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Summer temperatures and lake development during the MIS 5a interstadial: New data from the Unterangerberg palaeolake in the Eastern Alps, Austria

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ABSTRACT

Investigations of interstadials during early stages of glacial periods are of special interest, because they featured large-scale transformations of the climate system and the build-up of land-based ice sheets. Lacustrine sediment sequences are considered to be important natural archives that register past climate and environmental signals. Here, we present new multi-proxy data obtained from a palaeolake succession preserved in the inner-alpine terrace of Unterangerberg, Eastern Alps. These sediments formed during the second Early Würmian Interstadial, equivalent to Marine Isotope Stage (MIS) 5a, and were used to reconstruct changes in lake conditions and to infer past air temperatures. The sediment geochemical data and subfossil aquatic biota provide evidence of a cyclic lake–fen–lake development during this interstadial. The proxy records reveal stable lacustrine conditions with dense charophyte meadows and abundant aquatic fauna during the early part of the interstadial, a progressive shallowing of the lake resulting in the spreading out of fen vegetation in the middle part, and a transition from wetland to a renewed shallow lake stage towards the end of the interstadial. Chironomids were used to reconstruct mean July air temperatures, employing a combined Norwegian-Swiss chironomid temperature inference model. The reconstruction indicates a temperature close to present-day values of ca. 18 °C in the middle part of the record, while temperatures of ca. 13–14 °C are recorded for the lower and upper parts. The proxy data from this palaeolake provide evidence of heat and drought in the middle part of MIS 5a, supported by the chironomid-based temperature reconstruction. Our reconstruction shows a climate pattern broadly similar to that found in pollen-based estimates of mean July air temperatures from sites in the northern Alpine foreland and compares well to other European palaeoclimatic reconstructions of MIS 5a climate.

1. Introduction

The perspective of global climate change has drastically increased the interest in the palaeoecology of past warm periods, which left their traces in geological records. The inception of the last glacial period (115.0–11.7 ka, referred to as the Würmian in the European Alps) is of particular interest since this period is characterized by the transition from interglacial to glacial conditions with the occurrence of a series of strong and fast changes in climate and vegetation (stadials and interstadials) (NGRIP Members, 2004; Corrick et al., 2020). The transition was triggered by a decrease in summer insolation at high northern latitudes due to orbital forcing, which in turn led to a series of important feedback mechanisms involving all parts of the climate system – the ocean, the atmosphere, the cryosphere, the lithosphere and the biosphere (Köhler et al., 2010). The magnitude of temperature shifts at this transition and between stadials and interstadials varies greatly in palaeoclimate reconstructions, depending on the location and the methods and proxies used. Quantitative palaeoclimate data for this transitional period contribute significantly to our understanding of the role of the physical environment as a force driving ecological change.

In the Alps, the climatic deterioration that started at the end of the Last Interglacial (Eemian) resulted in an advance of alpine glaciers and the replacement of forests by steppe-tundra vegetation (Preusser, 2004; Ivy-Ochs et al., 2008). A general trend towards lower air temperatures was interrupted by two long and relatively warm interstadials, synchronous with Marine Isotope Stages (MIS) 5c and 5a in benthic oxygen isotope records of deep-sea sediments (Bond et al., 1993). These interstadials were referred to as Brørup and Odderade in northern Europe and St. Germain I and II in southern Europe, respectively. The complexity of this period is illustrated by the fact that it has been regarded

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by some as part of the MIS 5 interglacial complex (Shackleton et al., 2002; Guiter et al., 2003).

Most existing evidence for two warm intervals subsequent to the Last Interglacial in continental Europe relies on pollen data from terrestrial sediments. These data reveal that both interstadials of 5–10 kyr duration (Behre and van der Plicht, 1992; Wohlfarth, 2013) were forested in north-west, central and southern Europe (Behre, 1989). Reconstructions for northern Europe based on different types of proxies estimate winter and summer temperatures during the second interstadial to be mostly similar to those of the previous interstadial (Aalbersberg and Litt, 1998; Vandenberghe et al., 1998; Kühl et al., 2007). In the northern Alpine foreland, the second interstadial (MIS 5a) was characterized by coniferous forests dominated by spruce and the presence of the fern *Osmunda* (Grüger, 1979; Drescher-Schneider, 2000; Müller et al., 2003; Anselmetti et al., 2010; Dehnert et al., 2012) and is considered to be somewhat warmer than the first one (Klotz et al., 2004). A decline of closed forests in and around the Alps and a spread in tundra vegetation occurred at the end of the second interstadial (Drescher-Schneider, 2000; Müller and Sánchez Goñi, 2007) representing the boundary between the Early and Middle Würmian (MIS 5/4 boundary).

The ecological responses of lakes to climate change, as documented by empirical surveys, are pronounced (Havens and Jeppesen, 2018). Lacustrine sediment sequences preserving biological proxies are key archives for palaeovegetation and palaeoclimate reconstructions. Most valuable information is provided by subfossil remains of plants or amphibiotic insects which are sensitive to environmental changes in space and time. Quantitative reconstructions of climate parameters from these proxies are based on present-day plant/insect-climate relationships. The fastest response to climate warming can be expected to be recorded by rapid colonizers such as chironomids (non-biting midges; Insecta: Diptera: Chironomidae) which have aerial dispersal, relatively short life cycles and do not depend on soil formation. Summer temperature is one of the dominant drivers governing the distribution and abundance of chironomid species in lakes (Eggermont and Heiri, 2012).

Early and Mid-Würmian lake sediment successions are not widespread in the Alps due to the pervasive erosion and redeposition during the Last Glacial Maximum (Late Würmian) ice advance and decay. In some inner-alpine valleys and basins such sediments are preserved, however, and can be accessed e.g. by drill cores. Here, we present a multi-proxy environmental record from Early Würmian palaeolake deposits in the Unterangerberg terrace in the lower Inn Valley of Tyrol (Eastern Alps, Austria), one of the large longitudinal valleys of the Alps. This study aims to provide a record of changes in lake conditions and quantitative chironomid-inferred estimates of mean July air temperature for the second Early Würmian interstadial (MIS 5a, ca. 80 ka).

2. Site description and analysed core material

The inner-alpine Unterangerberg terrace is situated on the left side of the lower Inn Valley, Tyrol, northwest of the city of Wörgl (ca. 60 km northeast of Innsbruck) (Fig. 1). Surrounded by mountain ranges with altitudes of up to 1640 m a.s.l. to the north and northwest and bounded by the Inn River in the southeast, this terrace covers an area of ca 34 km^2 and lies approximately 100–150 m above the valley floor. According to the meteorological station Kirchbichl (498 m a.s.l.) situated close to the southeastern terrace edge, the mean July air temperature is 17.4 °C (1971–2000). Data from the meteorological station at Kufstein (492 m a.s.l.) located in the valley ca. 8 km downstream of the terrace show July temperature averages of 17.6 °C for 1971–2000 and 18.2 °C for 1981–2010 (data source: ZAMG – Central Institute for Meteorology and Geodynamics, Vienna, Austria (https://www.zamg.ac.at/cms/de/klima/klimauebersichten).

Geophysical investigations and a series of drillings conducted on the terrace during 1995–2006 in preparation for a tunnelling project resulted in a model of the bedrock topography in the subsurface of the terrace (Starnberger et al., 2013a, 2013b). Seventeen drill cores were recovered in 1998 and 2006 from a SW-NE oriented depression filled by up to 150 m of Pleistocene sediments. The lithostratigraphy varies significantly between the cores, highlighting the complex depositional pattern in the subsurface of the terrace. Only core A-KB 17/98 (47°30′03″N, 12°00′12″E; ca. 630 m a.s.l.) penetrated lacustrine sediments (ca. 44–40 m core depth) corresponding to MIS 5a (Starnberger et al., 2013a). A chronological framework of these organic-rich sediments was provided by pollen data described in detail in Starnberger et al. (2013a). A dominance of spruce in the pollen spectra, along with the presence of thermophilous tree species as well as the fern *Osmunda*, allows for correlation of this unit with the second Early Würmian Interstadial distinguished also in pollen records from other sites in the northern alpine foreland (e.g. at Mondsee and Samerberg). As derived from the palynological data, this interstadial is the warmest found in the entire Unterangerberg record covering the time interval ca. 118–40 ka (Starnberger et al., 2013a).

The sediments between 44 and 40 m depth are represented by fine detritus gyttja (ca. 44–43 m), calcareous gyttja (ca. 43–42 m), lignite (ca. 42.0–41.5 m) and again calcareous gyttja (ca. 41.5–40.0 m). Based on the lithological description, five sediment samples were taken as 5 cm thick slices (44.00–43.95, 42.90–42.85, 42.20–42.15, 41.85–41.80, and 40.35–40.30 m core depth) along this 4 m-thick interval.

3. Methods

3.1. Carbon and nitrogen analyses

Total carbon (TC) content and total nitrogen (TN) content were determined at the Forest Research Laboratory (Farnham, UK), using a combustion method (ISO 10694, 1995 and ISO 13878, 1998) with a Carlo Erba Flash 1112 series elemental analyser. Total inorganic carbon (TIC) content was analysed with the same device after pre-combustion in a furnace at 500 °C for 2 h to remove the organic fraction. The total organic carbon (TOC) fraction was calculated as the difference between TC and TIC. The TOC and TN data are expressed as percentages of dry weight of the sediment (wt%). The C/N ratio was calculated as the element mole ratio of TOC and TN (C_{TOC}/N_{TN}). The TIC content was converted into calcium carbonate ($CaCO_3$) content by multiplying with a factor of 8.33 based on the molar mass of carbon relative to $CaCO_3$. The amount of organic and inorganic matter (OM and IM) was determined by loss on ignition at 550 °C following the recommendations of Heiri et al. (2001). $CaCO_3$ content was expressed as percentages of dry weight of the IM fraction (im%).

3.2. Chironomid analysis

The sample pre-treatment procedure and the subsequent hand-sorting the chironomids were exceptionally long because of the dry and compact nature of the sediment. The densely packed sediments did not disintegrate completely using standard laboratory procedures for subfossil midges outlined in Walker (2013). The processing included chemical pre-treatment with warm 10% KOH for 1 h (to remove fine particles), subsequent rinsing through a 100 μm sieve, treatment of the residues in an ultrasonic bath (40 kHz) for 5 s (to disintegrate the compacted sediments), and another follow-up rinsing through a 100 μm sieve. The ultrasonic treatment based on the effect of cavitation was repeated in the case of samples that did not completely disintegrate after the first run. Chironomid larval head capsules (HC) were hand-picked from the residue in a Bogorov counting tray under a stereo-microscope at 20–40× magnification, dehydrated in 100% ethanol and permanently mounted ventral side up on microscope slides using Euparal® mounting medium. Chironomids were identified under a compound microscope at 200–400× magnification following taxonomic

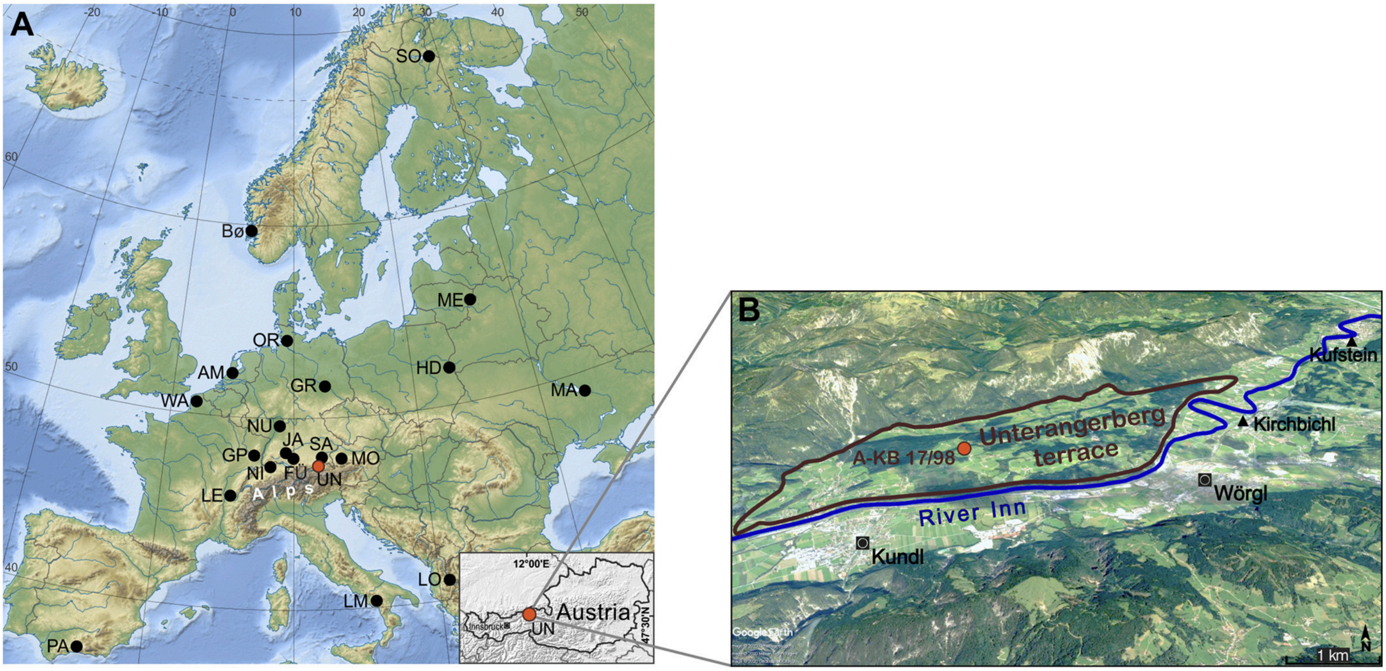

Fig. 1. (A) Maps showing the location of the Unterangerberg (UN) site in the northern Alps and other sites mentioned in the text: AM – Amersfoort, Bø – Bø, Fü – Füramoos, GP – La Grande Pile, GR – Gröbern, HD – Horoszki Duże, JA – Jammertal, LE – Les Echets, LM – Lago Grande di Monticchio, LO – Lake Ohrid, MA – Maksymivka, ME – Medininkai, MO – Mondsee, NI – Niederweningen, NU – Nussloch, OR – Oerel, PA – Padul, SA – Samerberg, SO – Sokli, WA – Watten, and (B) regional setting of the Unterangerberg terrace with the locations of the drill core site A-KB 17/98 (solid circle) and the meteorological stations (solid triangles) in the vicinity of the terrace (modified after Starnberger et al., 2013a).

keys for larvae (Brooks et al., 2007; Andersen et al., 2013). To provide a representative count for quantitative inferences (at least 45 chironomid HC, Heiri and Lotter, 2001), sediment samples of 15–68 g were processed.

3.3. Macrophytes and non-chironomid invertebrates

During the sorting chironomid subfossils, macro-remains of mosses and charophyte fructifications (oospores and gyrogonites) and of non-chironomid aquatic invertebrates, exoskeletons of oribatid mites (Acarina: Oribatida) and mandibles of caddisflies (Insecta: Trichoptera) and the alderfly *Sialis* (Insecta: Megaloptera) were also were picked out from the samples. Species identifications of mosses followed the key of van de Weyer and Schmidt (2018a, 2018b). The keys of Haas (1994) and Bazzichelli and Abdelahad (2009) were used to identify charophyte fructifications. Counts of macrofossils of plants and non-chironomid invertebrates were made for 50 g of dry sediment.

3.4. Chironomid-based palaeotemperature inferences

The quantitative inference model is based on a weighted averaging partial least squares (WA-PLS) regression (ter Braak and Juggins, 1993) and calibration, the statistical state-of-the art technique for palaeoecological reconstruction based on chironomid remains (e.g. Brooks and Birks, 2001; Heiri et al., 2014; Ilyashuk et al., 2019). This inverse regression approach assumes an explicit unimodal underlying taxon–environment response model, uses a weighted multivariate indicator-species approach, involves global estimation of environmental optima for all taxa across a full sampled environmental gradient, and is statistically robust (Birks, 2003; Birks et al., 2010). WA-PLS performs considerably better than direct analogue-matching procedures when none of the down-core assemblages is similar to the modern data (ter Braak et al., 1993; ter Braak, 1995). The method is therefore well suited for estimating past temperature changes even for fossil assemblages that do not have close modern analogues, as long as the individual taxa are well represented in the modern calibration data used to develop the model.

Quantitative mean July air temperature estimates were obtained using a chironomid-temperature transfer function based on a modern calibration dataset consisting of chironomid assemblage data from 274 lakes in the Alpine region and Norway (Heiri et al., 2011). This dataset contains information on the distribution of 154 chironomid taxa over a July air temperature range of 3.5–18.4 °C from lakes in temperate, subarctic, arctic, and alpine environments. The combined data-set covers a larger temperature range than other, more local, European calibration datasets and includes the majority of chironomid taxa expected in late Pleistocene sediments of European lakes. The resulting inference WA-PLS model using two components and square-root transformed percentage species data predicts mean July air temperature with a bootstrapped root mean square error of prediction (RMSEP) of 1.4 °C and a coefficient of determination between inferred and observed July air temperature values of 0.90. The model is described in detail in Heiri et al. (2011).

For numerical evaluation of the reconstruction several criteria were applied. Sample-specific errors as a quantitative estimate of the uncertainty in the reconstructed values (Juggins and Birks, 2012) were estimated using bootstrapping (9999 iterations). An evaluation of modern analogues for each sample was performed using the modern analogue technique (MAT). Every down-core chironomid assemblage was compared with all assemblages in the training set by using squared chi-square distance as a measure of dissimilarity. Samples with a minimum distance above the cut-level of the 5th percentile of all distances in the modern calibration data were considered as having ‘no good’ analogues in the modern calibration dataset (Birks et al., 1990). Goodness-of-fit to temperature of the down-core assemblages was tested by passively positioning the down-core samples on a canonical correspondence analysis (CCA) of the modern training set constrained solely by July air temperature. Any down-core samples with a squared residual distance to the first CCA axis greater than the 90th and 95th percentiles of all residual distances in the training set samples were

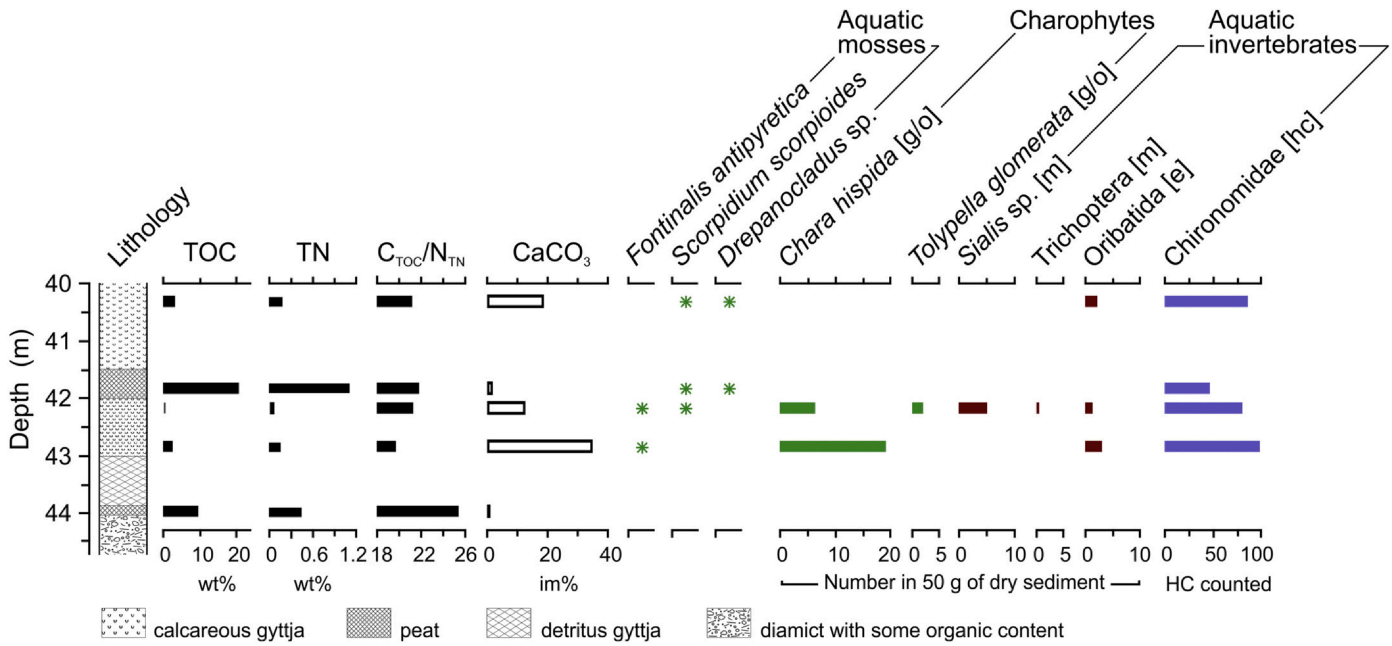

Fig. 2. Lithostratigraphic description, percentage values of total organic carbon (TOC) and total nitrogen (TN), atomic carbon to nitrogen (C_{TOC}/N_{TN}) ratio, percentage values of calcium carbonate ($CaCO_3$) in the inorganic fraction of sediments, abundances of macrofossils of charophytes and non-chironomid aquatic invertebrates, and chironomid head capsule count data in the Unterangerberg sediment profile dated to MIS 5a. Macrofossils: [e] – exoskeleton, [g/o] – gyrogonite and/or oospore, [hc] – head capsule, and [m] – mandible. The presence (*) of aquatic moss macrofossils is also shown.

identified as having a 'poor fit' or 'very poor fit' with temperature, respectively (Birks et al., 1990).

4. Results and interpretations

4.1. Sediment geochemistry and aquatic biotic proxies

The deepest layer (44.00–43.95 m depth) of the sediment sequence is characterized by high values of TOC (10 wt%) and TN (0.5 wt%), and a trace amount of $CaCO_3$ (0.9 im%) in the inorganic fraction of sediments (Fig. 2). The C/N ratio of 26 suggests that vascular land plants constituted the main source of the organic matter accumulated in this layer (cf. Meyers and Teranes, 2001). No remains of aquatic organisms were found in this layer. All these parameters suggest that the sediments were deposited in terrestrial environments.

The sediment between 43 and 42 m depth, characterized by an increase in $CaCO_3$ (12–35 im%), a decrease in TOC (0.5–2.7 wt%) and TN (0.03–0.16 wt%) contents, and an abundance of aquatic subfossils (charophytes, aquatic mosses, and invertebrates), was deposited in a lacustrine environment. Charophyte algae are represented by *Chara hispida* and *Tolypella glomerata*, and aquatic mosses by *Fontinalis antipyretica* and *Scorpidium scorpioides*. The invertebrate assemblages show a high taxonomic diversity. Chironomids, trichopterans, oribatids, and the alderfly *Sialis* were recorded among freshwater invertebrates.

The sediment between 41.85 and 41.80 m depth exhibits high levels of TOC (21 wt%) and TN (1.1 wt%), a small amount of $CaCO_3$ (1.6 im %), and contains abundant fragments of *S. scorpioides* and *Drepanocladus* sp. mosses. Invertebrate subfossils are represented only by chironomid remains. This sediment reflects the peat forming stage suggesting a shift of the palaeolake to a more palustrine environment.

The uppermost sample (40.35–40.30 m depth) is marked by relatively low values of TOC (3.4 wt%) and TN (0.18 wt%), and a relatively high $CaCO_3$ content in the inorganic fraction of sediments (18 im%). The subfossil aquatic biota are represented by residues of *S. scorpioides* and *Drepanocladus* sp. mosses, chironomids and oribatid mites. This sample is indicative of shallow lacustrine conditions.

The C/N ratio of all samples, except the deepest one, varies around 20. Since C/N ratios of 20 and greater typically characterize charophytes (Puche and Rodrigo, 2015; Rodrigo et al., 2016), aquatic mosses (Demars and Edwards, 2007; Riis et al., 2016), and vascular land plants (Meyers and Teranes, 2001), this suggests that the organic matter is a mixture mainly originating from aquatic (macrophytes) and terrestrial (vascular land plants) sources.

4.2. Chironomid succession

Chironomid head capsules (HC) were abundant in the record except for the bottommost layer (44.00–43.95 m depth) where no remains were found. In all other samples the minimum count sum of 45 HC usually recommended for palaeoenvironmental reconstruction (Heiri and Lotter, 2001) was reached. Counts of identifiable HC varied from 48 to 109 (mean = 81) per sample. A total of 28 taxa were identified, 21 of them have abundances > 2% in at least one sample (Fig. 3).

The assemblages in both samples obtained from the calcareous gyttja layer (43–42 m depth) are characterized by a dominance of *Paratanytarsus penicillatus*-type, *Phaenopsectra flavipes*-type, *Micropsectra insignilobus*-type, *Tanytarsus lugens*-type, and *Microtendipes pedellus*-type, the truly aquatic larvae of which can occur across a wide range of standing water bodies including lakes and ponds. At 41.85–41.80 m depth, where clay gyttja changed to peaty gyttja, taxa with larvae typical for semi-aquatic/terrestrial habitats (the edge of a lake, seepages, wet moss, water-logged peats and leaf litter, etc.) such as *Limnophyes/Paralimnophyes* and *Georthocladius* (Brooks et al., 2007; Przhiboro and Sæther, 2007; Cranston, 2010) prevail. Truly aquatic larvae of *Prodiamesa* were also present. In the uppermost sample (40.35–40.30 m depth), *Limnophyes/Paralimnophyes* persists as the dominant taxon, but chironomid larvae associated with lake littoral/profundal habitats (*T. mendax*-type, *P. flavipes*-type, *M. insignilobus*-type, *Paratendipes nudisquama*-type, and *T. lugens*-type) show well-defined occurrences (1–9%), suggesting a transition from a semi-aquatic to a lacustrine environment at the coring site.

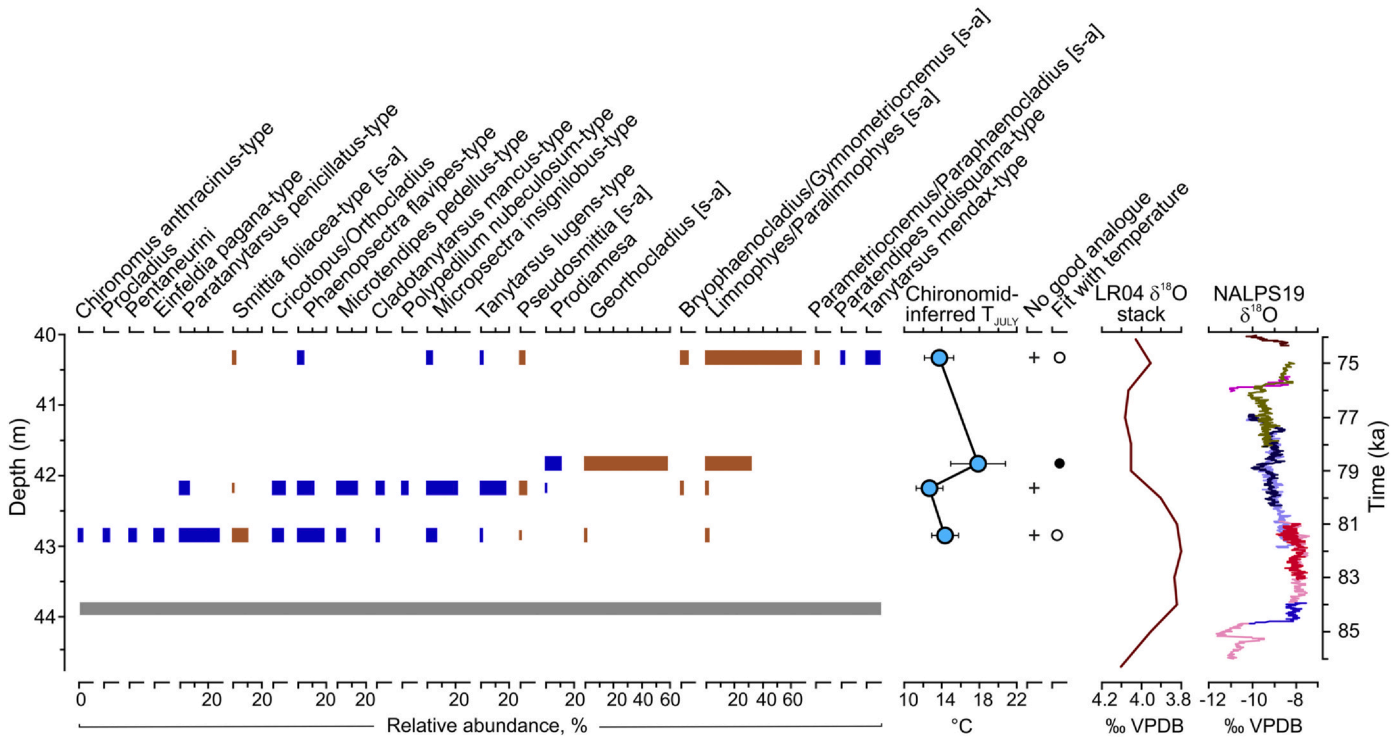

Fig. 3. Chironomid stratigraphy of the most common (> 2%) taxa in the Unterangerberg sediment profile. Taxa are arranged from bottom left to top right according to the position of their highest downcore relative frequency. No chironomid subfossils are present in the bottom-most layer (grey band). Semi-aquatic taxa are marked with [s-a]. Chironomid-inferred mean July air temperature (T_{JULY}) estimates are plotted with sample specific error bars. Samples lacking 'good' modern analogues in the training set (crosses) and those with 'poor' (open circles) or 'very poor' (solid circle) fit with temperature are also marked. MIS 5a as defined by the $\delta^{18}O$ stack from benthic foraminifera (LR04; Lisiecki and Raymo, 2005) and the NALPS19 speleothem $\delta^{18}O$ record (Moseley et al., 2020) are shown on the right for comparison. Colour coding of the $\delta^{18}O$ speleothem records of NALPS19 is the same as in Moseley et al. (2020).

4.3. Palaeotemperature estimates and their numerical evaluation

The quantitative reconstruction of mean July air temperature from the chironomid data revealed an amplitude of temperature variations of ca. 5 °C (Fig. 3). In the lower part of the interstadial sequence inferred July temperatures were ca. 13–14 °C. This was followed by a rise up to ca. 18 °C which is close to the modern values at the study site. At the end of the interstadial sequence, a return towards colder conditions with an inferred temperature of ca. 14 °C occurred.

All taxa of the record are currently known from the European Alps and are represented in the inference model. The relative chironomid abundances of the down-core samples, however, are not well reflected in the dataset and reconstruction diagnostic statistics revealed that all samples have no good analogues and/or a poor fit with temperature. This non-analogue situation may well be related to the fact that the A-KB 17/98 sediments represent littoral habitats of the ancient lake (Starnberger et al., 2013a), with a high predominance of semi-terrestrial taxa in some samples, whereas all training set samples originate from the deepest part of lakes. The modern analogue method, however, does not involve any underlying taxon-climate response model and a lack of modern analogues does not a priori imply that the results modeled with a transfer function for quantitative reconstruction are not valid (Birks, 1995). WA-PLS regression and calibration is based on the optima of the taxa included in the model and performs relatively well in poor analogue situations (Birks, 1998), interpolating temperature estimates for assemblages consisting of taxa that do not coexist in the modern training set samples. Transfer function-based reconstructions can be sensitive to the impact of confounding ecological factors (Juggins, 2013) and, therefore, poor fit scores of the samples with temperature may reflect potential effects of secondary variables. Nevertheless, given the good representation of the numerically important down-core chironomid taxa in the modern training set, it is expected that the inferences provide reasonable temperature estimates for the studied interstadial except for the sample at 41.85–41.80 m depth.

The chironomid assemblage at 41.85–41.80 m depth with high abundances of *Georthocladius* and *Limnophyes/Paralimnophyes*, which are common in very shallow water or even semi-aquatic/terrestrial habitats, has a good analogue but very poor fit to temperature. These taxa have abundances greater than their maximum value in the training-set incorporating purely lacustrine assemblages. In the inference model, *Georthocladius* is relatively rare, whereas *Limnophyes/Paralimnophyes* is frequent along a large temperature gradient (Heiri et al., 2011). This suggests that variables other than temperature may have influenced the response of the chironomid assemblage at that time, and therefore, the reconstructed temperature value may not be reliable. High abundances of these taxa provide indication of a low lake-level that will have impacted the size of the littoral zone. Changes in these variables may have invoked a stronger response in the chironomid fauna than temperature alone, giving the anomalous temperature inference.

5. Discussion

5.1. Empirical evidence from proxy records

Disentangling the direct and indirect linkages between climate, limnic processes and the preservation of their records in sediments is a challenging task (Anderson, 2014). Despite chironomid assemblages in lakes being influenced by a wide range of interacting environmental factors, inferring temperature changes from a chironomid sequence using a transfer function assumes that the chironomid assemblages respond, directly (through physiological constraints) or indirectly (through changes in lake and catchment processes altering chironomid habitats), to temperature (Velle et al., 2010; Eggermont and Heiri, 2012). Summer temperature has been shown to be a key factor driving chironomid communities in limnic environments, particularly on multidecadal to centennial time scales (e.g. Brooks and Birks, 2001). Alterations in lake water depth and aquatic vegetation mediated by climate-induced changes in catchment hydrology and soil processes are apparently also responsible for considerable variability in chironomid assemblages (Korhola et al., 2000; Luoto, 2010; Engels et al., 2012). However, water depth changes in small and shallow lakes that are commonly used for temperature reconstruction have apparently only a relatively minor influence on chironomid-inferred temperatures as long as they do not lead to a dramatic shallowing or drying of the lake (Heiri et al., 2003, 2014).

The multi-proxy record of the Unterangerberg palaeolake suggests cool summers and relatively stable lake conditions in the first half of the interstadial sequence. Most likely, shallow-water biotopes were well represented in the oligo-mesotrophic lake, where charophytes formed dense underwater meadows, which in turn provided habitats and shelter for aquatic invertebrates. The calcite encrustations formed around charophyte stems during photosynthetic activity of these algae (Raven et al., 1986) probably were major contributors to the relatively high $CaCO_3$ content in the lake sediments.

A prominent feature of the aquatic plant and chironomid records is the distinct change in assemblage composition and the increase in reconstructed temperatures in the middle part of the sequence (ca. 41.8 m depth) up to values similar to modern mean July air temperatures of ca. 18 °C. Ecological preferences of the moss and chironomid taxa suggest that the lake biota may have responded to a change in water depth, e.g. the lake surface area may have drastically shrunk or the lake even transformed into a wetland ecosystem. The predominance of *S. scorpioides* and *Drepanocladus* sp. mosses among aquatic plants and the low $CaCO_3$ concentration suggest an environment typical of a moderately nutrient-rich fen (cf. Vitt, 2019). A possible reason for the lake shallowing was a drought impacting surface water and/or groundwater input into the lake. Summer heat waves have most likely exacerbated these dry conditions by increasing evaporation and decreasing soil moisture and runoff.

Pollen-based inferences corresponding to this interval of the sediment record (between 42.20 and 41.15 m depth) also show a dramatic drop in tree pollen from ca. 80 to 5% and a large amount of charcoal particles (Starnberger et al., 2013a), providing evidence of forest fires disrupting the dominant vegetation (cf. Whitlock and Larsen, 2001). The development of a more open vegetation cover was mainly caused by the rapid decline of spruce (*Picea*) (Starnberger et al., 2013a) that is noted to be very fire-sensitive owing to its thin bark and particularly susceptible to heat and drought due to its shallow root system (Caudullo et al., 2016; Fréjaville et al., 2018). This interval is also characterized by the scattered distribution of pine (*Pinus*) that has a thick bark and is marked by a high resistance to fire (Fernandes et al., 2008) and birch (*Betula*), which generally functions as a pioneer tree genus with rapid early growth especially in secondary successional sequences following a disturbance, e.g. by fire (Beck et al., 2016). Important pioneers of disturbed habitats such as sedges (*Cyperaceae*) and grasses (*Poaceae*), prevailing in the herbal pollen spectrum of this interval, were infected with endophytic fungi (Starnberger et al., 2013a). The latter are known to be able to improve adaptation and mitigate responses of their host plants to abiotic stresses, including those resulting from major fire events, by regulating ecophysiological mechanisms leading to drought resistance and thermo-tolerance in infected plants (Rodriguez et al., 2004; Baynes et al., 2012; Nagabhyru et al., 2013). Taking in account that low winter temperatures and low moisture availability can limit tree growth or survival and that the predominance of non-arboreal taxa is a clear indication of habitat aridity (Prentice et al., 1992; Salonen et al., 2012), very low pollen concentrations and the pollen composition suggest that the climate during this period was characterized by warm, dry summers and cold winters.

All available proxy data from the Unterangerberg palaeolake record provide evidence for hot and dry summers promoting fires in the middle of the MIS 5a interstadial sequence. High summer temperatures during the time interval are supported by the chironomid-based quantitative reconstruction, although the inferred temperature of 18 °C is regarded as unreliable (see above). The increase in the reconstructed temperatures may reflect the indirect response of the chironomids to climate change which gave rise to dramatic changes in the hydrological regime of the lake. The inferred temperature may well be even underpredicted, given that the transfer function models have a tendency to pull predicted values towards the mean of the training set, leading to overestimation of low and underestimation of high temperatures (ter Braak and Juggins, 1993).

Towards the end of the interstadial sequence (ca. 40.3 m depth), the abundance of *S. scorpioides* and *Drepanocladus* sp. mosses and a relatively high $CaCO_3$ content of the inorganic fraction (18 im%) suggest an environment typical of a nutrient- and bicarbonate-rich fen (cf. Vitt, 2019). The chironomid assemblage comprises species characteristic of semi-aquatic/terrestrial and open water habitats and imply that the fen was at a transition to areas of open water, namely to lacustrine conditions. Such a lake-fen-lake cycle is usually repeated where surface-water and groundwater inputs vary over time (Haslam, 2003). The chironomid-based reconstruction implies that summer temperatures decreased by the end of the interstadial to those typical of the first half of the interstadial. Most likely, the rate of evaporation decreased under cool conditions, resulting in increased effective moisture and the transition from wetland to a lacustrine environment. This inference is supported by an increase of willow (*Salix*) at ca. 40–41 m depth (Starnberger et al., 2013a); this plant grows primarily on moist soils and on the banks of water bodies.

In general, the chironomid-based temperature inferences are in agreement with pollen data from the same sediment unit (Starnberger et al., 2013a) which provide evidence for the general pattern of the MIS 5a climate in the region: (1) a climate amelioration (reforestation phase) in the early part of the interstadial, (2) a subsequent warming indicated by the rise of *Picea*, (3) a climate optimum indicated by a maximum of thermophilous deciduous trees, (4) a climate deterioration (increased drought stress) favourable for open vegetation rich in sedges and grasses in the middle of the interstadial, (5) a slight climate improvement (apparently, an increase in humidity) indicated by a short re-expansion of scattered forest vegetation, and (6) cooler conditions favourable for the expansion of open grassland and shrub vegetation with *Salix* at the end of the interstadial. Subsequently, the pollen record shows the development of open vegetation, corresponding to a stadial environment (MIS 5a/4 transition); the lake dried out completely at this period.

5.2. Comparison with other MIS 5a palaeoclimatic reconstructions across Europe

A similar pattern of vegetation and climate development during the MIS 5a interstadial has been recorded from sites in the northern Alpine foreland, e.g. from Lake Mondsee, Austria (Drescher-Schneider, 2000), and Samerberg (Grüger, 1979; Müller and Sánchez Goñi, 2007), Füramoos (Müller et al., 2003; Müller and Sánchez Goñi, 2007) and Jammertal (Müller, 2000) in Germany. Similar to the climate inferences from the Unterangerberg palaeolake, a multi-proxy investigation of sediments at Niederweningen in the Swiss Alpine foreland revealed that after a climate improvement at the likely beginning of MIS 5a, a period of progressive lake shallowing and a transition to a wetland environment (swamp) occurred, after which a renewed lake phase started under moderate climate conditions at the end of the interstadial (Dehnert et al., 2012). Evidence of steppe expansion and drying of the soil in the middle/end part of MIS 5a has been observed in the records from La Grande Pile in eastern France (de Beaulieu and Reille, 1992;

Guiot et al., 1992), Horoszki Duże in eastern Poland (Granoszewski, 2003), Lago Grande di Monticchio in southern Italy (Allen and Huntley, 2000), Padul in southern Spain (Pons and Reille, 1988), and Watten in northern France (Emontspohl, 1995). The available palaeobotanical and sediment data suggest that a wet oceanic climate prevailed in central and southern Europe during the early part of the interstadial, a more continental climate with hot, dry summers in the middle part, and a cold and relatively humid climate during its final part (Wohlfarth, 2013 and references therein).

A subdivision of the MIS 5a interstadial into two very different climatic regimes is evident in the beetle (Coleoptera) record from Oerel, northwest Germany (Behre et al., 2005). Mild climate conditions with both summer (ca. 19 °C) and winter (2–4 °C) temperatures above present-day values (ca. 16 °C and ca. 1 °C for July and January, respectively) are recorded during the early part of the interstadial. During the later part, the climate at Oerel became much colder and more continental with temperatures of the warmest month of ca. 8–12 °C and temperatures of the coldest month (ca. –11 to −22 °C) significantly lower than the current mean January temperature (Behre et al., 2005). In the central German lowlands, at Gröbern, mean July temperatures of ca. 17 °C (ca. 18 °C at present) and January temperatures of ca. –12 °C (ca. –0.5 °C at present) during MIS 5a are reconstructed from pollen and plant macrofossil data (Kühl et al., 2007), suggestive of greater continentality than today. A forested environment with deep winter frost during the interstadial was identified by pedological analysis of the loess-palaeosol sequence at Nussloch, southern Germany (Antoine et al., 2001).

MIS 5a pollen records from central Europe (de Beaulieu and Reille, 1984; Granoszewski, 2003; Klotz et al., 2004) show a lower abundance of thermophilous plants at eastern sites due to factors related to increased continentality, less precipitation, thin snow cover, frost, and a shorter growing season. The reconstructions confirm that this temperate interstadial was markedly less influenced by air advection from the ocean probably due to the relatively large fall in sea level (Caspers and Freund, 2001). Globally averaged sea level for MIS 5a was ca. 9–30 m lower than at present (Creveling et al., 2017) and up to ca. 40 m lower than during MIS 5e (cf. Dutton and Lambeck, 2012; Grant et al., 2012). Warm season sea-surface temperature estimates from planktonic foraminifera assemblages in the eastern subpolar North Atlantic Ocean reveal that MIS 5a was ca. 4 °C colder than MIS 5e (Oppo et al., 2006). Biological proxies in western and central Europe also indicate that summer temperatures during the second post-Eemian interstadial were about 4 °C below those of the Eemian thermal maximum (Vandenberghe et al., 1998).

Applying different quantitative approaches, Klotz et al. (2004) used four high-resolution early Würmian pollen records at elevations ranging from 200 to 662 m a.s.l. in the northern Alpine foreland, Les Echets in France and Jammertal, Füramoos, and Samerberg in southern Germany, for a quantitative climate reconstruction (Table 1). For the sites Samerberg and Füramoos, the two nearest to our study site (Fig. 1), these reconstructions indicate mean temperatures of the warmest month of ca. 13–17 °C during MIS 5a. Similar estimates of mean July air temperatures (13–18 °C) are suggested by our record from Unterangerberg. Both reconstructions, pollen-based by Klotz et al. (2004) and our chironomid-based, suggest that peak mean July air temperatures in the interstadial may have reached values close to the present-day ones. The same way, stable isotope data of calcitic flowstones from the Inn Valley near Innsbruck imply that peak climatic conditions during MIS 5a were not drastically different from those that prevail in the area today (Spötl and Mangini, 2006). At Les Echets, France, the pollen-based reconstruction by Klotz et al. (2004) demonstrates that peak summer temperatures in the interstadial were close to modern values (Table 1). A chironomid record from Les Echets also documents the MIS 5a climatic improvement by higher percentages of warm-adapted taxa (Gandouin et al., 2007).

Other temperature inferences for MIS 5a from France (Guiot et al., 1992, 1993; Ponel, 1995), Germany (Kühl et al., 2007) as well as from Poland (Granoszewski, 2003) and Ukraine (Gozhik et al., 2014) also imply interstadial summer temperatures approaching those of today (Table 1). A pollen record from Medininkai in Lithuania suggests that the MIS 5a interstadial was the warmest interval of the last glacial period with July temperatures of 16.5–17.5 °C (ca. 16.2 °C at present; Šeirienė et al., 2014).

Based on marine fauna and/or pollen data sets in the maritime parts of NW-Europe from 40° to 80° N, MIS 5a temperatures in the north (on Svalbard) and in the south (the Netherlands, France) were very similar to today, but much cooler than today in between (Norway, NW Germany) (Sejrup and Larsen, 1991). Sea-surface temperature estimates, inferred from planktonic foraminifera in the Norwegian Sea and the eastern part of the North Atlantic, show MIS 5a summer temperatures equal or warmer than today for North Atlantic sites and ca. 6 °C lower than today in the Norwegian Sea, i.e. the same trend as inferred from the coastal sections (Sejrup and Larsen, 1991). These data confirm the close relationship between western European climate and North Atlantic sea-surface temperatures. Moreover, the precisely dated NALPS19 speleothem δ^{18}O record reveals rapid shifts in climate during the last glacial period along the northern rim of the Alps, highly consistent with the δ^{18}O variability recorded in Greenland ice cores on multi-decadal timescales (Moseley et al., 2020). This implies that due to the common North Atlantic moisture source, millennial-scale climate change was coherent between Greenland and Europe, with no evidence of a significant lag time (Moseley et al., 2020).

A comparison between records from central Europe and from western Europe and Fennoscandia demonstrates that the magnitude of the warming during the second post-Eemian interstadial was high at low latitudes in Europe and much lower in northern Europe (Behre, 1989; Guiter et al., 2003). Terrestrial records covering a large part of Europe show distinct north-south and west-east gradients in vegetation and climate (probably even steeper than today), and a more continental climate, mainly due to a lower sea level and a southward displacement of the Gulf Stream and a cold Norwegian Sea (Behre, 1989; Zagwijn, 1989; Guiter et al., 2003).

6. Conclusions

New multi-proxy data obtained from a palaeolake sediment sequence at the inner-alpine Unterangerberg site provide new quantitative insights into the climate in the Eastern Alps during the second Early Würmian interstadial (MIS 5a). The palaeolake was a highly dynamic system reflecting well the climate and environmental changes that have occurred during the interstadial. Sediment geochemistry data and biotic proxies provide evidence of a cyclic lake–fen–lake development. Stable lacustrine conditions were established soon after a general amelioration of the climate in the early part of the interstadial and shallow-water biotopes with dense charophyte meadows and abundant aquatic fauna were wide-spread in the lake. This was followed by a heat-drought period favourable for lake shallowing and giving rise to an environment typical of a moderately nutrient-rich fen. A transition from wetland to a lacustrine environment took place under cooler conditions towards the end of the interstadial, resulting in open water areas with adjoining fens.

Mean July air temperatures based on chironomids indicate a warming from ca. 13–14 °C at the beginning of the interstadial to temperatures close to present-day values (ca. 18 °C) in the middle part of the interstadial. Chironomid assemblages may have been influenced by changes in water depth and macrophyte richness during the middle of this interstadial, and the reconstructed temperatures may be regarded as unreliable. Nevertheless, all available proxy data provide evidence for a heat-drought period during this interval. A subsequent decrease in air temperature to ca. 14 °C is inferred towards the end of the interstadial. The temperature pattern reconstructed from the Unterangerberg palaeolake record broadly agrees with quantitative

Table 1
Palaeotemperature estimates for the MIS 5a interstadial from European terrestrial and coastal marine deposits. Reconstructions are based on: b – beetles, ch – chironomids, f – foraminifera, m – marine mollusks, p – pollen, and pm – freshwater plant macrofossils. Values in square brackets correspond to present-day temperature data reported in the references.

Site	Mean July air temperature, °C	Mean January air temperature, °C	Reference
Northern Europe	10–15[b, p]	–13[b, p]	Aalbersberg and Litt, 1998
Brøggerhalvøya (Svalbard)	5.0[f, m] [5.0]	–	Sejrup and Larsen, 1991
Sokli (Finland)	≥ 13.0[pm, ch] [13.0]	–	Helmens et al., 2018
Bø (Norway)	6.0[f, m] [15.0]	–	Sejrup and Larsen, 1991
Medininkai (Lithuania)	16.5–17.5[p, pm] [16.2]	–8.5[p, pm] [−5.1]	Šeirienė et al., 2014
Northwest Germany	15–16[b, p, pm]	< −10[b, p, pm]	Caspers and Freund, 2001
Oerel (Germany) early part	19[b] [16.0]	2–4[b] [1.0]	Behre et al., 2005;
and later part	8–12[b]	−11 to –22[b]	Helmens, 2014
Amersfoort (Netherlands)	16.0[p] [18.0]	–	Sejrup and Larsen, 1991
Gröbern (Germany)	17[p, pm] [18.3]	–12[p, pm] [−0.5]	Kühl et al., 2007;
	≥ 15[c]	—	Walkling and Coope, 1996
Horoszki Duże (Poland)	≥ 15–17[p, pm] [18.0]	≥ 0[p, pm]	Granoszewski, 2003;
			Helmens, 2014
Central and eastern Europe			
Maksymivka (Ukraine)	17.0–21.5[p] [22.5]	−7.5 to 3[p] [−2.9]	Gozhik et al., 2014
La Grande Pile (France)	13–18[p] [18.5]	−13 to –5[p] [−0.5]	Guiot et al., 1992;
	14–20[b, p]	—	Guiot et al., 1993;
	16–20[b]	—	Ponel, 1995;
			Rousseau et al., 2007
Northern Alpine foreland			
Les Echets (200 m a.s.l.)	15–20[p] [19.7]	−15 to 2[p] [1.9]	Klotz et al., 2004
Jammertal (578 m a.s.l.)	6 − 17[p] [17.3]	–17 to –4[p] [−1.4]	Klotz et al., 2004
Füramoos (662 m a.s.l.)	13–17[p] [17.8]	−15 to –2[p] [−0.8]	Klotz et al., 2004
Samerberg (660 m a.s.l.)	14–16[p] [15.7]	−12 to –5[p] [−2.8]	Klotz et al., 2004
Unterangerberg (630 m a.s.l.)	13–18[ch] [18.2]	–	This study
Southern Europe			
Monticchio (Italy)	–	−14 to 1[b]	Allen et al., 1999
Lake Ohrid (Macedonia/Albania)	19 − 23[p] [22.0]	–2 to 3[p] [2.0]	Sinopoli et al., 2019

pollen-based estimates of mean July air temperatures from the sites in the northern Alpine foreland. Further investigations of early glacial interstadials are needed to provide high-resolution palaeoecological records relevant for better understanding climate and environmental change during the early part of the last glacial.

Declaration of Competing Interest

The authors declare no conflicts of interest.

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The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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