ehippia), the pioneering, colonial green alga *Botryococcus braunii*, and the bryophyte *Sphagnum* (spores) are among the few taxa that are well represented in the fossil record other than diatoms (Fig. 3B).

The diatom assemblage (Fig. 3A) is dominated by Fragilariaceae (predominantly *Staurosira construens*) and *Aulacoseira*. Fragilariaceae species are generally considered to be opportunistic and pioneering due to their wide range of ecological preferences (Smol 1983; Anderson 2000). They are favoured by relatively high alkalinity (Battarbee 1986) and are often found in lakes that have some sort of disturbance such as proglacial environments (Risberg *et al.* 1999; Bigler *et al.* 2003). The encountered planktonic *Aulacoseira* species (*A. ambigua*, *A. subarctica*, *A. alpigena*) are all heavily silicified and indicate a high influx of silica into the lake and enhanced levels of turbulence to keep these diatoms suspended in the water column. The laminated silts in uppermost part of local zone I-1 show increased representations of periphyton (taxa attached to plants) *S. construens* var. *binodis*, *Pseudostaurosira robusta* and *Navicula scutelloides* and, in combination with LOI values rising to 5%, probably reflect an extension in the lake's littoral zone. Relatively nutrient-rich conditions (in particular phosphate) are suggested by eutrophic *Stephanodiscus* species (*S. neoastraea*, *S. medius*) and *A. granulata* (Anderson 2000).

*Local zone I-2 (11.80–11.00 m).* – The upper 80 cm of silty glacial lake sediment was deposited in a smaller and shallower lake (local zone I-2). This lake stage developed after the opening of a spillway along the retreating ice margin that led to partial drainage of the Sokli Ice Lake. The silt deposit shows laminae of varying grain sizes (clay to fine sand) and thicknesses and, together with the appearances of stream-inhabiting chironomid taxa (e.g. *Eukiefferiella*, *Rheocricotopus*; not shown in the diagram), suggest inflow of running water close to the coring site. The fossil remains of the soil fungus *Glomus* (HdV-207; van Geel *et al.* 1989), abundant fragments of bryophytes and small organic bits and pieces of wood were probably transported from the catchment/lake surroundings by running water as well. Statoblasts of *Fredericella* show high abundances in the lowermost part of local zone I-2. This bryozoan was identified as *F. indica* in the early MIS 3 glacial lake sediment (Helmens *et al.* 2017b) and its occurrence might be favoured by wave action (Økland & Økland 2001) and/or stony shores with sparse aquatic vegetation (Økland & Økland 2005). Macrophytes that are recorded in low abundances in the silt deposit include *Callitriche hermaphroditica*, *Myriophyllum* and narrow-leaved *Potamogeton*.

Local zone I-2 is characterized by a rich chironomid assemblage (Fig. 3A). The assemblage is dominated by the deep-water taxa *Conynocera oliveri*- and *Chironomus anthracinus*-types. Both taxa also have an affinity for pieces of wood were (Axford *et al.* 2009; Luoto &

Sarmaja-Korjonen 2011). The littoral taxon *Tanytarsus pallidicornis*-type is presently common in the sublittoral and littoral zones of boreal lakes mostly found living among *Phragmites* stands (Luoto 2010). The occurrences of *C. anthracinus*, *Procladius*, *Endochironomus albipennis*, *T. pallidicornis*, *T. mendax*, *Polypedilum nubeculosum*, *Cladotanytarsus mancus*, *Microtendipes pedellus* and *Chironomus plumosus* types suggest meso- to eutrophic water conditions. The latter is supported by the recording of the macro-alga *Nitella* (oospores) and the diatom taxa *S. medius* and *S. minutulus*.

The sediment becomes sandier in the uppermost part of local zone I-2 and, together with the fossil record, suggests a further shallowing of the glacial lake accompanied by an extension in the littoral zone. The littoral diatom taxon *Staurosirella pinnata* shows a sharp increase in percentage values and macrofossils of wetland plants (*Carex*, *Salix*, *B. nana*) and the aquatic plant *Callitriche hamulatea* are found. Also, pollen of sedges (Cyperaceae) increase in percentage values (Fig. 3C). The fossil record in the sandy sediment is further characterized by enhanced percentages for the diatom species *Aulacoseira granulata* var. *angustissima*. Together with the recording of *Amphora libyca* and *S. leptostauron*, this diatom assemblage indicates alkaline waters with high Ca concentrations (Gómez et al. 1995; Jones & Birks 2004).

*Local zone II (11.00–8.90 m).* – The Sokli Ice Lake drained at the transition from local zone I to II and lacustrine sedimentation continued in a relatively small depression within the Sokli basin. Fragilariaceae continue to show mass abundances throughout local zone II. This might be related to an increased influence of the local carbonate bedrock on the lake water chemistry in the now greatly reduced catchment.

*Local zone II-1 (11.00–10.15 m).* – Local zone II-1 records a dynamic lake environment with rapid turnover of aquatic and telmatic communities.

The lowermost samples indicate shallow water conditions. Spores of *Equisetum* and pollen of sedges and *Salix* are well represented in the fossil record, and it is possible that the enhanced pollen percentage values for Ranunculaceae, Rosaceae and Apiaceae are related to a local wetland or shore habitat as well (Fig. 3B, C). Macrofossil remains of wetland elements (*Salix*, *Carex*, *Ranunculus* sect. *Batrachium*) and aquatic taxa (*Callitriche hermaphroditica*, *C. cf. cophocarpa*, *Potamogeton*) are found. Open water is indicated by statoblasts of the bryozoa *Plumatella* and *Cristatella mucedo*. *Pediastrum boryanum* var. *pseudoglabrum*, a green alga associated with shallow, macrophyte-rich, eutrophic environments (Bradbury & Winter 1976; Cronberg 1982), also shows enhanced percentage values.

Following the initial lake stage with shallow waters, the deep-water taxon *Tanytarsus lugens*-type appears with high occurrences. The chironomid assemblage in the

organic-bearing silt layer further includes a variety of meso-eutrophic taxa (*E. albipennis*, *P. nubeculosum*, *E. C. mancus*- and *C. plumosus* types). This indicates that nutrient-rich conditions continued to prevail. *Cymbella ehrenbergii*, a diatom species found in calcareous lakes and slow-flowing rivers (Elliott et al. 2011), shows enhanced percentages as well.

*Tanytarsus lugens* has a relatively high oxygen demand and its sudden decline near the base of the finely laminated gyttja is probably related to increased anoxia. The latter decreases bioturbation and this allows preservation of laminae in the sedimentary record. *T. lugens* is replaced by high numbers of *Conynocera ambigua*, an oligo- to mesotrophic species common in clear alkaline waters. Compared with *P. boryanum* var. *pseudoglabrum*, which was recorded in the basal organic silts, the alga *P. integrum* is associated with oligotrophic and cool waters (Komárek & Jankovská 2001; Sarmaja-Korjonen et al. 2006).

The upper part of the finely laminated gyttja bed shows *C. ambigua* being replaced, as dominant taxon, by *P. sordidellus*- and *Cricotopus intersectus*-types. Both chironomids are related to macrophyte abundances. Aquatic plants have become well represented in the fossil record and include abundant leaf remains of narrow-leaved *Potamogeton* (*P. pusilus/pectinatus/rutilus*, *P. burchtoldii*) and pollen of *Potamogeton*, *Callitriche* and *Myriophyllum spicatum*-type. The overall increase in percentage values for the diatom taxon *Staurosira construens* var. *venter* probably reflects its periphytic habitat preference as well. *P. pusilus* and *P. pectinatus* are presently recorded in mesohaline waters.

The typical littoral chironomid type *C. intersectus* attains highest abundances in the upper portion of local zone II-1 and, together with the appearances of macrofossil remains of *Myriophyllum*, *Ceratophyllum* (see zone II-2) and *Carex*, most probably reflect an extension in the lake's littoral zone. The cyanobacteria (blue-green alga) *Gloeotrichia*-type is recorded, as well as the diatom *Epithemia sorex*, an epiphytic taxon that has cyanobacterial endosymbionts capable of nitrogen fixation (Marks & Power 2001). The imbalance in the P/N ratio might be the result of increased nutrient loading connected with terrestrial erosion. According to van Geel et al. (1996), *Gloeotrichia echinulata* depends on sediment P rather than epilimnic P. Increased percentage values for *S. leptostauron*, a diatom taxon often found growing attached to sediment grains, and rheophilic diatoms (e.g. *Meridion circulare*), suggest a closer proximity to inflow of running water. Alkaline lake water conditions are indicated by *S. construens* var. *subsalina* and *S. leptostauron*.

*Local zone II-2 (10.15–9.35 m).* – Characteristic for local zone II-2 are *Ceratophyllum* leaf spikes (HdV-137; van Geel et al. 1989) identified in the pollen analysis, which are particularly abundant in the lower part of the

local zone, and high percentage values of the green alga *Spirogyra* (Zygnemataceae) in the local zone's upper part. Two species of the aquatic plant *Ceratophyllum* presently occur in Finland, *C. demersum* and *C. submersum*. The latter has only a few localities along the southern coastline, which have established during the last two decades. *C. demersum* occurs in shallow, eutrophic, oligo- to mesosaprobic water bodies (i.e. exclusively oxidizing to partly reducing decomposition; Westhoff & den Held 1975). It tolerates highly polluted waterways where e.g. human-induced eutrophication has led to an impoverishment of the flora (Westhoff *et al.* 1981). *Spirogyra* is represented in the fossil record by four types (HdV-130, -132, -210, -315; Pals *et al.* 1980; van Geel *et al.* 1983, 1989; van der Wiel 1983) and is characteristic of stagnant, shallow, meso-eutrophic fresh waters (van Geel & Grenfell 1996). Local zone II-2 is further characterized by relatively high abundances of *Orthocladus oliveri*- and *Dicrotendipes nervosus*-types, chironomid taxa also related to shallow, eutrophic waters.

Other macrophytes that are recorded include *Myriophyllum spicatum*-type (including *M. verticillatum* and *M. sibiricum*), *M. alterniflorum*, narrow-leaved *Potamogeton compressus*, *Sparganium*, *Nuphar*, *Elatine triandra*, *Callitriche hermaphroditica* and *Hippurus*. *Paratanytarsus penicillatus*-, *Cladotanytarsus mancus*- and *Cricotopus cylindraceus*-types are chironomid taxa common in meso- to eutrophic waters, whereas *Zalutschia zalutschicola* is a humic indicator (Luoto 2013).

An extension in the wetland zone during local zone II-2 is indicated by high spore percentage values of *Equisetum* accompanied by conductive tissue (HdV-217; van Geel *et al.* 1989), bryophyte spores (HdV-340; van Geel *et al.* 1989), the recording of *Typha* and *Selaginella selaginoides*, and an overall increase in Cyperaceae pollen. The latter parallels strong increases in fern spores (*Dryopteris*-type, *Athyrium*, *Pteridium*), suggesting an extension/close proximity of wetland or shore habitats as well. *Tilletia sphagnii* (HdV-27; van Geel 1976) and *Ustilina deusta* (HdV-44; van Geel 1976) are fungi, the latter growing on wood substrate. The extension in the littoral was accompanied by a further encroachment of running water as indicated by increased values of rheophilic diatoms (e.g. *Diatoma mesodon*) and the occurrence of the semi-terrestrial chironomid *Limnophyes*.

The epiphytic diatom *Epithemia adnata* shows enhanced values in the uppermost part of local zone II-2 and, like *E. sorex*, is capable of N fixation. It is found in neutral to high pH environments. *Cocconeis placentula*, *Rhopalodia gibba* and *Amphora libyca* are all alkaliphiles species.

*Local zone II-3 (9.35–8.90 m).* – The sandy lithology of local zone II-3, and the fossil content, indicate an advanced stage of infilling and overgrowing of the lake

(terrestrialization), and an increased influence of running water close to the coring site. Macrofossils of a variety of wetland plants (*Carex*, *Salix*, *B. nana*, *Juncus*, *Eriophorum*, *Trichophorum*, *Ranunculus* sect. *Batrachium*) and woody pieces are abundantly present, and *Glomus* returns in the fossil record. *Staurosirella pinnata* is known to tolerate rapidly changing environments and often dominates shallow waters with sandy substrates (Haworth 1976; Jones & Birks 2004). *S. lapponica* indicates shallow, and possibly less productive, conditions.

#### *Regional vegetation development*

*Zone I (depth interval 12.15–11.00 m).* – Pollen of the shrub *Betula nana* were separated from pollen of the tree *B. pubescens/pendula* using a combination of size and morphological characteristics as described in Terasmaä (1951). The similarity between the pollen curves of *B. undifferentiated* and *B. nana* in the pollen diagram (Fig. 3C) indicates that the former probably represents *B. nana*. This means that *B. nana* is represented in the pollen assemblage of zone I by percentage values of up to ~20–30%. Dwarf shrubs (Ericales) and lycopods (including *Diphasiastrum*, *Huperzia selago*) are also well represented. Together with *B. pubescens/pendula* pollen reaching values of ~40%, and *Pinus* pollen to ~20%, this pollen assemblage suggests the presence of low-arctic shrub tundra vegetation in close vicinity to the birch forest ecotone (Prentice 1978). The latter is supported by macrofossil findings of tree birch in the glacial lake sediment, both in the 2/2010 (Fig. 3C) and B-series boreholes (Table 1). In addition, larch trees were present. *Larix* is generally very poorly represented in the fossil record due to short-distance dispersal and poor preservation (Gunin *et al.* 1999; MacDonald *et al.* 2000) and even low percentage values can be taken as evidence for its local presence. In contrast, the pollen of *Pinus* as well as *Picea* are most probably the result of long-distance transport (Aario 1940). Grasses (Poaceae) are well represented in the pollen record from the glacial lake sediment, both during early MIS 5a and MIS 3 and the Early Holocene (Helmens *et al.* 2018). High amounts of poid (grass) phytoliths in the latter records, and the recording of Poaceae fruits in the early MIS 5a deposit in borehole B-series (Table 1), point to a local, littoral/shore habitat and indicate that Poaceae are probably over-represented in the glacial lake pollen records.

*Zone II (11.00–10.15 m).* – The proportion of *B. pubescens/pendula* pollen sharply increases at the base of the gyttja deposit and records the establishment of birch forest in the Sokli region (zone II). *Larix* continues to be registered. *Lycopodium clavatum* is relatively well represented during zone II as well as in pollen samples from surface lake sediments in the present-day birch and pine-birch forests (Seppä *et al.* 2004).

Zone III (10.15–8.90 m). – *Pinus* pollen show a rising trend during zone III, and *Pinus* stomata are recorded, simultaneously when total tree pollen fall. Since the latter is due to increasing representations of sedges and ferns in the lake's littoral zone (see above), it does not reflect an opening of the regional vegetation. The start of rising *Pinus* pollen percentage values at the base of zone III-a coincides precisely with the transition to shallow water conditions in the Sokli basin recorded at the base of local zone II-2. It is possible that the increased representation of pine in the regional forest contributed to the lake shallowing, due to increased evapotranspiration and reduced runoff. In borehole 900 (Fig. 2), pollen of Cyperaceae reach percentages of 40% (Helmens et al. 2000), and *Carex* seeds dominate the macrofossil record from borehole B-series (Table 1), indicating even shallower lake conditions at this site compared to the location of the 2/2010 borehole.

Pollen of *Pinus* reach values of over 40% during zone III-b, after excluding both sedges and ferns from the pollen sum, and indicate the establishment of pine-birch forest at Sokli. *Alnus* probably occurred in a moist habitat around the lake, *Larix* and *Juniperus* were present, whereas pollen of *Quercus*, *Ulmus*, *Corylus* and *Fraxinus* are probably the result of long-distance transport.

#### Climate development

*Plant indicator species – inferred  $T_{jul}$ .* – Plant macrofossil remains are scarce in the glacial lake sediment at the base of the MIS 5a lake sequence. In the overlying, organic-bearing deposit, a variety of aquatic plants (*Ceratophyllum*, *C. cophocarpa*, *P. compressus*) indicate minimum  $T_{jul}$  values of around 13.5–14 °C, with *E. triandra* and the wetland element *Typha* suggesting minimum values up to around 15–15.5 °C (Table 2, Fig. 4B).

*Pollen assemblage – inferred  $T_{jul}$ .* – The pollen-based  $T_{jul}$  reconstruction (Fig. 4A) is characterized by a considerable variation between the general temperature levels during MIS 5a reconstructed by the six different pollen-climate calibration models. The disagreement between methods is in sharp contrast with the prior application of an identical ensemble reconstruction approach to the MIS 5e pollen sequence at Sokli (Salonen et al. 2018). A likely contributor to the comparatively large spread in  $T_{jul}$  values reconstructed by the model ensemble for MIS 5a (Fig. 4A(2)) is the worse quality of modern analogues found in the modern calibration data set. While for MIS 5e the analogue quality was excellent for the major part of the sequence (i.e. even better than for Late Holocene pollen samples from Lake Loitsana; Salonen et al. 2018), for the MIS 5a pollen samples the analogue distances are typically 2–3 times larger than during the Late Holocene. Modern analogues for the MIS 5a fossil samples with best analogue quality are found in northern Fennoscandia,

somewhat north of the location of Sokli (Fig. 4A(1)).

The general poor fit between the MIS 5a fossil and modern calibration samples are probably due to the character of the MIS 5a lake, i.e. a relatively small and shallow lake with an extensive littoral zone. In contrast, a large open water body with a fringe of wetland prevailed in the Sokli basin throughout a major part of MIS 5e. Particularly pollen of sedges (Cyperaceae) and spores of ferns (*Dryopteris*-type, *Athyrium*) show high and increasing percentage values (Fig. 3C) in concordance with an extension in the littoral (local zones II-2 and II-3; Fig. 3A, B) and these taxa were excluded from the pollen sum in the  $T_{jul}$  reconstruction. Nevertheless, there are indications that other herbs and shrubs (*Salix*, Poaceae, Ranunculaceae, Rosaceae, Apiaceae), that were not excluded from the sum, had a local wetland/shore habitat as well and, as such, can be expected to be over-represented in the pollen record and contribute to a poor analogue fit. Furthermore, *B. pubescens/pendula* pollen percentage values reach 70–80% in the birch forest assemblage of zone II, when applying a sum without sedges and ferns, i.e. greatly exceeding means of ~30–35% in the modern calibration data from Finland and Russia (Salonen et al. 2012). This might be an additional factor leading to poor modern analogues. The high percentages for *B. pubescens/pendula* in the early part of the MIS 5a vegetation development might reflect the strong pioneer character of *Betula* spp., i.e. producing abundant, wind-dispersed fruits, and revealing rapid reproductive rates, fast growth rates and a young reproductive-maturity age (Birks 1986).

In Fig. 4A(3), the median of the six-method ensemble based on all taxa (blue line) is compared with the median shown in Fig. 4A(2), i.e. produced by applying a pollen sum without sedges and ferns (red line). The largest difference in reconstructed  $T_{jul}$  is shown in zone III-b with pine-birch forest in the Sokli area, with the limited assemblage showing the highest  $T_{jul}$ , reaching near present-day values (13 °C). This value agrees with a minimum  $T_{jul}$  of 12 °C for pine forest in modern-day northern Fennoscandia (Väliranta et al. 2015). The low  $T_{jul}$  inferred by the full taxa assemblage for zone III-b can be ascribed to the low temperature optimum for Cyperaceae in the calibration data set (Salonen et al. 2012; see also Salonen et al. 2013).

*Chironomid assemblage – inferred  $T_{jul}$ .* – The chironomid-inferred  $T_{jul}$  reconstruction (Fig. 4C) shows overall increasing values from 12.7 °C at the base of the MIS 5a lake sequence to 15.8 °C at the top, with constant sample-specific errors of 0.7–0.9 °C. In general, the early part of the temperature record has high variability, but the mid-part is more stable (14–15 °C). Typical for pre-Holocene records, most samples have poor modern analogues according to MAT. Despite the poor fit between the fossil chironomid and modern calibration

samples, all fossil samples had good coverage of taxa present in the calibration data set with at least 94% of the fossil taxa present in the calibration data.

The low  $T_{jul}$  reconstructed near the base of the glacial lake deposit (base of local zone I-2), and in the overlying organic-bearing silt bed (lowermost part of local zone II-1), appear to be driven by the deep-water taxa *Corynocera oliveri*- and *Tanytarsus lugens*-types (Fig. 3A), which have temperature optima at 12.8 and 13.5 °C, respectively, in the modern calibration set. These taxa probably occurred in the cold profundal of the MIS 5a lake and therefore might reflect water temperature instead of air temperature. Although *C. oliveri*- and *T. lugens*-types are classical cold indicator taxa (Brooks 2006; Self *et al.* 2011), both are also typical pioneers in coarse substrates (Axford *et al.* 2009; Luoto & Sarmaja-Korjonen 2011).

*Corynocera ambigua* is one of the few other cold temperature chironomid taxa (optimum 13.7 °C) encountered in the MIS 5a sediment sequence. It shows overall high occurrences in the mid-part of the lake sequence (local zones II-1 and II-2) with more stable  $T_{jul}$  inferences. The modern distribution of *C. ambigua* in Finnish lakes is related to cold oligo-mesotrophic waters, but it is known to have a complex ecology (Brodersen & Lindegaard 1999). It is reported to dominate the assemblage in temperate lakes as well (Brodersen & Lindegaard 1999), and in the Holocene record from Lake Loitsana, high numbers of *C. ambigua* have been related to macrophyte density, particularly of *Myriophyllum* (Shala *et al.* 2014b). *Myriophyllum* is also well represented in the macrofossil record of local zone II-2 (Fig. 3B), but the high abundances of *C. ambigua* in the early half of local zone II-1 might be related to clear alkalinity water conditions.

The mid-part of the MIS 5a lake sequence is further characterized by a large number of intermediate- to warm-water chironomid taxa, including *Microtendipes pedellus*- (optimum  $T_{jul}$  at 14.6 °C), *Psectrocladius sordidellus*- (14.7 °C), *Cricotopus intersectus*- (15.2 °C), *Cladotanytarsus mancus*- (15.4 °C), *Cricotopus cylindraceus*- (15.6 °C) and *Chironomus anthracinus*-types (15.7 °C), suggesting warm summers, although the relatively high occurrences of *P. sordidellus*- and *C. intersectus*-types might be driven by habitat (affinity to macrophyte abundance) as well. The apparent increase in  $T_{jul}$  in the uppermost part of the record is probably caused by decreasing occurrences of *C. ambigua* as the lake became increasingly shallow and eutrophic.

Because of the influence of habitat preference on the chironomid assemblages, the trend in  $T_{jul}$  as well as the absolute  $T_{jul}$  values shown in Fig. 4C should be treated with caution. Nevertheless, the predominance of intermediate to warm chironomid taxa possibly indicates relatively warm summers. We used the calibration model by Luoto (2009) to accommodate for the overall shallow nature of the MIS 5a lake. However, the temperature

range of this calibration set is relatively short and was recently extended at the cold end from 11.3 to 7.9 °C (Luoto *et al.* 2014a, b). Based on the new model, the  $T_{jul}$  optima for the intermediate- to warm-water chironomid taxa are on average ~1 °C lower. They provide a  $T_{jul}$  range in the order of 13 to 15 °C, which is in line with the July temperature estimates inferred from the plant indicator species.

## Discussion

### *Environmental and climate developments at Sokli during MIS 5a*

The fossil remains analysed in the lake deposit of MIS 5a age in the Sokli basin, including pollen, spores, NPPs, macrofossils, diatoms and chironomids, record with great sensitivity the lake history and associated, successional developments in aquatic and telmatic ecosystems. Characteristic are the alkaline and nutrient-rich lake water conditions, which resulted from a combination of factors including: (i) the local carbonate bedrock; (ii) rapid leaching of carbonates and other soluble minerals from surface soils shortly after deglaciation (Engström *et al.* 2000; Helmens *et al.* 2018); (iii) sudden lake volume reductions (morphometric eutrophication; Hofmann 1998), such as following the drainage of the Sokli Ice Lake (Shala *et al.* 2014a); (iv) lake shallowing due to infilling; and (v) inflow of running water and sediment close to the coring site. Relatively high sedimentation rates, suggested by overall low LOI values (Korhola & Weckström 2004), allowed an exceptionally detailed reconstruction of the development of the Sokli Ice Lake and subsequent infilling of a relatively small and shallow lake confined to the Sokli basin.

The regional vegetation development that is recorded, following the moment of deglaciation, is typical for the early half of an interglacial at the latitude of Sokli. It is characterized by low-arctic shrub tundra being replaced by pioneer birch forest and then pine-dominated boreal forest. The latter vegetation is similar to that recorded in the Lake Loitsana sequence at the start of the Middle Holocene (Shala *et al.* 2017). The late part of the MIS 5a warm stage is missing in our records due to lake infilling.

Our study shows the importance of validating quantitative climate estimates inferred from fossil remains in lake sediments against the lake's own history. The multi-proxy based reconstruction of lake development shows that the chironomid assemblages in the MIS 5a lake deposit are strongly driven by non-climatic factors including changes in water depth, lake water geochemistry (alkalinity, eutrophication) and macrophyte abundances. Therefore, the trend as well as the absolute values of the chironomid-based  $T_{jul}$  reconstruction should be treated with caution. Never-

theless, most taxa are intermediate to warm indicators and show  $T_{jul}$  optima in the range of 13 to 15 °C, in line with the  $T_{jul}$  estimates inferred from the aquatic and wetland plant indicator species. The present-day distribution of the latter species is regulated by temperature, not edaphic factors or water chemistry (Väliranta *et al.* 2015 and references therein). For example, the distribution of *Typha* is currently restricted to southern Finland, and this taxon is not present at Sokli today, even though suitable habitats with moist, nutrient-rich soil are extensively available (Shala *et al.* 2017). However, since the presence of macrofossils in lake sediments strongly depends on taphonomic factors (e.g. distance to shore), the plant indicator species-inferred climate record is discontinuous. Finally, the expansion in the littoral caused by the infilling of the MIS 5a lake hampers the modelling of the pollen assemblage–climate relationship. The wetland element Cyperaceae is over-represented in the pollen record from the upper part of the MIS 5a lake deposits and, since Cyperaceae have some of the lowest temperature optima in the calibration set (corresponding to tundra conditions), this results, if uncorrected for, in an under-estimation of  $T_{jul}$ . By applying a pollen sum that excludes Cyperaceae as well as ferns, the pollen-based  $T_{jul}$  reconstruction reaches the present-day value of 13 °C in agreement with a minimum  $T_{jul}$  of 12 °C for pine forest in modern-day northern Fennoscandia.

Despite the shortcomings in the climate reconstructions, there is evidence for warmer-than-present summers during early MIS 5a. Warm, insolation-forced summers are also reported for the Early Holocene in northern Fennoscandia (Kullman 1999; Bigler *et al.* 2003; Väliranta *et al.* 2011, 2015; Luoto *et al.* 2014b; Paus & Haugland 2017; Shala *et al.* 2017). The apparent lag in terrestrial vegetation response, both during early MIS 5a and the Early Holocene, might be due to time needed for slow soil forming processes (e.g. Väliranta *et al.* 2015; Helmens *et al.* 2018), although the establishment of pioneer birch vegetation upon deglaciation might itself have delayed the development of boreal forest. Competition of niches (Giesecke & Bennett 2004) is mentioned by Väliranta *et al.* (2011) as a possible factor explaining the considerable time-lag by up to 3000 yr between the first macrobotanical and/or stomata finds of *Picea* and the establishment of closed (mixed) spruce forest in northeast European Russia during the Early Holocene. *Betula* pollen percentage values rise earlier, and values are higher and always exceed the threshold pollen accumulation rate (PAR) value for open birch forest (Seppä & Hicks 2006), than do *Picea* pollen records at the Russian sites. Our chronology for the MIS 5a deposit does not allow the calculation of PAR, but PAR values for the Early Holocene pioneer birch forest at Loitsana also greatly exceed those for the present-day birch forest in northern Europe (J. S. Salonen, pers. comm. 2014).

### *The Last Interglacial Complex (MIS 5) in the Sokli basin and wider implications*

The lake deposits of MIS 5e, 5c and 5a age in the Sokli basin each have their own unique signature in the basin's late Quaternary stratigraphy (Fig. 2). The successive developments in aquatic and terrestrial ecosystems depicted by their rich fossil records indicate that fossil remains occur *in situ* and are not the results of redeposition of older material as suggested in Forsström (1990). The distinctly different lake histories inferred from the sediment and fossil records also show that there is no evidence for a domino-like stacking of glaciotectonically upthrust interglacial sediment wedges as suggested by P. L. Gibbard in Otvos (2015). The near continuous sedimentary sequence of MIS 5 age in the Sokli basin provides an exceptionally long environmental and climate record for northern Europe, i.e. a region where deposits or fossil records dated to either of the substages of MIS 5 (MIS 5e, 5d, 5c, 5b, 5a) are rare. The data presented here for MIS 5a, and the earlier-published data for MIS 5c and MIS 5e, fully support Helmens (2014) in defining MIS 5 at Sokli as the Last Interglacial Complex, placing the start of the Last Glacial at the base of MIS 4 at c. 70 ka BP.

The up to 9-m-thick diatom gyttja of MIS 5e age at Sokli was deposited in a lake that was initially deep and stratified. A large open water body persisted until the last stages of infilling of the lake. A rich algal record (diatoms, green algae; Pliikk *et al.* 2016) characterizes the lake deposit. The sandy gyttja deposit of MIS 5c age accumulated in a small oxbow lake that remained flooded throughout its infilling process. An exceptionally abundant macrofossil record of plants and insects (Engels *et al.* 2010; Helmens *et al.* 2012) depicts the different stages of terrestrialization of the lake and return to stream channel deposition. Although macrofossils are not as abundant as in the MIS 5c gyttja, the fossil record in the lake deposit of MIS 5a age is diverse and traces in detail the development of the Sokli Ice Lake and subsequent infilling of a relatively small and shallow lake confined to the Sokli basin (this study). It is likely that the waterlogged depression in which the gyttja of MIS 5a age was deposited formed due to compression of the older sediments under the weight of the Fennoscandian Ice Sheet during the MIS 5b glaciation. A fluvial deposit of MIS 5d age separates the MIS 5e and 5c gyttja deposits (Fig. 2). The terrestrial vegetation developments during the warm stages of MIS 5 were similar to those recorded for the Holocene in the Sokli basin (Shala 2014). The vegetation succession starts with the replacement of pioneer birch vegetation by pine-dominated boreal forest. The establishment of spruce is recorded in the Late Holocene and late MIS 5c (Helmens *et al.* 2012). The presence of spruce is detected early during MIS 5e and *Picea* pollen percentages continuously rise through the MIS 5e lake deposit to a value of 20% (Salonen *et al.*

2018). MIS 5e further stands out by the local presence of *Corylus*; hazel reaches its current northern limit at over 500 km south of Sokli. Only the early half of the interglacial vegetation succession is recorded for MIS 5a (this study). Summer temperatures exceeding present-day values are inferred for the Early and Middle Holocene (Shala *et al.* 2017) and all three warm MIS 5 substages (Väliranta *et al.* 2009; Engels *et al.* 2010; Pliikk *et al.* 2018; Salonen *et al.* 2018; this study), whereas warmer-than-today winters are additionally reconstructed for MIS 5e (Salonen *et al.* 2018).

Similarly to at Sokli, MIS 5 has been defined as the Last Interglacial Complex in southwest-central Europe (Wol-lard 1978; Turon 1984). Bolikhovskaya & Molodkov (2014) also report the persistence of interglacial climate conditions until the end of MIS 5a for northeast-central Europe. The latter results agree with pollen records from loess-palaeosol sequences on the East European Plain, and a mollusc-based electron spin resonance (ESR) chronostratigraphy for the continental margin of northern Eurasia, indicating that during most of MIS 5 the vegetation cover in eastern Europe has evidently been of interglacial character (Molodkov & Bolikhovskaya 2009, 2010). MIS 5c and 5a have been respectively defined as the Brörup and Odderade Interstadials of the Last Glacial in the northwest European mainland stratigraphy. The interstadials show mainly boreal forest compared to temperate forest during the Eemian Interglacial (MIS 5e). Particularly winter temperatures are reconstructed to well below present-day values in northwest-central Europe during MIS 5c and 5a (Kühl *et al.* 2007) compared to minor winter temperature depressions in the east (Šeirienė *et al.* 2014). The overall warm conditions during all three substages of MIS 5 on the European mainland, and at Sokli, can be ascribed to higher-than-present summer insolation (Berger & Loutre 1991), with possible feedback mechanisms causing the strong decrease in winter temperature in northwest-central Europe during MIS 5c and 5a (Šeirienė *et al.* 2014).

Finally, the warm MIS 5c and 5a interglacial conditions at Sokli, i.e. the near-central area of Fennoscandian glaciation, preclude the persistence of any significant ice mass in Fennoscandia during MIS 5c and 5a. This is in agreement with data from southern Europe where speleothem encrustations in coastal caves on the island of Mallorca indicate a sea-level highstand that was slightly higher than today, and only slightly lower than the MIS 5e sea-level, during late MIS 5a (Dorale *et al.* 2010). The data from Mallorca are consistent with a number of relative sea-level estimates from tectonically stable locations around the world for MIS 5a.

## Conclusions

The integration of an extensive multi-proxy data set including a large variety of micro- and macrofossils of

plants and animals has allowed a comprehensive reconstruction of environmental and climate changes at the Sokli site in northern Finland during the early half of MIS 5a. In contrast with earlier suggested cold tundra conditions, our study indicates the development towards pine-dominated boreal forest and summer temperatures that exceed present-day values. Studying the climate evolution and dynamics in northern Europe during MIS 5 has long been hampered by a highly fragmented stratigraphical record resulting from glacial erosion. The unique MIS 5 record now available for Sokli shows the persistence of interglacial conditions into MIS 5a, thereby constraining the Last Glacial to MIS 4-2. Furthermore, our study shows the reconstruction of local, azonal environmental changes (e.g. lake development, successions in aquatic and telmatic ecosystems) as being an essential component when inferring regional vegetation and climate changes from biotic proxies.

*Acknowledgements.* – The Swedish Nuclear Fuel and Waste Management Company (SKB) provided funding for this study; furthermore, the Bolin Centre for Climate Research at Stockholm University is acknowledged for funding to the Sokli studies (KFH). JSS acknowledges funding from the Academy of Finland (project 1310649). We thank Sanna Piilo (University of Helsinki) for the LOI measurements and Jens-Ove Näslund (SKB) for comments on the manuscript. Bas van Geel (University of Amsterdam) and an anonymous reviewer are thanked for their useful comments that further improved the manuscript.

*Author contributions.* – KFH conceived the study and wrote the manuscript, with input from all authors. CK, NK, TPL and MV performed proxy analyses, and TPL and JSS made quantitative climate reconstructions.

## References

- Aario, L. 1940: Waldgrenzen und subrezentenen Pollenspektren in Petsamo Lappland. *Annales Academiae Scientiarum Fennicae A. LIV* 8, 120 pp.
- Alexanderson, H., Eskola, K. O. & Helmens, K. F. 2008: Optical dating of a Late Quaternary sediment sequence from northern Finland. *Geochronometria* 32, 51–59.
- Anderson, N. J. 2000: Diatoms, temperature and climatic change. *European Journal of Phycology* 35, 307–314.
- Axford, Y., Briner, J. P., Miller, G. H. & Francis, D. R. 2009: Paleocological evidence for abrupt cold reversals during peak Holocene warmth on Baffin Island, Arctic Canada. *Quaternary Research* 71, 142–149.
- Battarbee, R. W. 1986: Diatom analysis. In Berglund, B. E. (ed.): *Handbook of Holocene Palaeoecology and Palaeohydrology*, 527–570. John Wiley & Sons, Chichester.
- Berger, A. & Loutre, M. F. 1991: Insolation values for the climate of the last 10 million years. *Quaternary Science Reviews* 10, 297–317.
- Bigler, C., Grahn, E., Laroque, I., Jeziorski, A. & Hall, R. I. 2003: Holocene environmental change at Lake Njulla (999 m a.s.l.), northern Sweden: a comparison with four small nearby lakes along an altitudinal gradient. *Journal of Paleolimnology* 29, 13–29.
- Birks, H. J. B. 1986: Late-Quaternary biotic changes in terrestrial and lacustrine environments, with particular reference to north-western Europe. In Berglund, B. E. (ed.): *Handbook of Holocene Palaeoecology and Palaeohydrology*, 3–65. John Wiley & Sons, Chichester.

- Birks, H. J. B., Heiri, O. & Seppä, H. 2010: Strengths and weaknesses of quantitative climate reconstructions based on late-Quaternary biological proxies. *The Open Ecology Journal* 3, 68–110.
- Bolikhovskaya, N. S. & Molodkov, A. N. 2014: Chronology and climatic peculiarities of the period between c. 94 and 70 ka (MIS 5b–5a) inferred from palynological and IR-OSL analyses of the Voka reference section (south-eastern coast of the Gulf of Finland). Abstracts, International Conference INQUA-SEQS 2014, Ekaterinburg, Russia, September 10–16, 2014, 20–22.
- Bradbury, J. P. & Winter, T. C. 1976: Areal distribution and stratigraphy of diatoms in the sediments of Lake Sallie, Minnesota. *Ecology* 57, 1005–1014.
- Brodersen, K. P. & Lindegaard, C. 1999: Classification, assessment and trophic reconstruction of Danish lakes using chironomids. *Freshwater Biology* 42, 143–157.
- Brooks, S. J. 2006: Fossil midges (Diptera: Chironomidae) as palaeoclimatic indicators for the Eurasian region. *Quaternary Science Reviews* 25, 1894–1910.
- Cleveland, W. S. 1979: Robust locally weighted regression and smoothing scatterplots. *Journal of the American Statistical Association* 74, 829–836.
- Cronberg, G. 1982: *Pediastrum* and *Scenedesmus* (Chlorococcales) in sediments from lake Väckjösjön, Sweden. *Algological Studies, Archiv für Hydrobiologie, Supplement* 29, 500–507.
- Davis, B. A. S. & 68 others. 2013: The European Modern Pollen Database (EMPD) project. *Vegetation History and Archaeobotany* 22, 521–530.
- Donner, J. 1995: *The Quaternary History of Scandinavia. World and Regional Geology* 7, 200 pp. Cambridge University Press, Cambridge.
- Donner, J. 1996: The Early and Middle Weichselian interstadials in the central area of the Scandinavian glaciations. *Quaternary Science Reviews* 15, 471–479.
- Dorale, J. A., Onac, B. P., Fornós, J. J., Ginés, J., Tuccimei, P. & Peate, D. W. 2010: Sea-level highstand 81,000 years ago in Mallorca. *Science* 327, 860–863.
- Drehs, A., Nordlund, A., Karlsson, P., Helminen, J. & Rissanen, P. 2002: *Climatological Statistics of Finland 1971–2000*. 99 pp. Finnish Meteorological Institute, Helsinki.
- Elliott, S. M., Roe, H. M. & Patterson, R. T. 2011: Testate amoebae as indicators of hydrosere change: an 8500 year record from Mer Bleue Bog, eastern Ontario, Canada. *Quaternary International* 268, 128–144.
- Engels, S., Helmens, K. F., Väiliranta, M., Brooks, J. & Birks, H. J. B. 2010: Early Weichselian (MIS-5d and 5c) temperatures and environmental changes as recorded by chironomids and macroremains at Sokli (northern Fennoscandia). *Boreas* 39, 689–704.
- Engström, D. R., Fritz, S. C., Almendinger, J. E. & Juggins, S. 2000: Chemical and biological trends during lake evolution in recently deglaciated terrain. *Nature* 408, 161–166.
- Forsström, L. 1990: Occurrence of larch (*Larix*) in Fennoscandia during the Eemian interglacial and the Brörup interstadial according to pollen analytical data. *Boreas* 19, 241–248.
- van Geel, B. 1976: *A palaeoecological study of Holocene peat sections, based on the analysis of pollen, spores and macro and microscopic remains of fungi, algae, cormophytes and animals*. 75pp. Academisch proefschrift, HugodeVries laboratorium, University of Amsterdam.
- van Geel, B. & Grenfell, H. R. 1996: Spores of Zygnemataceae. In Jansonius, J. & McGregor, D. C. (eds): *Palynology: Principles and Applications*, 173–179. American Association of Stratigraphic Palynologists Foundation, Dallas.
- van Geel, B., Coope, G. R. & van der Hammen, T. 1989: Paleoeology and stratigraphy of the Lateglacial type section at Usselo (The Netherlands). *Review of Palaeobotany and Palynology* 60, 25–129.
- van Geel, B., Hallewas, D. P. & Pals, J. P. 1983: A Late: Holocene deposit under the Westfriesee Zeedijk near Enkhuizen (Prov. of Noord-Holland, The Netherlands): paleoecological and archaeological aspects. *Review of Palaeobotany and Palynology* 38, 269–335.
- van Geel, B., Odgaard, B. V. & Ralska-Jasiewiczowa, M. 1996: Cyanobacteria as indicators of phosphate-eutrophication of lakes and pools in the past. *PACT* 50, 399–415.
- 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.
- Gómez, N., Riera, J. L. & Sabater, S. 1995: Ecology and morphological variability of *Aulacoseira granulata* (Bacillariophyceae) in Spanish reservoirs. *Journal of Plankton Research* 17, 1–16.
- Gunin, P. D., Vostokova, E. A., Dorofeyuk, N. I., Tarasov, P. E. & Black, C. C. 1999: *Vegetation Dynamics of Mongolia*. *Geobotany* 26, 233 pp. Kluwer, Dordrecht.
- Haworth, E. Y. 1976: Two Late-Glacial (Late Devensian) diatom assemblage profiles from northern Scotland. *New Phytologist* 77, 227–256.
- Helmens, K. F., Risberg, J., Jansson, K. N., Weckström, J., Berntsson, A., Kaislahti Tillman, P., Johansson, P. W. & Wastegård, S. 2009: Early MIS 3 glacial lake evolution, ice-marginal retreat pattern and climate at Sokli (northeastern Fennoscandia). *Quaternary Science Reviews* 28, 1880–1894.
- Helmens, K. F. 2014: The Last Interglacial-Glacial cycle (MIS 5-2) re-examined based on long proxy records from central and northern Europe. *Quaternary Science Reviews* 86, 115–143.
- Helmens, K. F., Bos, J. A. A., Engels, S., Van Meerbeeck, C. J., Bohncke, S. J. P., Renssen, H., Heiri, O., Brooks, S. J., Seppä, H., Birks, H. J. B. & Wohlfarth, B. 2007b: Present-day temperatures in northern Scandinavian during the Last Glaciation. *Geology* 35, 987–990.
- Helmens, K. F., Johansson, P. W., Räsänen, M. E., Alexanderson, H. & Eskola, K. O. 2007a: Ice-free intervals continuing into Marine Isotope Stage 3 at Sokli in the central area of the Fennoscandian glaciations. *Bulletin of the Geological Society of Finland* 79, 17–39.
- Helmens, K. F., Katrantsiotis, C., Salonen, S. J., Shala, S., Bos, J. A. A., Engels, S., Kuosmanen, N., Luoto, T. P., Väiliranta, M., Luoto, M., Ojala, A., Risberg, J. & Weckström, J. 2018: Warm summers and rich biotic communities during N-Hemisphere deglaciation. *Global and Planetary Change* 167, 61–73.
- Helmens, K. F., Räsänen, M. E., Johansson, P., Jungner, H. & Korjonen, K. 2000: The Last Interglacial-Glacial cycle in NE Fennoscandia: a nearly continuous record from Sokli (Finnish Lapland). *Quaternary Science Reviews* 19, 1605–1623.
- Helmens, K. F., Väiliranta, M., Engels, S. & Shala, S. 2012: Large shifts in vegetation and climate during the Early Weichselian (MIS 5d-c) inferred from multi-proxy evidence at Sokli (northern Finland). *Quaternary Science Reviews* 41, 22–38.
- Hirvas, H. 1991: Pleistocene stratigraphy of Finnish Lapland. *Geological Survey of Finland Bulletin* 354, 123 pp.
- Hofmann, W. 1998: Cladocerans and chironomids as indicators of lake level changes in north temperate lakes. *Journal of Paleolimnology* 19, 55–62.
- Howett, P. J., Salonen, V.-P., Hyttinen, O., Korkka-Niemi, K. & Moreau, J. 2015: A hydrostratigraphical approach to support environmentally safe siting of a mining waste facility at Rautuvaara, Finland. *Bulletin of the Geological Society of Finland* 87, 51–66.
- Iivonen, E. 1973a: *Eem-interglasiaalinen kerrostuma Savukosken Soklilla, Pohjois-Suomessa, orgaanisten kerrostumien ja glasiaaligeologisen tutkimuksen valossa*. Licentiate's thesis, University of Turku, 144 pp.
- Iivonen, E. 1973b: *Eem-Kerrostuma Savukosken Soklilla*. *Geologi* 25, 81–84.
- Johansson, P. W. 1995: The deglaciation in the eastern part of the Weichselian ice divide in Finnish Lapland. *Geological Survey of Finland Bulletin* 383, 72 pp.
- Johansson, P. W. & Räsänen, M. 1994: Nya preliminära undersökningar av moräntäckta organiska avlagringar i Sokli, Norra Finland. *Nordiska Geologiska Vintermöten Abstracts* 21:a, p. 92.
- Jones, V. J. & Birks, H. J. B. 2004: Lake-sediment records of recent environmental change on Svalbard: results of diatom analysis. *Journal of Paleolimnology* 31, 445–466.
- Kleman, J., Hätttestrand, C., Borgström, I. & Stroeven, A. P. 1997: Fennoscandian paleoglaciology reconstructed using a glacial geological inversion model. *Journal of Glaciology* 43, 283–299.

- omárek, J. & Jankovská, V. 2001: Review of the green algal genus *Pediastrum*: Implication for pollen-analytical research. *Bibliotheca Phycologica* 108, 1–127.
- Korhola, A. & Weckström, J. 2004: Paleolimnological studies in Arctic Fennoscandia and the Kola Peninsula (Russia). In Pienitz, R., Douglas, M. S. V. & Smol, J. P. (eds.): *Long-term environmental change in Arctic and Antarctic lakes*, 381–418. Springer, Dordrecht.
- Kühl, N., Litt, T., Schölzel, C. & Hense, A. 2007: Eemian and Early Weichselian temperature and precipitation variability in northern Germany. *Quaternary Science Reviews* 26, 3311–3317.
- Kullman, L. 1999: Early Holocene tree growth at a high elevation site in the northernmost Scandes of Sweden (Lapland): a paleobiogeographical case study based on megafossil evidence. *Geografiska Annaler* 81A, 63–74.
- Lisiecki, L. E. & Raymo, M. E. 2005: A Pliocene-Pleistocene stack of 57 globally distributed benthic  $\delta^{18}\text{O}$  records. *Paleoceanography and Paleoclimatology* 20, PA1003, <https://doi.org/10.1029/2004pa001071>.
- Lundqvist, J. 1992: Glacial stratigraphy in Sweden. In Kauranne, K. (ed.): *Glacial Stratigraphy, Engineering Geology and Earth Construction*, 43–59. Geological Survey of Finland Special Paper 15.
- Lunkka, J. P., Sarala, P. & Gibbard, P. L. 2014: The Rautuvaara section, western Finnish Lapland, revisited – new age constraints indicate a complex Scandinavian Ice Sheet history in northern Fennoscandia during the Weichselian Stage. *Boreas* 44, 68–80.
- Luoto, T. P. 2009: Subfossil Chironomidae (Insecta: Diptera) along a latitudinal gradient in Finland: development of a new temperature inference model. *Journal of Quaternary Science* 24, 150–158.
- Luoto, T. P. 2010: Hydrological change in lakes inferred from midge assemblages through use of an intralake calibration set. *Ecological Monographs* 80, 303–329.
- Luoto, T. P. 2013: Dystrophy in determining midge community composition in boreal lakes. *Ecoscience* 20, 391–398.
- Luoto, T. P. & Sarmaja-Korjonen, K. 2011: Midge-inferred Holocene effective moisture fluctuations in a subarctic lake, northern Lapland. *Boreas* 40, 650–659.
- Luoto, T. P., Kaukolehto, M. & Nevalainen, L. 2014a: The relationship between water and air temperature in chironomid-based paleoclimate reconstructions: records from boreal and subarctic Finland. *The Holocene* 24, 1584–1590.
- Luoto, T. P., Kaukolehto, M., Weckström, J., Korhola, A. & Välranta, M. 2014b: New evidence of warm early-Holocene summers in subarctic Finland based on an enhanced regional chironomid-based temperature calibration model. *Quaternary Research* 81, 50–62.
- MacDonald, G. M., Velichko, A. A., Kremenetski, C. V., Borisova, O. K., Goleva, A. A., Andreev, A. A., Cwynar, L. C., Riding, R. T., Forman, S. L., Edwards, T. W. D., Aravena, R., Hammarlund, D., Szeicz, J. M. & Gattaulin, V. N. 2000: Holocene treeline history and climate change across Northern Eurasia. *Quaternary Research* 53, 302–311.
- Marks, J. C. & Power, M. E. 2001: Nutrient induced changes in the species composition of epiphytes on *Cladophora glomerata* Kütz. (Chlorophyta). *Hydrobiologia* 450, 187–196.
- Molodkov, A. N. & Bolikhovskaya, N. S. 2009: Climate change dynamics in Northern Eurasia over the last 200 ka: evidence from mollusc-based ESR-chronostratigraphy and vegetation successions of the loess-palaeosol records. *Quaternary International* 201, 67–76.
- Molodkov, A. N. & Bolikhovskaya, N. S. 2010: Climato-chronostratigraphic framework of Pleistocene terrestrial and marine deposits of Northern Eurasia based on pollen, electron spin resonance, and infrared optically stimulated luminescence analyses. *Estonian Journal of Earth Sciences* 59, 49–62.
- Økland, K. A. & Økland, J. 2001: Freshwater bryozoans (Bryozoa) of Norway II: distribution and ecology of two species of *Fredericella*. *Hydrobiologia* 459, 103–123.
- Økland, K. A. & Økland, J. 2005: Freshwater bryozoans (Bryozoa) of Norway V: Review and comparative discussion of the distribution and ecology of the 10 species recorded. *Hydrobiologia* 534, 31–55.
- Otvos, E. G. 2015: The Last Interglacial Stage: definitions and marine highstand, North America and Eurasia. *Quaternary International* 383, 158–173.
- Overpeck, J. T., Webb, T. I. I. & Prentice, I. C. 1985: Quantitative interpretation of fossil pollen spectra: dissimilarity coefficients and the method of modern analogs. *Quaternary Research* 23, 87–108.
- Pals, J. P., van Geel, B. & Delfos, A. 1980: Paleocological studies in the Klokkeweel bog near Hoogkarspel (prov. of Noord Holland). *Review of Palaeobotany and Palynology* 30, 371–418.
- Paus, A. & Haugland, V. 2017: Early to Middle Holocene forest-line and climate dynamics in southern Scandes mountains inferred from contrasting megafossil and pollen data. *The Holocene* 27, 361–383.
- Pliikk, A., Helmens, K. F., Fernández-Fernández, M., Kylander, M., Löwemark, L., Risberg, J., Salonen, S. J., Välranta, M. & Weckström, J. 2016: Development of an Eemian (MIS 5e) Interglacial palaeolake at Sokli (N Finland) inferred using multiple proxies. *Palaeogeography, Palaeoecology, Palaeoclimatology* 463, 11–26.
- Prentice, I. C. 1978: Modern pollen spectra from lake sediments in Finland and Finnmark, north Norway. *Boreas* 7, 131–153.
- Risberg, J., Sandgren, P., Teller, J. T. & Last, W. M. 1999: Siliceous microfossils and mineral magnetic characteristics in a sediment core from Lake Manitoba, Canada: a remnant of glacial Lake Agassiz. *Canadian Journal of Earth Sciences* 36, 1299–1314.
- Salonen, J. S., Helmens, K. F., Brendryen, J., Kuosmanen, N., Välranta, M., Goring, S., Korpela, M., Kylander, M., Philip, A., Pliikk, A., Renssen, H. & Luoto, M. 2018: Abrupt high-latitude climate events and decoupled seasonal trends during the Eemian. *Nature Communications* 9, 2851, <https://doi.org/10.1038/s41467-018-05314-1>.
- Salonen, S. J., 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.
- Salonen, J. S., Ilvonen, L., Seppä, H., Holmström, L., Telford, R. J., Gaidamavicius, A., Stancikaite, M. & Subetto, D. 2012: Comparing different calibration methods (WA/WA-PLS regression and Bayesian modelling) and different-sized calibration sets in pollen-based quantitative climate reconstruction. *The Holocene* 22, 413–424.
- Salonen, J. S., Korpela, M., Williams, J. W. & Luoto, M. 2019: Machine-learning based reconstructions of primary and secondary climate variables from North American and European fossil pollen data. *Scientific Reports* 9, 15805, <https://doi.org/10.1038/s41598-019-52293-4>.
- Sarmaja-Korjonen, K., Seppänen, A. & Bennike, O. 2006: *Pediastrum* algae from the classic late glacial Bølling Sø site, Denmark: response of aquatic biota to climate change. *Review of Palaeobotany and Palynology* 138, 95–107.
- Šeiriėnė, V., Kühl, N. & Kisiėlienė, D. 2014: Quantitative reconstruction of climate variability during the Eemian (Merkinė) and Weichselian (Nemunas) in Lithuania. *Quaternary Research* 82, 229–235.
- Self, A. E., Brooks, S. J., Birks, H. J. B., Nazarova, L., Porinchi, D., Odland, A. & Jones, V. J. 2011: The distribution and abundance of chironomids in high-latitude Eurasian lakes with respect to temperature and continentality: development and application of new chironomid-based climate-inference models in northern Russia. *Quaternary Science Reviews* 30, 1122–1141.
- Seppä, H. & Hicks, S. 2006: Integration of modern and past pollen accumulation rate (PAR) record across the arctic tree-line: a method for more precise vegetation reconstructions. *Quaternary Science Reviews* 25, 1501–1516.
- Seppä, H., Birks, H. J. B., Odland, A., Poska, A. & Veski, S. 2004: A modern pollen-climate calibration set from northern Europe: developing and testing a tool for paleoclimatological reconstructions. *Journal of Biogeography* 31, 251–267.
- Shala, S., Helmens, K. F., Jansson, K., Kylander, M. E., Risberg, J. & Löwemark, L. 2014a: Palaeoenvironmental record of glacial lake evolution during the early Holocene at Sokli, NE Finland. *Boreas* 43, 362–376.
- Shala, S., Helmens, K. F., Luoto, T. P., Salonen, J. S., Välranta, M. & Weckström, J. 2017: Comparison of quantitative Holocene temperature reconstructions using multiple proxies from a northern boreal lake. *The Holocene* 27, 1745–1755.

- Shala, S., Helmens, K. F., Luoto, T. P., Väiliranta, M., Weckström, J., Salonen, J. S. & Kuhry, P. 2014b: Evaluating environmental drivers of Holocene changes in water chemistry and aquatic biota composition at Lake Loitsana, NE Finland. *Journal of Paleolimnology* 52, 311–329.
- Smol, J. P. 1983: Paleophycology of a high arctic lake near Cape Herschel, Ellesmere Island. *Canadian Journal of Botany* 61, 2195–2204.
- Talvitie, J., Lehmuspelto, P. & Vuotovesi, T. 1981: Airborne thermal surveying of the ground in Sokli, Finland. *Geological Survey of Finland, Report of Investigation* 50, 1–13.
- Terasmaä, J. 1951: On the pollen morphology of *Betula nana*. *Svensk Botanisk Tidskrift* 45, 358–361.
- Turon, J. L. 1984: Direct land/sea correlations in the last interglacial complex. *Nature* 309, 673–676.
- Väiliranta, M., Birks, H. H., Helmens, K. F., Engels, S. & Piirainen, M. 2009: Early Weichselian interstadial (MIS 5c) summer temperatures were higher than today in northern Fennoscandia. *Quaternary Science Reviews* 28, 777–782.
- Väiliranta, M., Kaakinen, A., Kuhry, P., Kultti, S., Salonen, J. S. & Seppä, H. 2011: Scattered late-glacial and early-Holocene tree populations as dispersal nuclei for forest development in NE European Russia. *Journal of Biogeography* 38, 922–932.
- Väiliranta, M., Salonen, J. S., Heikkilä, M., Amon, L., Birks, H. H., Helmens, K. F., Klimaschewski, A., Kuhry, P., Kultti, S., Poska, A., Shala, S. & Veski, S. 2015: Plant macrofossil evidence for an early onset of the Holocene summer thermal maximum in Northern Europe. *Nature communications* 6, 6809, <https://doi.org/10.1038/ncomms7809>.
- Vartiainen, H. 1980: The petrography, mineralogy and petrochemistry of the Sokli carbonatite massif, northern Finland. *Geological Survey of Finland Bulletin* 313, 126 pp.
- van der Wiel, A. M. 1983: Apalaeoecological study of a section from the foot of the Hazendonk (Zuid-Holland, The Netherlands), based on the analysis of pollen, spores and macroscopic plant remains. *Review of Palaeobotany and Palynology* 38, 35–90.
- Westhoff, V. & den Held, A. J. 1975: *Plantengemeenschappen in Nederland*. 324 pp. Thieme & Cie b.v., Zutphen.
- Westhoff, V., Bakker, P. A., van Leeuwen, C. G. & van der Voo, E. E. 1981: *Wilde planten, deel 2, Het Lage Land*. 303 pp. De Lange/van Leer b.v., Deventer.
- Woillard, G. M. 1978: Grande Pile peat bog: a continuous pollen record for the last 140,000 years. *Quaternary Research* 9, 1–21.