Chironomid- and pollen-based quantitative climate reconstructions for the post-Holsteinian (MIS 11b) in Central Europe

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Abstract. Investigating climatic and environmental changes during past interglacials is crucial to improve the understanding of the mechanisms that govern the changes related to current global warming. Among the numerous proxies that can be used to reconstruct past environmental and climatic conditions, pollen allow quantitative reconstructions of annual, warmest month and coldest month air temperatures as well as precipitation sums, while the head capsules of Chironomidae larvae are widely used to infer past summer air temperature as well as in the trophic state or pH of water bodies. Nevertheless, the latter have so far mostly been used for reconstructing Holocene and Late Weichselian summer temperatures while there are to date only four sites in Europe with chironomid-based summer air temperature reconstructions for the Late Pleistocene and no such records for any Middle Pleistocene warm period. In this study we present the first quantitative palaeoclimate reconstruction for the post-Holsteinian (Marine Isotope Stage - (MIS) 11b) in Central Europe that is based on both pollen and fossil chironomid remains preserved in palaeolake sediments recovered at Krępa, southeastern Poland. Besides being used for the palaeoclimatic reconstruction, pollen analyses provide the biostratigraphic framework and a broader perspective of climate development at the end of Holsteinian Interglacial. Fossil Chironomidae assemblages at Krępa consist mainly of oligotrophic and mesotrophic taxa (e.g. *Corynocera ambigua*, *Chironomus anthracinus*-type) while eutrophic taxa (e.g. *Chironomus plumosus*-type) are less abundant. The chironomid-based summer temperature reconstruction yields July air temperature between 15.3 and 20.1°C

during the early post-Holsteinian. Similar summer air temperature changes during the first stadial after the Holstein Interglacial are also reflected by the pollen data, which, however, show a certain delay compared to the chironomid-based temperature reconstruction. In any case, results from Krępa prove that conducting Chironomidae analysis is feasible for periods as early as the Middle Pleistocene, improving our understanding of the mechanisms that control present-day climatic and environmental changes.

1 Introduction

Earth's history is characterised by repeated climate fluctuations, which had until the present interglacial, the Holocene (marine isotope stage (MIS) 1), only natural causes and were not influenced by humans. This offers the opportunity to compare natural climatic changes in the past with the current ones in order to better assess the anthropogenic impact on the present climate. With respect to human impact during the Holocene, the so-called "Anthropocene" is presently widely debated across various scientific disciplines though its exact timing as well as the actual dimension of human influence on the environment are still debated (Brondizio et al., 2016).

Holocene environmental archives, such as lake, palaeolake and ocean sediments provide material for comprehensive palaeoecological analyses. The sensitivity of some groups of organisms in these archives to changing hydrological or climatic conditions allows to reconstruct past events that directly affected the abundance or structure of the communities (Battarbee, 2000). Species, which are characterised by narrow ecological preferences, whether it be air temperature, water chemistry or water depth, are used for certain palaeoenvironmental reconstructions (Juggins and Birks, 2012). Many ecological parameters can be reconstructed using different proxies. For example, Foraminifera can be used to reconstruct ocean pH (Foster and Rae, 2016; Roberts et al., 2018), pollen provide information about changes in vegetation (Ralska-Jasiewiczowa et al., 2004; Kupryjanowicz et al., 2018) and can be used to reconstruct past human activity (Chevalier et al., 2020) or past climate conditions (e.g. Rylova and Savachenko, 2005; Hrynowiecka and Winter, 2016). Head capsules of chironomids can serve as the basis for summer air temperature reconstructions (Eggermont and Heiri, 2012) as well as for assessing the trophic state or pH of freshwater ecosystems (Płóciennik, 2005).

In general, palaeoecological and palaeoclimatological reconstructions indicate a considerable human impact on the environment during the last 300 years (Zalasiewicz et al., 2010). However, these reconstructions neither provide unequivocal information about air temperature changes nor allow to distinguish between the relative contribution of natural drivers and human impact to these changes. To gain a deeper understanding of the present human impact on climate and environment, it is therefore essential to investigate natural climate variability and environmental changes during past warm periods prior to any anthropogenic impact. In this regard, a particularly suitable target is the Holsteinian Interglacial (or Mazovian Interglacial in Poland), which is commonly estimated to have lasted from 423 to 395 ka BP, thus corresponding to MIS 11c (Lauer and Weiss, 2018; Lauer et al., 2020; Fernández Arias et al., 2023). To date, there are only very few chironomid-based reconstructions of climatic and ecological conditions for the Middle and Late Pleistocene in Europe available (Engels et al., 2008; Bolland et al., 2021; Ilyashuk et al., 2022; Rigterink et al., 2024) but none for the Holsteinian Interglacial and the time thereafter in particular. Hence, knowledge about climatic conditions at this time is mainly derived from pollen data, e.g. from the Praclaux maar in southern France (Reille and de Beaulieu, 1995), Tenaghi Philippon in north-eastern Greece (Tzedakis et al., 2006; Ardenghi et al., 2019) and Lake Ohrid on the North Macedonian-Albanian border (Kousis et al., 2018). In Central Europe, high-resolution MIS 11 pollen records are for example available from the Ossówka palaeolake in eastern Poland (Nitychoruk et al., 2005, 2018; Bińka et al., 2023) as well as from Nowiny Żukowskie in eastern Poland (Hrynowiecka and Winter, 2016) and Dethlingen in northern Germany (Koutsodendris et al., 2010). Another site worth mentioning is Bilhausen in central Germany, which provided a pollen record for the so-called Bilshausen Interglacial, which might correspond to MIS 11 or MIS 13 (Kühl and Gobet, 2010). In Northern Europe, there are even fewer records covering MIS 11 e.g. the record from Hoxne in eastern England (Horne et al., 2023) where temperature reconstructions were performed using chironomids (e.g., (Brooks, 2006), ostracods (Horne, 2007) and beetle remains (Atkinson et al., 1987).

The contemporary state of knowledge considering MIS 11 has recently been reviewed by Candy et al. (2014). Climate conditions in Central Europe were in general temperate at that time (Nitychoruk et al., 2018), but vegetation reconstructions suggest warmer and more humid conditions compared to the Holocene climatic optimum (Hrynowiecka and Winter, 2016). Two major climatic oscillations have so far been documented during the Holsteinian Interglacial, the Older Holsteinian Oscillation (OHO) and the Younger Holsteinian Oscillation (YHO). The OHO occurred around 418 BP (Koutsodendris et al., 2010, 2012; Górecki, 2023) and is clearly connected to a rapid cooling as indicated by the disappearance of temperate vegetation (mostly *Picea-Alnus* forests) and the spread of pioneer tree taxa including *Betula*, *Pinus* and *Larix* (Koutsodendris et al., 2010, 2012; Candy et al., 2014; Hrynowiecka and Pidek, 2017; Górecki et al., 2022). Although the OHO has been described at multiple sites across northern Europe (Koutsodendris et al., 2012), it has so far not been identified in southern Europe (Kousis et al., 2018). In contrast to the OHO, the YHO occurred around 400 ka BP within the climatic optimum of the Holsteinian Interglacial (*Carpinus-Abies* phase) and was apparently not connected to a significant cooling (Górecki et al., 2022). Records from Germany and eastern Poland suggest a sudden regression of *Carpinus* from the forest communities (Koutsodendris et al., 2010; Hrynowiecka et al., 2019; Górecki et al., 2022) and particularly in Poland a rapid spread of *Abies* with an admixture of *Corylus* and at southern sites also *Taxus* is observed (Górecki et al., 2022), suggesting that temperature was not limiting the growth of *Carpinus*.

Aiming at improving the knowledge about climate variability at the demise of the Holsteinian Interglacial, we present in the following the first quantitative climate reconstructions for the post-Holsteinian in Central Europe, which are based on chironomid and pollen analyses.. In addition, we discuss the potential of chironomid analysis for palaeoecological studies of Quaternary sediments as well as the challenges for chironomid analysis arising from both the evolution and interchanging adaptations to species ecological preferences and the preservation of fossil remains.

2 Study site and methods

2.1 Study area

The Krępa palaeolake sediment succession (51°37’53.2’’N, 22°18’38.1’’E, 146 m asl.) is located in SE Poland, near the city of Kock, approximately 120 km southeast of Warsaw (Fig. 1).It is under influence of humid continental climate (Dfb) in terms of the Köppen-Geiger climate classification (Peel et al., 2007). Average annual temperature for this region is ~ 8.6 °C, with July mean temperature of ~ 19 °C and January mean temperature of ~ -1 °C, while average annual precipitation is ca. 600 mm (Ustrnul et al., 2021). In a geomorphological sense it is situated in the central-eastern part of the North European Plain behind the maximum extent of the Saalian glaciation (Marks et al., 2018) and the sediment core analysed in this paper was obtained on a moraine plateau related to this ice sheet. Holsteinian Interglacial deposits in the area were first identified by Jesionkiewicz (1982) during cartographic work for the 1:50 000 Detailed Geological Map of Poland (DGMP; Sheet 676 - Kock) (Drozd and Trzepla, 2007). On the moraine plateau, the interglacial deposits are found under a thin cover of moraine deposits, whereas at the slopes of the nearby Wieprz River valley, they are exposed directly at the surface. This study’s material was obtained from a sediment core that was drilled at Krępa in 2015 by using a Geoprobe drilling device (Górecki, 2023).

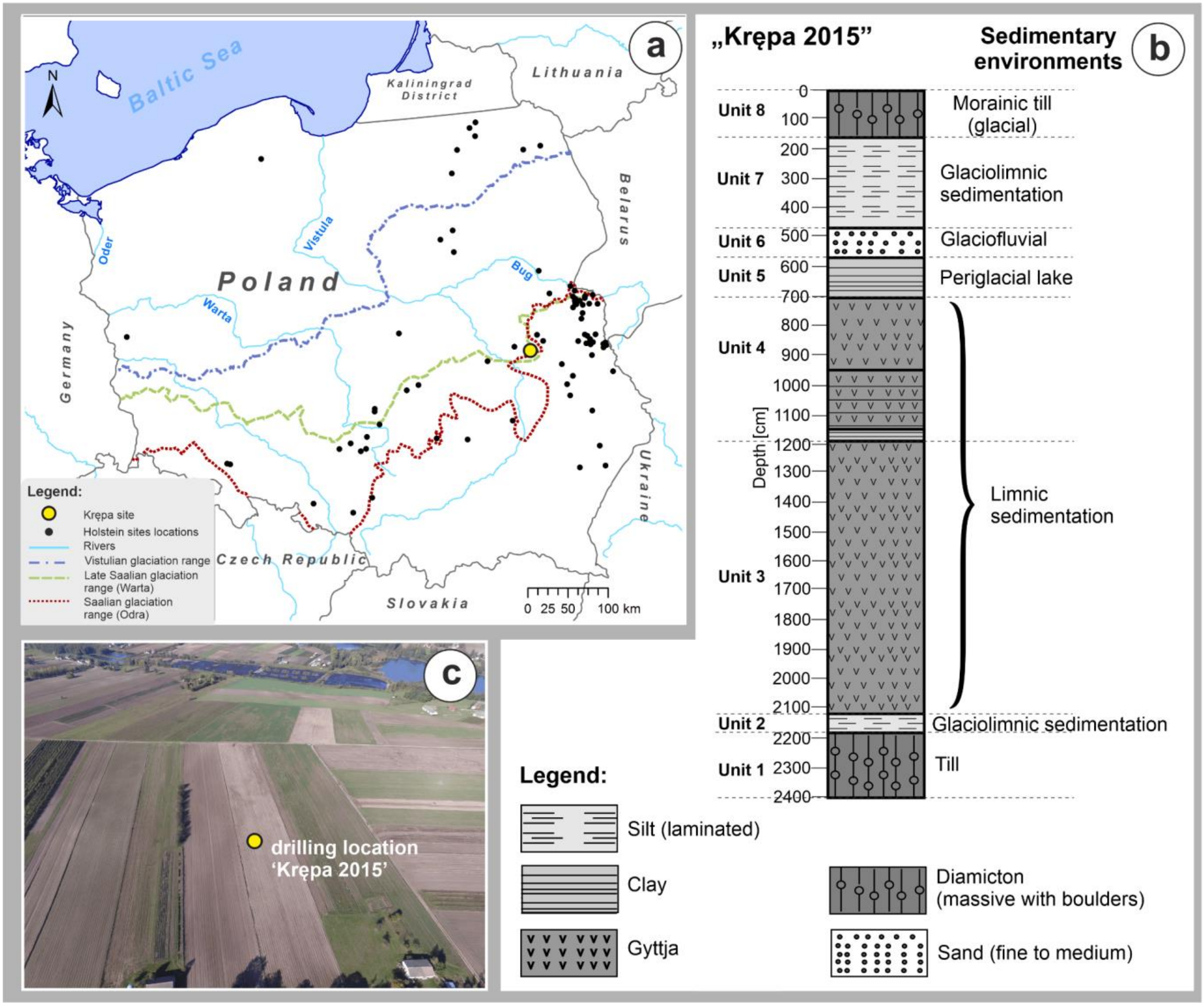

Figure 1: (a) Location of selected sites with deposits from the Holsteinian Interglacial in Poland with the Krępa site indicated by the big yellow dot. Glaciation ranges are based on Żarski et al. (2024), Pochocka-Szwarc et al. (2024) and Marks (2023). (b) Lithological profile of the Krępa sediment succession and (c) location of the drilling site (foto M. Żarski).

2.2 Holsteinian Interglacial

The climate during MIS 11c was characterised by relatively stable warm and moist conditions with global temperatures approximately 1.5–2 °C above the pre-industrial level (Masson-Delmotte et al., 2010). According to Raymo and Mitrovica (2012) and Muhs et al. (2012), the sea level was possibly 6–13 m higher than present. This can be partly attributed to the melting of the Greenland Ice Sheet (Robinson et al., 2017), as pollen and palaeoDNA data suggest the existence of spruce forests in Greenland at this time (Willerslev et al., 2007; de Vernal and Hillaire-Marcel, 2008).

In Europe, warm and wet oceanic climate conditions extended far to the east as evidenced by the presence of Taxus and Abies pollen at sites in Lithuania (Kondratiene and Gudelis, 1983), Belarus (Mamakowa and Rylova, 2007), and the western Ukraine (Łanczont et al., 2003; Benham et al., 2016), while modern distribution limits of these taxa are estimated further to the west (Benham et al., 2016). Evidence from several terrestrial records from Eurasia suggests that the MIS 11c climate was also highly complex, with pronounced climate variability occurring on both centennial and millennial timescales (Koutsodendris et al., 2010; Prokopenko et al., 2010; Tzedakis, 2010; Oliveira et al., 2016; Tye et al., 2016; Górecki et al., 2022).

The pollen succession of the Holsteinian Interglacial in Poland is characterised by a dominance of first Picea-Alnus and then Carpinus and Abies, as well as by a significant proportion of Taxus, and a frequent occurrence of thermophilic taxa such as Pterocarya, Celtis, Juglans, Ilex, Carya, Parrotia, Buxus, Vitis, Brasenia, Trapa, and Azolla (Janczyk-Kopikowa, 1991). Temperature reconstructions based on the indicator species method suggest for the warmest period, the Carpinus-Abies phase, temperatures of 0–3 °C in January and 21–26 °C in July, which along with high precipitation amounts created a suitable environment for the spread of rare warmth-adapted taxa (Krupiński, 1995; Hrynowiecka and Winter, 2016). Palaeotemperature reconstructions from Dethlingen (Koutsodendris et al., 2012) suggest, however, slightly lower temperatures in Western Europe for both January (-2.2 ± 3.1 °C) and July (17.8 ± 2.1 °C).

The warm character of the Holsteinian Interglacial was also confirmed by oxygen isotope analyses on endogenic lake carbonates (Nitychoruk et al., 2005) and snail shells (Szymanek, 2018). These showed significant changes in climatic conditions throughout the Holsteinian Interglacial, during which, continental and maritime influences intertwined in Central Europe. Continental influences resulted in a shortened vegetation period with long winters, while the opposite situation occurred under maritime influence, i.e. the vegetation period was significantly longer, temperatures were milder and precipitation rates were higher, also reflected by the appearance of stenothermal plant species (Nitychoruk et al., 2005).

2.3 Pollen analysis

The Krępa sediment core obtained in 2015 was sampled for palynological analyses at 5-cm intervals between 770 and 2180 cm depth, resulting in a total of 281 samples. A volume of 1 cm^3 was collected from organic sediments (peat, gyttja), while minerogenic sediments (clays, silts, sands) were sampled with a volume of 3 cm^3 due to the anticipated low pollen grain concentration. Samples were further processed following the standard methodology outlined by Erdtman (1960) with modifications such as involving the use of HF (Berglund and Ralska-Jasiewiczowa, 1986). Prior to laboratory processing, a

Lycopodium tablet (Lund University, batch number 100320201, 20,408±543 spores per tablet) was added to each sample to determine the absolute sporomorph concentration (Stockmarr, 1971). Pollen grains were counted using a ZEISS Axio Imager A2 light microscope. Palynomorphs were identified using pollen keys and atlases (Beug, 1961; Stuchlik, 2001, 2002, 2009; Lenarczyk, 2014), as well as online resources (PalDat, 2000; NPP Database, Shumilovskikh et al., 2022). For most samples, counts were conducted up to a sum of 500 pollen grains from arboreal (AP) and non-arboreal (NAP) plants. However, samples from glacial sediments with low palynomorph concentration were counted up to a sum of 300 pollen grains only. Percentages were calculated based on the sum of pollen grains from trees and shrubs (AP), as well as herbaceous plants, and dwarf shrubs (NAP). The results of the palynological analysis are depicted in a simplified pollen diagram (Fig. 2) that was plotted using R Studio with the package riojaPlot (Juggins, 2022). Local Pollen Assemblage Zones (LPAZ) were established using the CONISS cluster analysis function within riojaPlot and were visually adjusted if necessary.

2.4 Pollen-based climate reconstructions

Climate variables reconstructed using pollen data include mean annual air temperature (Tann), annual precipitation sum (Pann), mean July air temperature (Tjul), and mean January air temperature (Tjan). Two reconstruction approaches were applied: the Modern Analog Technique (MAT; (Overpeck et al., 1985; Guiot and Pons, 1986) and Weighted Averaging Partial Least Squares regression (WA-PLS; ter Braak et al., 1993; ter Braak and Juggins, 1993). In the MAT approach, the optimal number of analogues (k) was determined using leave-group-out (LGO) cross-validation, while WA-PLS model selection, including the determination of the optimal number of components, was based on predictive accuracy assessed through leave-one-out (LOO) cross-validation and supported by randomization tests, following the methodology outlined by Chevalier et al. (2020). For each reconstruction model, the coefficient of determination (R^2) and root mean square error (RMSE) were calculated to evaluate model performance. Standard errors of prediction (SEP) were also computed and used as uncertainty estimates, displayed as error bars in the respective figures. Modern pollen data used in the reconstructions were sourced from the Northern Hemisphere database compiled by Herzschuh et al. (2023a, b). To enhance spatial relevance, the modern dataset was geographically filtered to include only samples within a 3000 km radius of the fossil site. Taxa with zero abundance following filtering were removed to reduce noise and improve model robustness. All modelling and data processing were performed in RStudio using the rioja package (Juggins, 2022). The pollen-based reconstructions were restricted to the interval of the succession where chironomid remains were also present.

2.5 Chironomidae analysis

Initially, 79 sediment samples of 1 cm³, taken between 800 and 2160 cm depth at 5-40 cm intervals, were investigated for the presence of Chironomidae head capsules. However, only 30 of them (965-1155 cm depth) simultaneously contained more than 0-2 individuals, creating a sequence that enabled a summer temperature reconstruction. Chemical preparation followed Brooks et al. (2007). The precipitate was initially heated with KOH. The wet sediment was then passed through 212 μm (to remove larger sediment particles) and 100 μm mesh sieves and subsequent residues were treated in an ultrasonic bath for 3 sec. The processed sediment was subsequently examined under a stereomicroscope (Zeiss Axio Lab A1) at 25× magnification. Chironomid head capsules from each sample were picked and mounted in Euparal. In case of damaged head capsules, individuals were counted as one if more than half of a body was preserved. Identification of chironomid head capsules followed Wiederholm (1983), Schmid (1993), Klink and Moller Pillot (2003), Brooks et al. (2007) and Andersen et al. (2013). Ecological preferences of identified taxa are based mainly on Brooks et al. (2007), Brundin (1949), Brodersen and Lindegaard (1999a) and Saether (1979).

Preliminary tests of sample preparation avoided the use of chemicals and included soaking the samples in water for a long time instead to reduce mechanical stress exerted to the head capsules during sample sieving as much as possible. Nevertheless, intact head capsules could not be extracted from some sediment samples even when using this gentle way of sample preparation, likely because of the already highly compacted sediment. As small numbers of head capsules may hinder palaeoecological and palaeoclimatic reconstructions, it was therefore partly necessary to combine samples (see below) or to increase the volume of the analysed sediment material (some samples were even as large as 20 cm3).

2.6 Chironomid-based mean July air temperature reconstruction

In order to reconstruct mean July air temperatures ($T_{jul\text{-}Ch}$) from the Krępa chironomid assemblage, the Swiss-Norwegian-Polish (SNP) training set (Kotrys et al., 2020) was used as this covers a higher temperature span than other available European training sets (e.g. the Finnish, Russian, Swiss-Norwegian training sets) (Kotrys et al., 2020). The SNP training set includes 357 lakes, 134 taxa, covers a temperature range between 3.5 and 20.1 °C. and uses the weighted averaging-partial least squares transfer function (WA-PLS). The RMSEP for this combined training set is 1.39°C, and the R^2 is 0.91 (Kotrys et al., 2020). Detrended Correspondence (MinDC) was also calculated. The temperature reconstruction was carried out using the C2 (v. 1.6) software (Juggins, 2007).

Chironomidae subfossil larvae were obtained from a total of 30 samples from the gyttja sediments (unit 4 on Fig. 1). Samples that contained fewer than 50 head capsules were merged except for a solitary sample at 1000 cm core depth. For 5 samples the required number of 50 head capsules was obtained and the remaining 24 samples were merged into seven clusters. After merging, sample clusters at 975 cm, 1080 cm, 1120 cm and 1125 cm core depth still did not reach 50 head capsules, but nonetheless, these samples and the one from 1000 cm core depth were included in the reconstruction as preliminary results seemed credible in terms of obtained temperature values.

. The lowest number of head capsules used for the $T_{jul\text{-}Ch}$ reconstruction was 5 individuals at 1070 cm core depth whereas the highest number was 78 at 985 cm core depth. After merging, the total number of samples used for the $T_{jul\text{-}Ch}$ reconstruction was 13.

3. Results and interpretation

3.1 Lithological description of the Krępa sediment succession and palaeoenvironmental interpretation

The basal part of the 23.8-m-long sediment core that was recovered from the Krępa sediment succession in 2015 (Fig. 1) consists of a 2-m-thick layer of massive, light greyish brown sandy clays with a large number of rock fragments (unit 1), which is interpreted as till. As indicated by its stratigraphic position and its petrographic characteristics (Drozd and Trzepla, 2007), this till was accumulated during the Elsterian glaciation (Sanian 2 glaciation in Poland), which is considered to correspond to MIS 12. Directly above the till, a 0.6-m-thick layer of laminated sandy silts and sandy-clayey silts is found (unit 2). These sediments are interpreted as the result of glaciolimnic sedimentation in a relatively shallow water body between blocks of dead ice during the recession of the Elsterian ice-sheet. The glaciolimnic sediments of unit 2 gradually turn into a carbonate gyttja with small interlayers of carbonatic-minerogenic gyttja (unit 3), which was most likely deposited in the profundal of an already relatively deep lake. Between 1187 and 760 cm core depth, non-carbonatic organic-minerogenic gyttjas with a generally increasing mineral content towards the top are found (unit 4). The limnic sediments of unit 4 are interpreted to reflect the gradual shallowing of the lake due to continuing sediment infill. At the same time, the systematic increase in mineral components in the sediments most probably reflects increased denudation and erosion in the catchment, likely favoured by reduced vegetation cover in response to a change towards colder climate conditions. The gyttja sequence of unit 4 is overlain by a 1.9-m-thick layer of massive clays (unit 5), which probably represent accumulation in a periglacial lake. The following 1.1-m-thick layer of fine- to medium-grained sands (unit 6) as well as the overlying 3.1-m-thick layer of rhythmically laminated sandy silts (unit 7) are interpreted as proglacial sediments (units 6 and 7) of the transgressing Early Saalian (MIS 6) ice sheet. Above this succession, the profile is capped by a 1.5-m-thick layer of sandy morainic till with rock fragments (unit 8) related to the Saalian glaciation.

The origin of the sedimentary basin at Krępa is difficult to interpret. Most sites with deposits from the Holsteinian Interglacial in this region of Poland are associated with tunnel valleys that formed during the Elsterian glaciation (Żarski et al., 2005; Nitychoruk et al., 2006). However, these sites are usually located beyond the maximum extent of the Older Saalian glaciation (Drenthe Stage in Germany; Odra glaciation in Poland; MIS 6) and thus subtly visible in the present surface morphology. In the case of Krępa, the covering of these deposits by the Older Saalian glacial advance has resulted in the complete obliteration of the post-Elsterian landscape. Based on the geological cross section presented in the DGMP sheet 676 - Kock (Drozd and Trzepla, 2007) and the distribution of interglacial deposits in the study area (Jesionkiewicz, 1982), it can only be inferred that the depression hosting the Krępa palaeolake was a relatively extensive kettle hole, formed during the recession of the Elsterian ice sheet.

3.2 Vegetation changes during the Holsteinian Interglacial and the Early Saalian Glacial at Krępa site

LPAZ KR-1 (2120.0-2180.0 cm) - NAP values peak at >40 % (mostly *Poaceae*, but also *Artemisia* and *Betula nana*). Open communities are dominant. Tree pollen primarily comprises *Pinus* and *Betula* with both taxa potentially existing locally as small trees. Pollen of temperate species is sourced from redeposition. **No Chironomidae.**

LPAZ KR-2 (2027.5-2110.0 cm) - Initially, a conspicuous dominance of pollen originating from pioneering arboreal species, notably *Pinus* (up to 61 %) and *Betula* (up to 38%), coupled with a negligible representation of herbaceous plant pollen, signifies the prevalence of dense birch and pine forests. Subsequently, *Picea* (up to 24%) becomes established and *Alnus* (up to 35 %) colonises areas with higher soil moisture, probably adjacent to the lake. Rising pollen values of riparian species, e.g. *Fraxinus* (3.,5 %), *Ulmus* (2.,5 %), and *Quercus* (4 %), suggest local presence. **No Chironomidae.**

LPAZ KR-3 (1957.5-2027.5 cm) - At the beginning, the percentage of *Taxus* increases sharply (<40 %), suggesting a key role in the formation of forest communities. Continued presence of riparian forests. *Corylus*, *Viburnum*, *Sambucus nigra* and thermophilic species such as *Pterocarya fraxinifolia*, *Vitis*, *Hedera helix*, *Ligustrum* and *Buxus* sempervirens appeared in the forest understorey. Despite favourable climatic conditions, high *Pinus* percentages (>40 %) persisted, suggesting that this taxon was still important in the formation of forest communities. **No Chironomidae.**

LPAZ KR-4 (1892.5-2027.5 cm) - Rapid decline of *Taxus* forests (<5 %). *Alnus* (<25 %) and *Picea* (<30 %) regain significance in the forest communities. Contribution of riparian taxa remains low (*Fraxinus* and *Ulmus* <1,.5 %). Appearance of *Carpinus*, reaching up to 7 %. Continued presence of thermophilic taxa (*Viscum*, *Pterocarya fraxinifolia*, *Vitis*, *Hedera helix*, *Ligustrum*, *Buxus sempervirens*) indicates favourable climate conditions. **One specimen of *Chironomus anthracinus*-type.**

LPAZ KR-5 OHO (1855.0-1892.5 cm) - Clear change in the composition of forest communities Rapidly disappearing temperate vegetation was replaced by pioneer trees such as *Betula* (25 %) and *Pinus* (45 %). Forest communities remain a dominant element of the landscape, as suggested by the lack of an increase in NAP. Temperate species survived but at a much lower share. The clear shift in species composition suggests a much colder and drier climate compared to the previous zones. **No individuals of Chironomidae.**

LPAZ KR-6 (1697.5-1855.0 cm) - This zone is associated with the dominance of *Abies* and *Carpinus* (both up to 27 %). Mixed *Abies* forests most likely occupied poorer soils, while more fertile soils were covered by deciduous forests consisting of *Carpinus*, *Quercus* (<15 %) and *Corylus* (<15 %) in the understorey. *Taxus* persists but only as an admixture (<2 %). The entire zone is characterised by the undisturbed occurrence of Alnus, which proves the persistence of this taxon near the lake. Similarly, no significant changes in forest density are recorded as evidenced by low NAP percentages. Abundant thermophilic taxa, including *Viscum*, *Pterocarya fraxinifolia*, *Vitis*, *Hedera helix*, *Ligustrum*, *Buxus sempervirens*, *Parrotia persica*, *Celtis*, *Carya* and *Juglans* indicate favourable climate conditions. **No Chironomidae.**

LPAZ KR-7 YHO (1647.5-1697.5 cm) - This zone encompasses an apparent change in forest communities, reflected by a breakdown of *Carpinus* (to 3 %) and an increase of *Abies* (up to 34 %), *Corylus* (22 %) and *Taxus* (5 %). Mixed fir forests replaced deciduous forests at that time, while *Corylus* could be both an admixture in mixed forests and create its communities in bright places on more fertile soils. The *Carpinus* crisis probably did not last long, and it soon began to rebuild its presence. A continuous occurrence of thermophilic taxa is observed throughout the zone. **One specimen of *Glyptotendipes pallens*-type.**

LPAZ KR-8 (1497.5-1647.5 cm) - As in LPAZ KR-6, the two key taxa were *Abies* and *Carpinus*. Although percentages of the latter were rising to 36 %, *Abies* (up to 26 %) remained important and, in some parts, dominated over *Carpinus*. *Buxus* deserves special attention among the abundant thermophilic taxa since it occurs at a greater frequency than in the previous zone. The end of the zone is associated with a decline in the percentage of *Abies*. **No Chironomidae.**

LPAZ KR-9 (1362.5-1497.5 cm) - A characteristic feature of this zone is the dominance of *Carpinus* (up to 44 %) and a significant decrease in the importance of *Abies* (<10 %). Mixed forests with a significant share of *Quercus* (up to 33 %) could develop on poor soils instead of *Abies* forests. Thermophilic species were the most abundant in the entire profile, especially *Pterocarya fraxinifolia* (1 %) and *Buxus sempervirens* (<2 %). Slow overgrowth of the lake is reflected by the slow decline in the proportion of aquatic plants and the decline in *Alnus* percentages. The zone ends with the decline of *Carpinus* and *Corylus* and the reappearance of *Picea*. **No Chironomidae.**

LPAZ KR-10 (1312.5-1362.5 cm) - The beginning of the zone is marked by the slow disappearance of temperate deciduous species, including *Alnus*, *Quercus*, *Corylus*, and *Carpinus*. Abies gains importance again (up to 32 %), forming conifer forests together with *Picea* (up to 13 %) and *Pinus*. Thermophilic taxa are still present. The end of the zone is associated with the disappearance of *Abies*, the dominance of *Pinus* (67 %), and the appearance of *Larix* (<1.5 %). **No Chironomidae.**

LPAZ KR-11a (1257.5-1312.5 cm) - In this zone, the dominance of pioneer trees and herbs begins. The palynological record suggests the development of sparse *Betula* and *Pinus* forests with an admixture of *Larix* (12 %) and possibly locally occurring *Alnus* (3 %) and *Picea* (5 %). Pollen of other temperate trees likely originate from redeposition or long-distance transport and are not indicative of local occurrence. The high share of NAP pollen also proves the openness of forest communities in this period. A rapid change in vegetation is observed in the middle part of this zone. Open communities began to dominate the landscape (NAP <40 %), and woody vegetation was reduced to scattered birch-larch tree stands that occurred locally under favourable conditions. *Juniperus* (33 %) and *Poaceae* (23 %) had the highest share among the herbaceous plants, suggesting the presence of shrub tundra. Vast areas of open ground likely favoured soil erosion and redeposition of older material, which is visible in the palynological record as a sudden increase in the proportion of pollen from temperate taxa. Following the dominance of herbaceous vegetation, *Betula-Larix* forests re-established in the area. The zone ends with a sudden increase in the percentage of *Pinus* pollen. **No Chironomidae.**

LPAZ KR-11b (1222.5-1257.5 cm) - *Pinus-Betula* forests spread within this zone with an admixture of *Larix* and *Picea*. Although forest communities dominated most of the landscape, there were still patches of herbaceous plant communities, as indicated by high NAP percentages. The zone ends with a sudden decrease in *Pinus* percentages and an increase in the *Betula* share. **No Chironomidae.**

LPAZ KR-11c (1187.5-1222.5 cm) - Initially, loose birch forests with an admixture of *Larix* and *Pinus* spread. In the middle of the zone, the landscape was further opened and likely dominated by *Juniperus* shrub tundra. The zone ends with a sharp increase in the percentage of *Pinus* and a decrease in *Betula* and NAP. Single specimens of *Chironomus plumosus*-type.

LPAZ KR-12a (1122.5-1187.5 cm) - At the beginning of the zone, the development of *Pinus* forests with an admixture of *Picea* (up to 6 %) is observed. Low NAP percentages suggest a very dense vegetation. However, percentages of *Pinus* and other tree species gradually decrease, and open herbaceous communities appear. The end of the zone is associated with a decrease in the percentage of *Pinus* pollen. **Low number of Chironomidae head capsules (approximately 15 per sample). Dominance of *Chironomus anthracinus*-type (25 %) and Corynocera ambigua (16 %).**

LPAZ KR-12b (1072.5-1122.5 cm) - A further decrease in *Pinus* pollen is observed. At the end of the zone, the landscape was likely already dominated by open communities (NAP up to 40 %) and sparse *Pinus* forests. Dominance of Corynocera ambigua (24 %) and high contents of *Chironomus anthracinus*-type. **Disappearance of *Glyptotendipes pallens*-type and appearance of *Glyptotendipes severini*-type.**

LPAZ KR-12c (1022.5-1072.5 cm) - Initially, dense *Betula* forests with *Larix* as an admixture dominated the landscape. Subsequently, a rapid development of *Pinus* forests is observed. The end of the zone is associated with a sudden drop in the percentage of *Pinus* pollen. **The number of Chironomidae declines. Dominant species are *Chironomus anthracinus*-type (17 %), Corynocera ambigua and *Glyptotendipes pallens*-type (13 %).**

LPAZ KR-13a (967.5-1022.5 cm) - Initially, there was a significant opening in the vegetation, and herbaceous plants and shrubs dominated the landscape. In the middle of this zone, there was a temporary return of very sparse *Pinus* and *Betula* forests, followed by another expansion of herbaceous vegetation. The end of the zone is associated with an increase in *Betula* pollen. **Significant increase in the number of Chironomidae (on average 45 individuals per sample). Dominant species are Corynocera ambigua (approx. 29 %) and *Chironomus anthracinus*-type (18 %).**

LPAZ KR-13b (877.5-967.5 cm) - Relatively high percentages of *Pinus* (15-48 %) and *Betula* (29-49 %) suggest the existence of sparse *Pinus-Betula* forests in the vicinity of the lake. The presence of *Betula nana* (<5 %) indicates patches of shrub tundra in the area. The end of the zone is associated with the further spread of open communities. **Unidentifiable Chironomidae. At the end of the zone, the number increases slightly. The dominant species is *Propsilocerus lacustris*-type and single *Chironomus plumosus*-type and *Dicrotendipes nervosus*-type occur. Corynocera ambigua is also abundant.**

KR-14 (765.0-877.5 cm) - Within this zone, open communities further expanded, likely steppes dominated by *Poaceae* and *Artemisia*. The vegetation also featured shrubs, such as *Juniperus* and *Betula nana*. Tree species of the *Betula* genus were present throughout the zone, and percentage variations for this taxon were low. Conversely, *Pinus* percentages considerably fluctuated. Both pioneer tree species might have formed sparse patches of forest vegetation in favourable environmental conditions. **Low abundance of Chironomidae. Only two individuals of *Chironomus plumosus*-type were recorded.**

3.3 Ecological reconstruction based on Chironomidae assemblages from the Krępa site

In general, the chironomid assemblages preserved in the Krępa sediments are dominated by the two species *Corynocera ambigua* and *Chironomus anthracinus*-type. *Corynocera ambigua* is a species that is often described as cold-adapted oligotrophic (Fjellberg, 1972; Pinder and Reiss, 1983; Walker and Mathewes, 1988; Brooks et al., 2007; Luoto et al., 2008; van Asch et al., 2012), inhabiting shallow lakes in arctic and subarctic regions, though it is also found in eutrophic lakes (Halkiewicz, 2008; Kotrys et al., 2020) Adults do not fly and breed on the water surface when the temperature reaches approximately 7-8 °C (optimum 13.7 °C). Mothes (1968) concluded that *Corynocera ambigua* larvae develop in autumn and winter, while the eggs do not develop but only survive during summer. The decline in their numbers may be due to the growth of filamentous algae in summer. Larvae of *Corynocera ambigua* are eurythermic, while the pupae are cold-stenothermic (Brundin, 1949). They only reproduce at low temperatures and inhabit water bodies with a maximum depth of approximately 25 m. The abundance of *Corynocera ambigua* has been shown to correlate with the content of charophytes (Brodersen and Lindegaard, 1999b). Although this species does not feed on charophytes, their presence may increase the number of diatoms and stabilise the trophic status and water clarity (Forsberg, 1965; Blindow, 1992). *Corynocera ambigua* lives in dendritic tubes. Its food is diatom/algal detritus. (Fjellberg, 1972; Boubee, 1983).

This species has been recorded during cold episodes or glacial periods, at sites in England (Bedford et al., 2004), Norway (Velle et al., 2005), Poland (Płóciennik et al., 2015), and the Baltic region (Hofmann and Winn, 2000). However, *Corynocera ambigua*, cannot be considered a merely cold species. Some authors believe that its occurrence depends on high oxygen contents in the water (Brodersen and Lindegaard, 1999a) and for some authors, it is a pioneer species that appears first after glacier retreats, just like *Chironomus anthracinus*-type (e.g. Heiri and Millet, 2005; Ilyashuk et al., 2005, 2013, 2022; Gandouin et al., 2016). Luoto and Sarmaja-Korjonen (2011)2011 claim that this is how the species adapts to existing climatic conditions. The locally observed decline in *Corynocera ambigua* numbers in the Krępa sediments could also be attributed to changes in lake productivity related to changes in the environment. For example, when the production of soil and trees increased, the number of this species has been found to decrease (Magny et al., 2006; Larocque-Tobler et al., 2009).

Chironomus anthracinus-type occurs in various zones of lakes and is capable of surviving approximately 2–4 months of oxygen deficiency in the water (Hamburger et al., 1994). It is a species that easily occupies niches that are inaccessible to other species. According to some authors, it is a eutrophic (Kansanen, 1985; Brodersen and Lindegaard, 1999b) or cold-adapted species (Rohrig et al., 2004; Brooks et al., 2007; Płóciennik et al., 2011) and it prefers soft and more organic sediments (McGarrigle, 1980). The appearance of *Chironomus anthracinus*-type and *Glyptotendipes pallens*-type in the Krępa sediment may thus indicate the onset of eutrophication. Both *Chironomus anthracinus*-type and *Corynocera ambigua* are found in stratified lakes (e.g., Saether, 1979; Heiri, 2004). As we can see, both species are relatively resistant to unfavourable environmental conditions, thus having a fairly wide range of conditions in which they can occur.

The following description of Chironomidae assemblages follows the pollen zonation because (1) it reflects climatic changes better than the chironomid assemblages and (2)the low number of Chironomidae head capsules and the small species diversity prevented the statistically robust determination of a good modern analogue reconstruction of Chironomidae zones.

At the base of the sediment sequence (2120.0-2027.5 cm), there are no remains of chironomids preserved. The first individuals occur in LPAZ KR-4 and LPAZ KR-7. In these zones, eurytopic *Chironomus anthracinus*-type in a poor state of preservation is observed (Fig. 3). There are no remains of Chironomidae in the following LPAZ belonging to the Holsteinian Interglacial and the first head capsules of *Chironomus plumosus*-type are recorded again in LPAZ KR-11c, which is already considered as post-Holsteinian. This species occurs in a wide range of habitats and is particularly resistant to anoxia (Saether, 1979, Brooks et al., 2007). The following LPAZ KR-12a is characterised by a low abundance of chironomid head capsules. Assemblages could indicate a wide range of environmental conditions (e.g. *Chironomus anthracinus*-type is a profundal species that is tolerant to a wide thermal spectrum (Brooks et al., 2007; Luoto et al., 2019) and *Corynocera ambigua* is indicative for colder conditions (Brooks, 2006; Brooks et al., 2007). LPAZ KR-12b (1072.5-1122.5 cm) contains mainly cold-adapted species like *Corynocera ambigua* and freeze-resistant species like *Glyptotendipes pallens*-type and *Glyptotendipes severini*-type, which are often associated with algae and diatoms or mine leaves, (Tarkowska-Kukuryk, 2014). LPAZ KR-12c is characterised by species highly resistant to difficult environmental conditions, such as *Chironomus anthracinus*-type, which is typical for nutrient-rich conditions with wide environmental tolerances (Saether, 1979; Self et al., 2011), *Corynocera ambigua*, which has a broad thermal tolerance (Brodersen & Lindegaard 1999a and *Glyptotendipes pallens*-type, which can better tolerate harsh winter conditions and lives in different types of substrates (Moller Pillot, 2013; Čerba et al., 2022). LPAZ KR-13a is a phase with mainly cold-adapted species such as *Corynocera ambigua*. During LPAZ KR-13b the number of chironomid head capsules gradually increased with indicators of progressive eutrophication (e.g. *Chironomus plumosus*-type and *Dicrotendipes nervosus*-type (Iwakuma and Yasuno, 1981) and cold oligotrophic species (such as *Corynocera ambigua*) (Brooks et al., 2007) still occurring frequently. During LPAZ KR-14 the number of Chironomidae is low. Only eurytopic, warm stenotherm species, which are resistant to anoxia such as *Chironomus plumosus*-type appear (Brooks et al., 2007). The disappearance of *Corynocera ambigua* could also be the result of changes in oxygen concentration, reduced production of benthic algae or changes in the structure of the sediment (Brodersen and Lindegaard, 1999b).

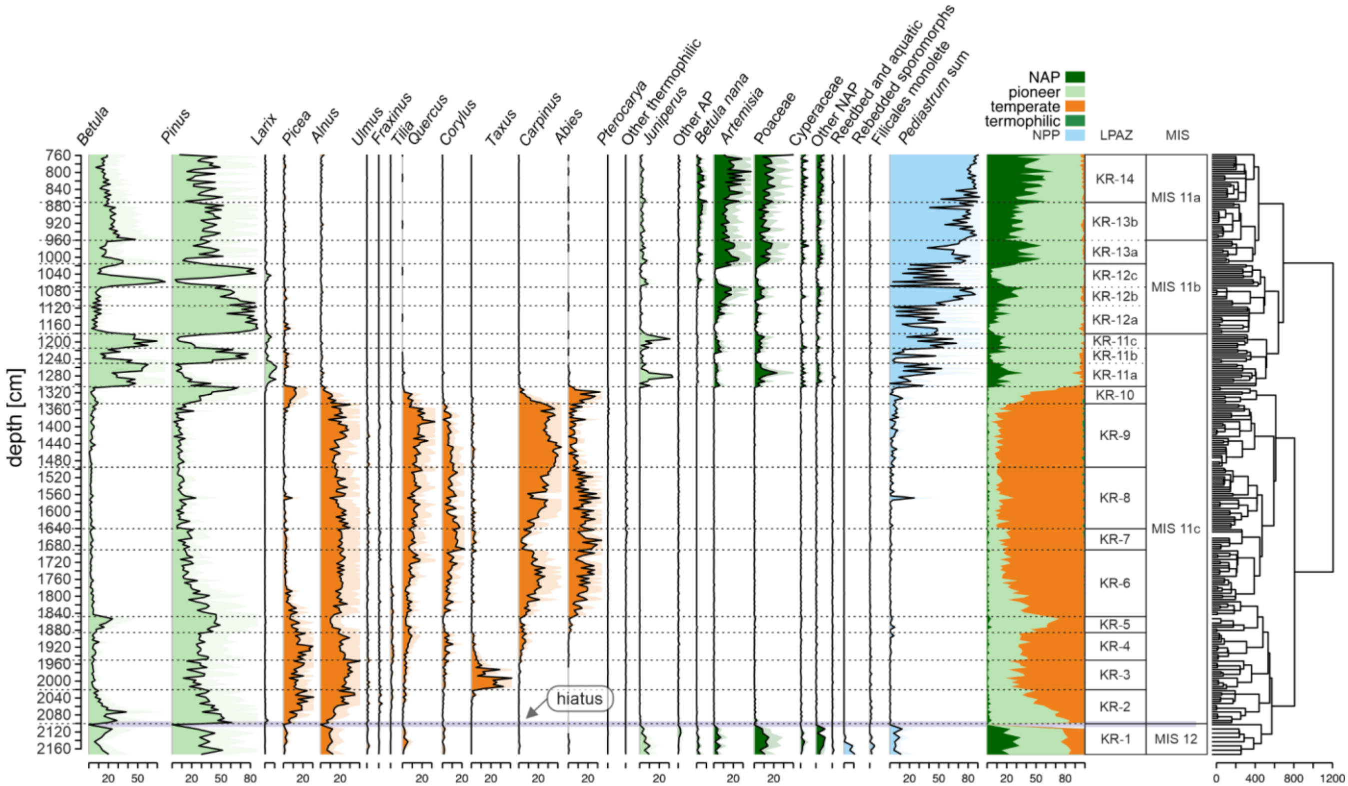

Figure 2: **Percentage diagram of selected pollen, spore, and algal taxa form the Krępa 2015 sediment core on depth scale (cm) with zonation of the diagram.**

3.4 Summer air temperature reconstruction based on Chironomidae assemblages from the Krępa site

Due to the low number of chironomid head capsules preserved in the Krępa sediments, a chironomid-based summer temperature reconstruction was only possible for the uppermost part of the sediment core, encompassing the post-Holsteinian stadial that is most likely equivalent to MIS 11b (Table 1). In LPAZ KR-12a, which marks the onset of MIS 11b that directly follows the Holsteinian Interglacial, average summer temperatures still ranged between 17 and 19 °C before shortly dropping to about 16 °C and increasing again to 18-20 °C in LPAZ KR-12b. Summer temperatures remained at this level throughout LPAZ KR-12c before significantly dropping to 15-17 °C in the middle of LPAZ KR-13a. Only at the end of LPAZ KR-13a, which is equivalent to the transition to the following interstadial that most likely corresponds to MIS 11a, summer temperatures markedly increased again to about 20 °C.

Table 1: Air temperature reconstruction from Chironomidae preserved in the Krępa sediments with reconstructed mean July air temperature (T_{jul-Ch}), error of the estimated T_{jul-Ch}, minimum dissimilarity between the chironomid assemblage in the Krępa sediments training set samples (MinDC), principal component analysis values (PCA) and corresponding LPAZ

Core depth (cm)	T_{jul-Ch}	error of est. (T_{jul-Ch})	MinDC	PCA	Number of Chironomidae head capsules	LPAZ
969	20.10	1.60	9.82830	-1.8144135	51	KR-13a
975	15.26	1.64	6.08105	-1.2383560	48	
980	16.82	1.57	7.89471	-1.7518844	67	KR-12c
985	17.23	1.59	8.37351	-1.4636110	78	
990	15.93	1.70	7.35685	-1.9244674	52	KR-12b
995	15.84	1.72	6.77137	-0.6709448	53	
1000	18.77	1.52	8.27430	6.5934818	42	KR-12a
1011	18.09	1.63	7.90763	0.4039345	51	
1022	19.25	1.50	7.06444	0.4114688	53	
1080	20.20	1.53	8.02666	0.5281182	52	
1102	18.55	1.52	8.95789	1.3132870	48	
1125	17.69	1.52	8.63666	-0.2629876	64	
1148	18.97	1.56	6.86405	-0.1236256	57	

According to the SNP training set-based reconstruction, 10 samples with good modern analogues remain below the 5 % percentile threshold (minDC), while 3 samples with average modern analogues have values above the 5 % percentile threshold (6.08105 < minDC > 9.82830). PCA values range between ~ –1.92 and 6.59 (Tab. 1).

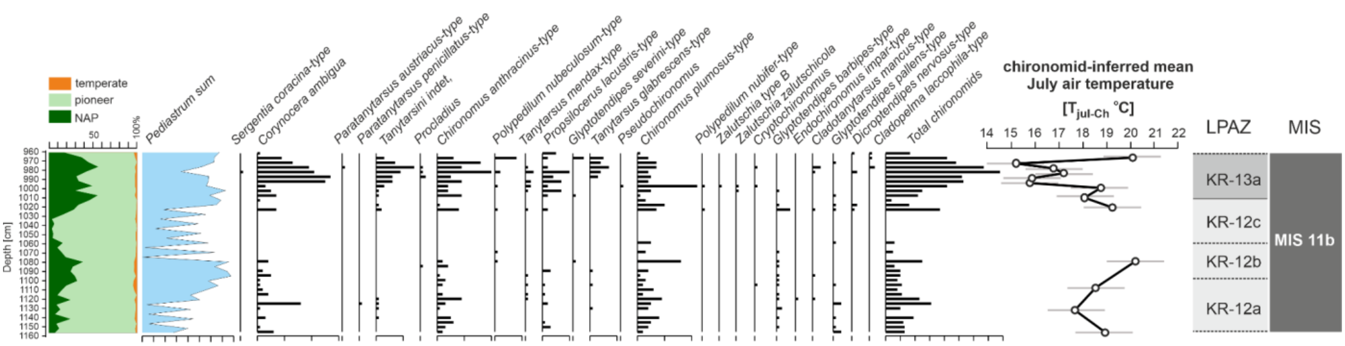

Figure 3: Chironomid-inferred mean July temperature reconstruction from Krępa with stratigraphic diagram of the Chironomidae assemblages. Caption: Chironomidae species are presented as counted numbers of specimens. Grey bars in the T_{jul-Ch} curve indicate error range.

3.5 Pollen-based climate reconstructions from the Krępa site

The pollen-based climate reconstructions from the Krępa sediment core reveal a distinct climate variability throughout MIS 11b, in general following the vegetation-indicated stadial-interstadial transitions (Fig. 4). Conducted cross-validation indicated that MAT reconstructions achieved the highest predictive skill, particularly for the reconstructed temperatures (Table 2). WA-PLS reconstructions were somewhat less robust, especially for precipitation, while the Tann and T_{jan} estimates still showed moderate predictive ability (Tab. 2).

Table. 2 Cross-validation results for pollen-based MAT and WA-PLS reconstructions, showing optimal model parameters, R^2, and RMSE for each climate variable.

Method	Climate Variable	Optimal component/k	R^2	RMSE
WA-PLS	P_{ann}	1	0.21	328 mm
	T_{ann}	2	0.59	3.53 °C
	T_{jul}	1	0.46	3.42 °C
	T_{jan}	2	0.59	4.7 °C
MAT	P_{ann}	2	0.56	252 mm
	T_{ann}	2	0.77	2.71 °C
	T_{jul}	2	0.69	2.63 °C
	T_{jan}	2	0.81	3.23 °C

Reconstructed T_{jul} from both pollen-based methods generally ranged between approximately 14 °C and 19 °C. In the LPAZ where chironomid data are available, the pollen-based T_{jul} values show a consistent trend and are within the respective uncertainty ranges broadly in line with the chironomid-inferred temperatures. During LPAZ KR-12a, MAT- and WA-PLS-derived T_{jul} averaged at ~17.3 and ~15.9 °C, respectively, aligning with the chironomid-inferred mean $T_{jul\text{-}Ch}$ of 18.3 °C. In LPAZ KR-12b, both pollen methods indicate further warming (~18.8 °C MAT, ~17.1 °C WA-PLS), which is in good agreement with the chironomid-based estimate of 19.4 °C, reflecting peak interstadial conditions. In LPAZ KR-12c, T_{jul} values dropped to ~14.7 °C (MAT) and ~15.0 °C (WA-PLS), indicating cooling during this interval. A moderate rebound is evident in LPAZ KR-13a, which is reconstructed similarly across pollen- and chironomid-based models, with Tj_{ul} increasing again to ~17.5 °C (MAT) and ~17.3 °C (WA-PLS), while the mean $T_{jul\text{-}Ch}$ is 17.5 °C.

T_{ann} values generally follow the summer temperature trends, beginning with relatively warm conditions in LPAZ KR-12a, where T_{ann} was 1.5°C. A slight increase is observed in LPAZ KR-12b, reaching peak interstadial warmth at approximately 2.0°C. This is followed by a marked cooling in LPAZ KR-12c, where T_{ann} drops to about –2.0°C. In LPAZ KR-13a, a modest recovery occurs with T_{ann} values rising to around –0.9°C.

Tjan generally exhibits a greater variability. In LPAZ KR-12a and LPAZ KR-12b, winters were comparably cold, with T_{jan} values around –11.1 and –10.5 °C, respectively. LPAZ KR-12c shows a slight increase in winter severity with T_{jan} values of approximately –11.3°C. A more pronounced decline follows in LPAZ KR-13a, where T_{jan} reaches around –12.7°C.

P_{ann} reconstructions show some uncertainty but annual precipitation sums generally range between 500 and 900 mm. LPAZ KR-12a is characterized by relatively high precipitation (~690–770 mm), followed by still moderately high values in LPAZ KR-12b (~670–740 mm). A notable decrease occurs in LPAZ KR-12c, with Pann values around 640 mm, indicating drier conditions. In LPAZ KR-13a, P_{ann} remains lower, typically between 615 and 655 mm, suggesting a continued reduction in annual precipitation.

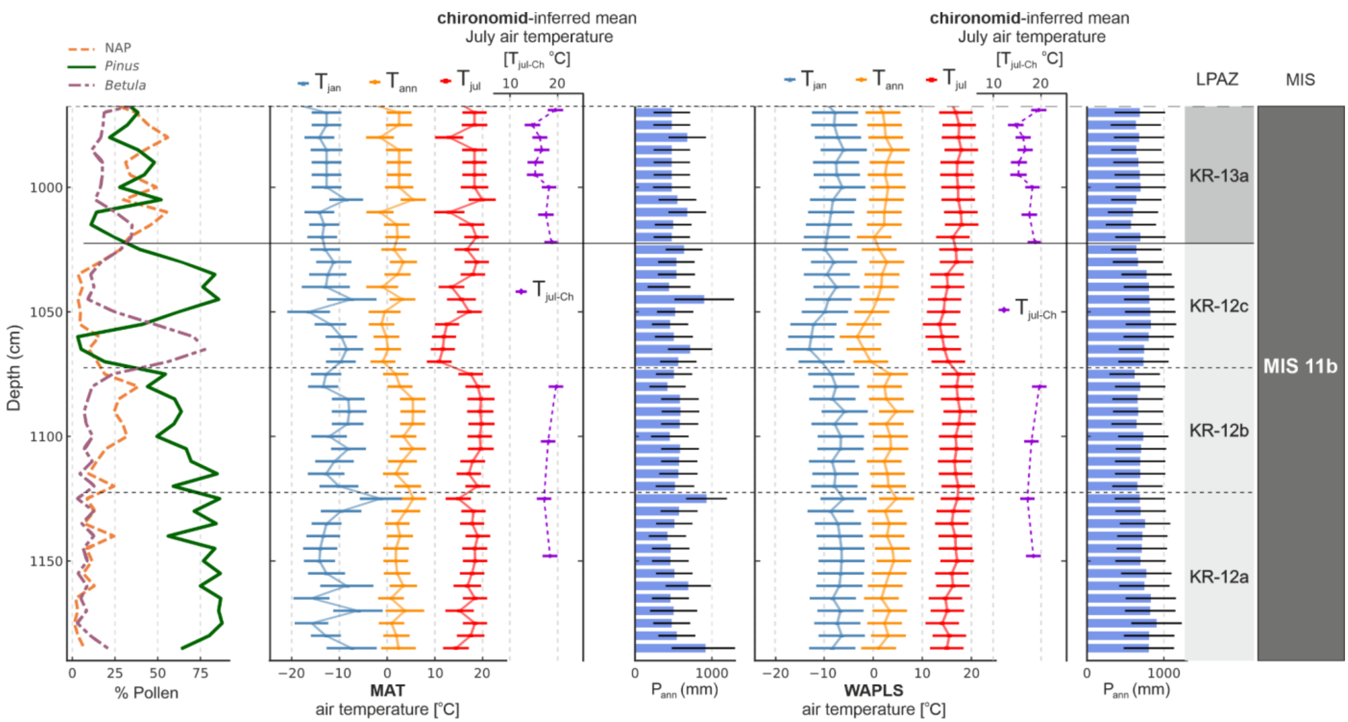

Figure 4: **Pollen-based reconstructions of mean July air temperature (T_{jul}), mean annual temperature (T_{ann}), mean January air temperature (T_{jan}), and annual precipitation sum (P_{ann}) for the Krępa site using MAT and WA-PLS. Error bars indicate the standard error of prediction (SEP). The chironomid-based $T_{jul\text{-}Ch}$ reconstruction is given for comparison.**

4. Discussion

4.1 Chironomidae analysis as a method of palaeoclimate reconstruction

The analysis of subfossil Chironomidae is part of the palaeoecological analysis conducted in geological, geomorphological, and archaeological research. Chironomidae, which are insects belonging to the suborder of Nematocera, are common and inhabit various types of aquatic environments, from moist soil to lakes. Their development cycle can last from 20 days to several years as they can extend the duration of the larval stage depending on environmental conditions (Butler, 1982). Because of the excellent preservation of their larvae's head capsules in lake and peat bog sediments for several hundreds of thousands of years, the analysis of their subfossil remains offers the possibility to reconstruct environmental and climatic changes in the past, quantitative reconstructions of the average July air temperature and the trophic state of the inhabited water body as well as the type and dynamics of the lake, the water pH, and microhabitats. Furthermore, training sets are also available to reconstruct the water level, salinity or oxygen content (Lotter et al., 1997).

4.1.1 Possible difficulties in climate reconstruction based on Chironomidae analysis during past interglacials

The basic principle of palaeoecological reconstructions is geological actuality implying that processes taking place on Earth in the past were the same as today (Krzeminski and Jarzembowski, 1999). This, for example, allows to reconstruct temperature based on fossil Chironomidae *assemblages by assuming* that a given species still has the same habitat requirements as thousands or hundreds of thousands years ago. The oldest recorded chironomid remains date back to the Late Triassic, i.e. ~200 1 Ma BP (Krzeminski and Jarzembowski, 1999). Data from the MIS 11 Krępa sediments indicate a large difference in the number and state of preservation of the chironomid remains compared to Holocene sites. In general, at least 50 individuals per sample are required for robust reconstructions of the average July temperature. As smaller numbers of identified head capsules considerably increase the error range of the air temperature reconstruction, it is commonly recommended to combine adjacent samples in case of low head capsule amounts (Heiri and Lotter, 2001). To enable selection of sites that could potentially yield chironomid-based palaeoenvironmental reconstructions, it is therefore critical to analyse the factors that could limit the degree of preservation or cause the disappearance or decrease in the number of individuals. .

Chironomidae inhabit all moist or aquatic habitats from moist wood to the ocean, between the tropics and the Arctic. The high specialisation of individual species is thereby decisive for their common occurrence and their ability to survive even under difficult environmental conditions. Among the features that allow the family to succeed are: a short life cycle (in some cases only 8 days) (Reyes-Maldonado et al., 2021), osmoregulation that enables survival in high-salinity waters (Kokkinn, 1986) or parthenogenesis that implies a high efficiency of population reproduction, faster colonisation rate and high fertility (Lencioni, 2004; Nondula et al., 2004; Donato and Paggi, 2008; Orel and Semenchenko, 2019; Lackmann et al., 2020), as well as a short DNA chain (Gusev et al., 2010; Cornette et al., 2015). Some species are able to change food resources depending on the availability in their habitat (Tokeshi, 1995; Davis et al., 2003). Large lakes like the one that most probably existed at Krępa (1) have a greater variety of habitats, thus being characterised by a larger biodiversity of Chironomidae (Allen et al., 1999;

Heino, 2000; Tarr et al., 2005). and (2) are more resilient to extreme droughts and other extreme events. In contrast, small lakes with less diverse and isolated habitats reveal a reduced species diversity and dispersal (Roberts, 2003).

Despite the specialisation of chironomids, there are many conditions in the environment that limit the number of communities. One of the main factors limiting and determining the life processes of Chironomidae is temperature as each life stage is dependent on this factor. The development of eggs, larvae and pupae, nutrition and growth, the emergence of individuals or the ability to fly are constrained by temperature maxima and minima, beyond which the given processes no longer take place. Most groups can tolerate low sub-zero temperatures; the temperature below which the development of most species does not occur is -15°C (Walker and Mathewes, 1989; Płóciennik, 2005). At Krępa, however, our summer temperature reconstruction indicates temperatures well above that threshold, so even in case of severe winters, Chironomids should have been able to develop during the warmer periods of the year. Frost tolerance is highest in the Orthocladinae family and lowest in the Tanypodinae family (Danks, 1971). In the case of the Krępa sediments, species of both families were found (e.g. *Propsilocerus lacustris*-type and *Procladius* respectively) with Orthocladinae being more abundant than Tanypodinae (57 vs. 5 head capsules) and the highest number of head capsules being preserved during a period with relatively cool summers (15-17°C).

Another important factor causing the decline of Chironomidae populations is the lack of oxygen in the water, although this cannot be directly captured by palaeoreconstructions. Instead, low-oxygen conditions are in general only indicated by the abundant occurrence of organic matter in the sediments. Such increases in organic matter commonly increase bacterial respiration and cause in consequence an oxygen deficiency in the profundal of water bodies (Charlton, 1980; Matzinger et al., 2010; Müller et al., 2012). Another factor limiting the preservation of chironomid head capsules in sediments are mechanical factors that cause damage to the head capsules. For example, Tanypodinae remains are, due to their large size, not very resistant to disintegration and the number of preserved capsules may therefore be smaller (Walker et al., 1984). This would be consistent with our finding of only 5 Tanypodinae individuals in the Krępa sediments at four different depths. The preservation of remains from the 3rd and 4th larval stages only is most likely related to the increased amount of chitin in these developmental stages, making remains of these stages more resistant to disintegration. The remains of Chironomidae may also not be preserved if accumulation rate is low and remains of species from shore habitats could be poorly preserved. However, studies confirm a positive relationship between biocenosis and thanatocoenosis (Iovino, 1975; Walker et al., 1984). The number of generations per year may also affect the abundance of Chironomidae, i.e. subfossils of multivoltine species can be overrepresented compared to bivoltine species, however, it is difficult to determine whether changes in species composition correspond with voltinism (Tokeshi, 1995).

The main factor influencing the preservation of Chironomidae remains is the content of $CaCO_3$, especially in moderately and strongly acidified lakes. This factor is often more important than pH, depth or time deposition of remains (Bailey et al., 2005). The microenvironment and the presence of organic matter are of great importance for the preservation of remains (Briggs and Kear, 1993; Sageman and Hollander, 1999). The faster mineralisation occurs, the better the preservation of the remains (Briggs and Kear, 1993; Park, 1995). Further factors reducing the abundance of chironomids are extreme temperatures, low nutrient levels, acidic waters, high Se concentrations (Del Wayne et al., 2018; Mousavi, 2002) , the content of hydrogen sulphide during holomixis, as well as paludification of the lake (Takagi et al., 2005; Płóciennik et al., 2020).

The lack of oxygen in the sediment could have limited not only the number of Chironomidae but also the number of preserved head capsules in the sediment. In particular, chitin usually does not accumulate in anaerobic sediments because it is more easily broken down by bacteria, effectively mineralising it into CH4 and CO2 (Wörner and Pester, 2019).

Chironomid species found in the Krępa sediments have a wide range of environmental conditions in which they occur. In particular, we observe dominance of species resilient to harsh conditions such as the oxygen-deficiency-resistant *Chironomus anthracinus*-type and the eutrophic *Chironomus plumosus*-type (18.7 and 22.2 % of the total number of head capsules, respectively), the cold-adapted *Corynocera ambigua* (25.7%) and the freeze-resistant *Propsilocerus lacustris*-type (7.5 %). However, both eutrophic and oligotrophic species as well as warm- and cold-adapted species occur in the Krępa sediments. As there are obviously only very few habitats where no invertebrates occur, the absence of chironomid remains during most of the Holsteinian Interglacial might be best explained by sediment-related disintegration and/or anoxic conditions at the bottom of a fairly deep lake. The lack of Chironomidae remains in the Krępa sediments could also be explained by mineralisation of the chitin. This would be in agreement with the parallel observed lack of cellulose remains from plants as well as with the very low number of Tanypodinae head capsules, which are particularly prone to disintegration. However, satisfyingly explaining the lack of chironomid remains in most of the interglacial lake deposits requires further research as well as a comparison of our results with other lake sediments that lack chitinous remains.

4.1.2 Chironomid-inferred reconstructions from the Krępa site in relation to pollen-based reconstructions

A chironomid-based summer temperature reconstruction was only possible for the part of the Krępa sediment core that corresponds to LPAZ KR-12 and early LPAZ KR-13, which most probably correspond to MIS 11b. Chironomid-based summer temperatures during the early part of this interval (LPAZ KR-12a and LPAZ KR-12b), i.e. directly after the Holsteinian Interglacial, were most probably still relatively high and stable, ranging from 19 to 21 °C, but dropping rapidly in LPAZ KR-12c and LPAZ KR-13a to 15-17 °C. The following re-increase to about 20 °C at the top of LPAZ KR-13a possibly reflects the transition into the post-Holsteinian interstadial that corresponds to MIS 11a. These data indicate that the summer temperature maximum during the post-Holsteinian is consistent with the temperature range of the SNP training set (3.5-20.0 °C) (Kotrys et al., 2020). On the other hand, there were periods with colder summers than today (15°C). Comparing MIS 11 to the Holocene, it is crucial to mention that insolation patterns for both periods differ - MIS 11 was characterised by two insolation maxima, while there was only one (though more distinct) during the Holocene (Rohling et al., 2010). In fact, summer temperature increase during MIS 11b might be explained by increasing insolation at that time.

In general, Chironomidae remains in the Krępa sediments occur mostly during cool periods while they are absent during warm periods. For example, in the interglacial part of the sediment record isolated remains were only found in LPAZ KR-4, which precedes the OHO, and in LPAZ KR-7, which corresponds to the YHO. In contrast, Chironomidae were most abundant in LPAZ KR-12, which is thought to roughly correspond to MIS 11b, the first cold phase after the Holsteinian Interglacial (Imbrie et al., 1984; Fawcett et al., 2011).. To date, studies using subfossil Chironomidae to reconstruct past climate conditions mainly focused on the Weichselian Late Glacial and the Holocene (Gandouin et al., 2016; Nazarova et al., 2018; Druzhinina et al., 2020). In contrast, there are only very few chironomid-based summer temperature reconstructions for the Late and Middle Pleistocene prior to 20 ka BP available so far (Gandouin et al., 2007; Samartin et al., 2016; Plikk et al., 2019; Ilyashuk et al., 2020; Bolland et al., 2021; Rigterink et al., 2024), and actually none for the MIS 11 complex. In general, chironomid records from other sites and time intervals are characterised by a higher abundance and species diversity of Chironomidae, while at Krępa Chironomidae occur only during the early glacial period following the Holsteinian Interglacial. A similar phenomenon has so far only been observed in the Laptev Sea region (Arctic Siberia), where Chironomidae also appear only in the cold period after the Eemian Interglacial, when the site was surrounded by wet grass-sedge shrub tundra period (Andreev et al., 2004).

In contrast to the patchy occurrence of chironomids, pollen-based climate reconstructions using MAT and WA-PLS provide continuous and robust records, successfully applied across various European regions and time periods (Mauri et al., 2015; Chevalier et al., 2020). During LPAZ KR-12a, pollen reconstructions indicate relatively stable and moderate summer temperatures. Additionally, P_{ann} remains relatively high during this phase, suggesting consistently moist conditions supporting dense forest coverage. This is in agreement with the observed dominance of *Pinus* forests with possibly still some admixed *Picea* during this phase, reflecting more humid but not necessarily warmer conditions (Caudullo et al., 2016).

The significant NAP increase during following LPAZ KR-12b suggests a substantial forest decline, although the pollen-based T_{jul} reconstructions indicate relatively warm summers. This combination of ecological and climatic signals strongly suggests that the decline in forest cover was primarily driven by colder winter temperatures rather than by summer thermal conditions. The pollen-based T_{jul} reconstruction confirms peak interstadial warmth in terms of summer temperatures comparable to current mean July temperatures in Eastern Poland (Mauri et al., 2015; Kotrys et al., 2020; Gedminienė et al., 2025). Furthermore, the pollen-based T_{ann} reconstruction also highlights peak interstadial warmth during LPAZ KR-12b, indicating overall favourable climatic conditions during the growing season. The pronounced increase in open-ground vegetation (NAP dominance) and herbaceous taxa thus likely reflects an ecological response to severe winter conditions that restricted the establishment and survival of forest taxa, particularly those sensitive to extreme winter frosts (Körner and Paulsen, 2004; Harrington and Gould, 2015).

LPAZ KR-12c begins with pioneer Betula-Larix forests, reflecting a significant climatic shift towards colder and possibly drier conditions. The appearance of *Larix*, a cold-tolerant, light-demanding taxon adapted to short growing seasons and low temperatures, reinforces the interpretation of subarctic or boreal-like climate conditions. *Larix* is typically associated with northern coniferous forests and reaches its distributional limits in areas with low winter temperatures and moderate precipitation (San-Miguel-Ayanz et al., 2022). Our MAT and WA-PLS reconstructions support this shift, showing notable declines in T_{jul} and T_{ann} as well as in P_{ann}, aligning with the development of tundra-like sparse forest communities. Gradually increasing pollen signals from Pinus indicate a modest rise in thermal conditions later within LPAZ KR-12c, yet still within a generally cool and moisture-limited climatic regime. The absence of chironomids during this interval corroborates the interpretation of sustained cooler and drier conditions. Chironomid assemblages are sensitive to environmental harshness, and under extremely cold or oligotrophic conditions, their production may be so low that remains are not preserved in sediment records (Eggermont and Heiri, 2012).

The gradual cooling indicated by our chironomid- and pollen-based reconstructions during subsequent LPAZ KR-13a is consistent with the presence of sparse Betula forests at the onset of this zone. Pollen-based reconstructions suggest that T_{jul} remained relatively mild (~17.5 °C MAT, ~17.3 °C WA-PLS), closely aligning with the chironomid-inferred mean $T_{jul\text{-}Ch}$ value of ~17.5°C for this interval. Although the chironomid data exhibit a broader range (15–20°C), this variability falls within typical reconstruction uncertainties and does not suggest a fundamentally different climatic signal. Meanwhile, declines in T_{ann} and especially T_{jan} indicate that cold-season severity remained the primary constraint on forest development (Nienstaedt, 1967; Körner and Paulsen, 2004; Harrington and Gould, 2015). In parallel, a reduction in P_{ann} further supports increasing climatic stress, potentially limiting moisture availability and forest resilience during this transitional phase (Körner and Paulsen, 2004).

The broader relevance of the climate conditions reconstructed from the Krępa pollen data is given by the comparison with other MIS 11 palaeotemperature reconstructions from Southern Europe (Oliveira et al., 2016; Kousis et al., 2018; Sassoon et al., 2023, 2025). These Mediterranean records indicate generally warm conditions during MIS 11b, punctuated by recurrent cooling and drying events that led to repeated forest contractions. For instance, the Lake Ohrid from SE Europe record shows a transition from temperate deciduous to cold mixed forests, with T_{ann} dropping to ~2 °C and mean temperature of the coldest month below −8 °C during the coldest events, despite precipitation often remaining near or above 800–900 mm (Kousis et al., 2018). Meanwhile, records from the SW Mediterranean reflect similar climate oscillations, with Sassoon et al. (2025) documenting synchronous declines in T_{ann} and P_{ann} centered around 398 ka BP. In contrast, the Krępa record reflects relatively steady summer cooling alongside more marked declines in winter temperatures and moderately decreasing precipitation. Mediterranean vegetation is primarily water-limited, making it especially vulnerable to fluctuations in atmospheric moisture and reductions in winter rainfall (Giorgi, 2006; Lionello et al., 2006). In contrast, vegetation in Eastern Europe is highly responsive to winter climate extremes. In particular, cold-season frost events, snow cover variability, and late-winter cold snaps affect plant performance, especially in temperate and continental zones (Kreyling, 2010; Camarero et al., 2022).

The lack of accurate absolute dating for terrestrial sediment sequences from the Holsteinian Interglacial makes it difficult to directly compare the results from Krępa to other MIS 11 sites. However, as there are a few quantitative temperature reconstructions based on pollen and biomarkers from other sites in Europe for the post-Holsteinian, a general comparison of temperature levels during this interval seems feasible. For example, pollen analyses on marine sediments from the Iberian margin show similar climatic and ecological patterns for MIS 11b as observed at Krępa namely repeated forest decline events. These were paralleled by reductions in sea surface temperatures, although temperatures were in general still relatively high during most of MIS 11b, i.e. only about 1 °C below the MIS 11c level (Oliveira et al., 2016). A similar pattern with still relatively high air temperature during early MIS 11b and a temperature drop only during late MIS 11b is also seen in palynological data from Lake Ohrid in SE Europe (Kousis et al., 2018). In line with our chironomid-based summer temperature reconstruction from Krępa, these results show that the temperature decline at the demise of the Holsteinian Interglacial was not abrupt and that at least summer temperatures most probably remained at a relatively high level for several thousand years. The general summer temperature variability that is seen in the Krępa record throughout the post-Holsteinian, i.e. the moderate drop during early MIS 11b, the following increase and the more pronounced drop during late MIS 11b as well as the marked re-increase at the transition into MIS 11a, closely resembles vegetation and sea surface temperature variability at the Iberian margin and might indicate a substantial impact of insolation variability (Oliveira et al., 2016).

Conclusion

This study presents the first combined chironomid- and pollen-based palaeoclimatic reconstruction for the post-Holsteinian i.e. MIS 11b, offering a new perspective on climate variability in Eastern Europe during this time interval. The results highlight the complementarity and reliability of both proxy types, as pollen-based MAT and WA-PLS reconstructions show strong internal consistency and correspond well with chironomid-inferred summer temperatures where data are available. The summer temperatures range from 14 to 19 °C and between 15 and 20 °C for the pollen- and chironomid-based reconstruction respectively. This indicates colder summers compared to present times for most of the post-Holsteinian period. Among the models, the pollen-based MAT reconstructions exhibit particularly high predictive skill, especially for temperature variables. The analysed part of Krępa sediment record reveals a progressive shift towards more continental climate conditions throughout MIS 11b. This is reflected by gradually cooling summers, increasingly severe winters, and a decline in annual precipitation. These climatic trends coincide with marked vegetation changes, including forest retreat and a rise in herbaceous taxa during colder phases.

To date, the vast majority of studies addressing palaeoclimate variability in the terrestrial realm during the Middle Pleistocene relies on pollen analysis. Nevertheless, this does not prejudge the lack or low abundance of Chironomid-inferred reconstruction in sites other than Holocene. More than that, they might prove to be a priceless source of knowledge about temperature, considering potential differences between pollen and Chironomid-inferred records. By comparing the results from different sites, it will be possible to find the factor that influenced the preservation of subfossil remains of Chironomidae.

Ultimately, this study underscores the value of multi-proxy approaches in palaeoclimate reconstruction, particularly for pre-Holocene periods. Chironomids show significant potential as a summer temperature proxy in older sediments as long as preservation conditions are favourable.

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Authors contribution

TP proposed the idea of the main text, and contributed to the figures. TP,AGr and AG wrote the original draft version of the manuscript. BK performed the chironomid-inferred summer temperature reconstruction. AG performed the pollen-inferred climate reconstructions. MŻ collected and described the core in the field. AG, AH, and MS analysed the pollen data. TP, AGr and MS analysed the chironomid data. TP, AGr, AG, MB and MS did the visualisations (graphs and maps). AG, AH, MŻ, MB, JN, MC, SL and MS reviewed the paper. All authors have made substantial contributions to the submission of this manuscript.

Competing interests

The authors declare that they have no conflict of interest.

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