# Chironomid- and pollen-based quantitative climate reconstructions for the post-Holsteinian (MIS 11b) in Central Europe~~Non-biting midges (Chironomidae) as a proxy for summer temperatures during the post-Holsteinian (MIS 11b) - a central European perspective~~

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**Abstract.** Investigating climatic~~Climatic~~ and environmental changes during past interglacials ~~periods~~ is crucial~~can be investigated~~ to improve the understanding of the mechanisms that govern~~governing~~ the changes related to~~which are~~ current~~ly~~ global warming~~observed~~. Among the ~~N~~numerous proxies that can~~might~~ be used~~tilised~~ to reconstruct past~~various~~ environmental and climatic conditions~~parameters. For instance~~, pollen allow~~can be used for~~ quantitative reconstructions~~ng~~ of ~~the~~ annual, warmest month and coldest month air temperature~~s, the temperature of the warmest month, the temperature of the coldest month,~~ as well as precipitation sums, while the head capsules of ~~and vegetational season duration.~~ Chironomidae larvae ~~head capsules~~ are widely used to infer past~~recreate~~ summer ~~thermal conditions~~air temperature~~.~~ as well as~~but~~ ~~Chironomid remains can also be used to trackindicate changes~~ in the trophic state or pH of water bodies. ~~Non-biting midges remains indicate trophy and pH of water bodies as well.~~ Nevertheless, the latter~~they~~ have so far mostly been used ~~mostly in the studies of~~ for reconstructing ~~the~~ 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 ~~with hardly any cChironomid inferred temperature reconstructions conducted for the MIS 11 period~~. In this study we present the first quantitative palaeoclimate~~summer temperature~~ reconstruction for the post-Holsteinian (Marine Isotope Stage - (MIS) 11b) in Central Europe that is based on both pollen and~~the analysis of~~ fossil chironomid remains preserved in palaeolake sediments recovered at Krępa, southeastern Poland. Besides being used for the palaeoclimatic reconstruction, ~~P~~pollen analyses~~is~~ provide the biostratigraphic framework ~~was used to determine the time chronology~~ and ~~to give~~ a broader perspective of climate~~of the climate~~ development at the end of Holsteinian Interglacial. Fossil ~~Pollen phases were extracted to~~ Chironomidae assemblages at ~~the~~ Krępa ~~site~~ consist mainly of oligotrophic and mesotrophic ~~species~~ taxa (e.g. *Corynocera ambigua* ~~*type*~~, *Chironomus anthracinus*-type ~~*type*~~) while~~with lower abundance of~~ eutrophic ~~species~~ taxa (e.g. *Chironomus plumosus*-type) are less abundant. The chironomid-based summer temperature reconstruction yields~~indicates~~ July air temperature ~~ranging~~ between 15~~,~~,3~~°C~~ and 20,~~,~~1°C during the early post-Holsteinian~~., which is in good agreement with the pollen-based reconstruction.,~~ Similar summer air temperature~~Temperature~~ changes during the first stadial after the Holstein Interglacial ~~period~~ are also reflected by the pollen data, which, however, show a certain delay compared to the chironomid-based temperature reconstruction~~s~~. In any case, results from Krępa prove that conducting Chironomidae analysis is ~~even~~ feasible for periods as early as the Middle ~~mid~~ Pleistocene, improving~~enhancing~~ our understanding of the mechanisms that control present-day climatic and environmental changes. ~~The additional element of this research is indicating sites within the Polish borders that were investigated so far – mostly on the basis of pollen analysis, occasionally *Cladocera*, isotopes, etc. – and might be new objects of studies based on Chironomid inferred temperature reconstructions. However, bringing cChironomid analysis with particular emphasis of challenges of conducting it with the use of sediments older than Holocene is the primary aim of this publication. Data from the MIS 11 complex are unique. There are only 4 sites with pre-Late Glacial chironomid-based summer temperature reconstructions in Europe.~~

## 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). ~~Climatic fluctuations occurred repeatedlynumerously throughout Earth's history and they were driventriggered by natural causes – without human participation. This situation creates the opportunity to compare those changes with the current ones, as the Holocene is the only interglacial during which human activity was considerable. The widely debated topic of the Anthropocene is presently taking place in the scientific community in various scientific disciplines. Both the time frame of the unit and the scale of human influence on the environment are under discussion (Brondizio et al.,~~

2016). The widely debated topic of the Anthropocene is presently taking place in the scientific community in various scientific disciplines. Both the time frame of the unit and the scale of human influence on the environment are under discussion (Brondizio et al., 2016).

Holocene i.e. stratigraphic units corresponding to marine isotope stages (MIS) 1), whose time frame ihas from 11,500 years BP – present (Mayewski et al., 2017) is an abundant source of environmental archives, such as i.a. lakes, palaeolakes, and ocean sediments provide ice cores, trees, oceans which provide material for comprehensive palaeoecological analyses. Taking advantage of Tthe The sensitivity of some groups of organisms in these archives to changing hydrological or climatic conditions change, allowswe can use this knowledge to to reconstructthe reconstruction of past events that directly affected the abundance or structure of the communitiesspecies structure of these groups of organisms ((Battarbee, 2000)Battarbee, 2000). Species, which are characterised by narrow ecological preferencesrequirements, whether it be air temperature, water chemistry or water table depth, are used for certain palaeoenvironmental reconstructions (Juggins and Birks, 2012). Many ecological parameters can be reconstructed using different proxies. For example, Fforaminifera is a reconstruction tool forcan be used to reconstruct ocean pH (Foster and Rae, 2016; Roberts et al., 2018), pollen provide information aboutindicates changes in vegetation migration (Ralska-Jasiewiczowa et al., 2004; Kupryjanowicz et al., 2018) and can be used to reconstructas a proxy showing the activities of a human in the pastpast human activityies (Chevalier et al., 2020) or past climate conditionsserve as a palaeoclimatic proxy (e.g. Rylova and Savachenko, 2005; Hrynowiecka and Winter, 2016). whereas Head capsules of cChironomids can serve as the basis for summer air temperature reconstructions (Eggermont and Heiri, 2012) as well as for assessing. Chironomidae remnants analysis allows the assessment of the water reservoir trophy and pH as well (Płóciennik, 2005).The analysis of chironomid subfossilsremains also allows the assessment of 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. However, these reconstructions do not providegive unequivocal information about exact changes in air temperature. The question also remains whether these changes and their pace are caused by natural factors or human activityacitivity. To gain a deeper understanding of the present day 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 impacthuman activity. In this regard, aone 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 and is considered as corresponding to MISMarine Isotope Stage (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~~Northern~~ Europe were in general temperate at that time ~~(~~(Nitychoruk et al., 2018), but vegetation reconstructions suggest warmer and more humid conditions compared to ~~climate during~~ the Holocene ~~(MIS 1)~~ 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~~an~~ (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*.

~~In this research we focus on the *Chironomidae* state of research in the Holstein Interglacial. Although non-biting midges remains are widely used in climate and palaeoenvironmental reconstructions (Eggermont and Heiri, 2012), there are only very few chironomid-based is still not much research considering using them to recreate reconstructions of climatic and ecological conditions for the Middle and Late Pleistocene in Europe available so far during the Holsteinian Interglacial (.Bolland et al., 2021; Engels et al., 2008; Ilyashuk et al., 2022; Rigterink et al., 2024). but none for the Holsteinian Interglacial and the time thereafter in particular. HenceIn fact, knowledge about climatic conditions at this time is mainly derived from pollen data, e.g. quantitative reconstructions based on terrestrial archives for this period are rare, regardless of the proxy used. Exceptions from this rule include palynological reconstructions from PraclauxVelay maar sites 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). Pollen data from the Ossówka palaeolake (eastern Poland) has also been~~

~~analysed, covering entire Holsteinian Interglacial (Nitychoruk et al., 2005), YHO (Nitychoruk et al., 2018) and post-Holsteinian (Bińka et al., 2023). Vegetation development during MIS11 has been also studied based on material from Nowiny Żukowskie site (E Poland) (Hrynowiecka and Winter, 2016). Another site worth mentioning is Bilhausen in central Germany, which provides pollen record for Bilhausen Interglacial, however, it remains unclear whether this period is MIS 11 or MIS 13 analogue (Kühl and Gobet, 2010). There are even fewer Northern European chironomid inferred palaeoecological reconstructions covering MIS 11 period.~~ ~~One of the exceptions is Hoxne site in eastern England (Horne et al., 2023).~~ In this study, temperature reconstructions were performed, combined three proxy methods based on invertebrate fossils: the ~~Chironomid Transfer Function method (e.g., Brooks, 2006), the Mutual Ostracod Temperature Range method (Horne, 2007) and the Beetle Mutual Climatic Range method (Atkinson et al., 1986).~~ ~~Contemporary state of knowledge considering MIS11 has been reviewed by Candy et al. (2014). That is why extension of using Chironomidae proxy on other periods (i.e.~~ Holsteinian Interglacial) ~~is crucial to understand current climate changes.~~

Aiming at improving the knowledge about climate variability at the demise of the Holsteinian Interglacial, ~~Here~~ we present in the following the first quantitative climate reconstructions ~~combined chironomid-based and pollen-based summerJuly air temperature reconstruction from Poland~~ for the post-Holsteinian in Central Europe, which are based on chironomid and pollen analyses. ~~periodWe tested temperature reconstruction using the Swiss-Norwegian Polish Training Set and presented the first Chironomid-inferred temperature reconstruction from Poland before the Last Glacial Period and even for the post-Holsteinian~~. ~~The literature contains data from pollen analysis for this period, but the~~ combined chironomid- and pollen-based temperature reconstruction ~~is~~will be one of the first for this time range. ~~This work~~ ~~sheds~~gives new light on the possibilities of analysing ~~subfossil Chironomidae.~~

~~Additionally, we have reviewed sites documenting lake sediments from the Holsteinian Interglacial period. Based on this we selected sites with a probable continuous sequence of interglacial sediments, which represent a potential archive for reconstructing the palaeotemperatures of the summer period on the basis of Chironomidae.~~ In addition, we discuss ~~T~~the potential of chironomid ~~that non-biting midges~~ analysis for palaeoecological studies ~~brings to the wide range of proxies used in the palaeoecology~~ of Qquaternary sediments ~~has also been discussed~~ as well as the challenges for chironomid analysis ~~such as those~~ arising from both the evolution and interchanging adaptations to species ecological preferences ~~ecological requirements~~ and the preservation ~~behaviour~~ of fossil remains. ~~In the presented article, we have collected all known sites of Holsteinian age from Poland. We have collected nearly 80 sites that were researched in Poland on the map. We also created an up-to-date set of sites. We hope that our list will be a handy syllabus for people interested in palaeoclimate research in Poland.~~

## 2 Study site~~Data~~ 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).

## ~~2.1 Data compilation~~

~~The research included sites located in Poland and covering the Holsteinian (Mazovian) interglacial~~The research covered sites located in Poland. Holsteinian (Mazovian) Interglacial has been included. This analysis encompasses 80 sites. They are concentrated mainly in the eastern and central part of Poland (east of Warta valley), with only several sites located in the western half of the country (Fig. 1). In general, they are focused in the area contained between Wartanian Glaciation and Odranian Glaciation maximum ranges (Krupiński, 2000). The sites' locations were are presented in tabular form (Tab. 1). As the Holsteinian cores were often researched as early as in 1930–1960's, their exact location is not always known from scientific papers and therefore it had to be estimated. In this case, the approximate geolocation was determined based on terrain descriptions, drawings and maps from the articles and comparing them to resources from Google Earth. In this case, location sketches and Google Earth were used as the location estimation tools.


**Figure 1: Holsteinian sites location in Poland with different glaciation ranges. The number of each location corresponds with Supplement Table 2. Sites from area in frame (A) are labelled in Supplement Figure 12. Krępa site is highlighted with a big red dot. Glaciation ranges are based on Żarski et al. (2024), Pochocka-Szwarc et al. (2024), Marks (2023). Caption: map created with the use of EU-15s Digital Elevation Model; rivers downloaded from: https://www.naturalearthdata.com/. Map created in ArcMap programme.**

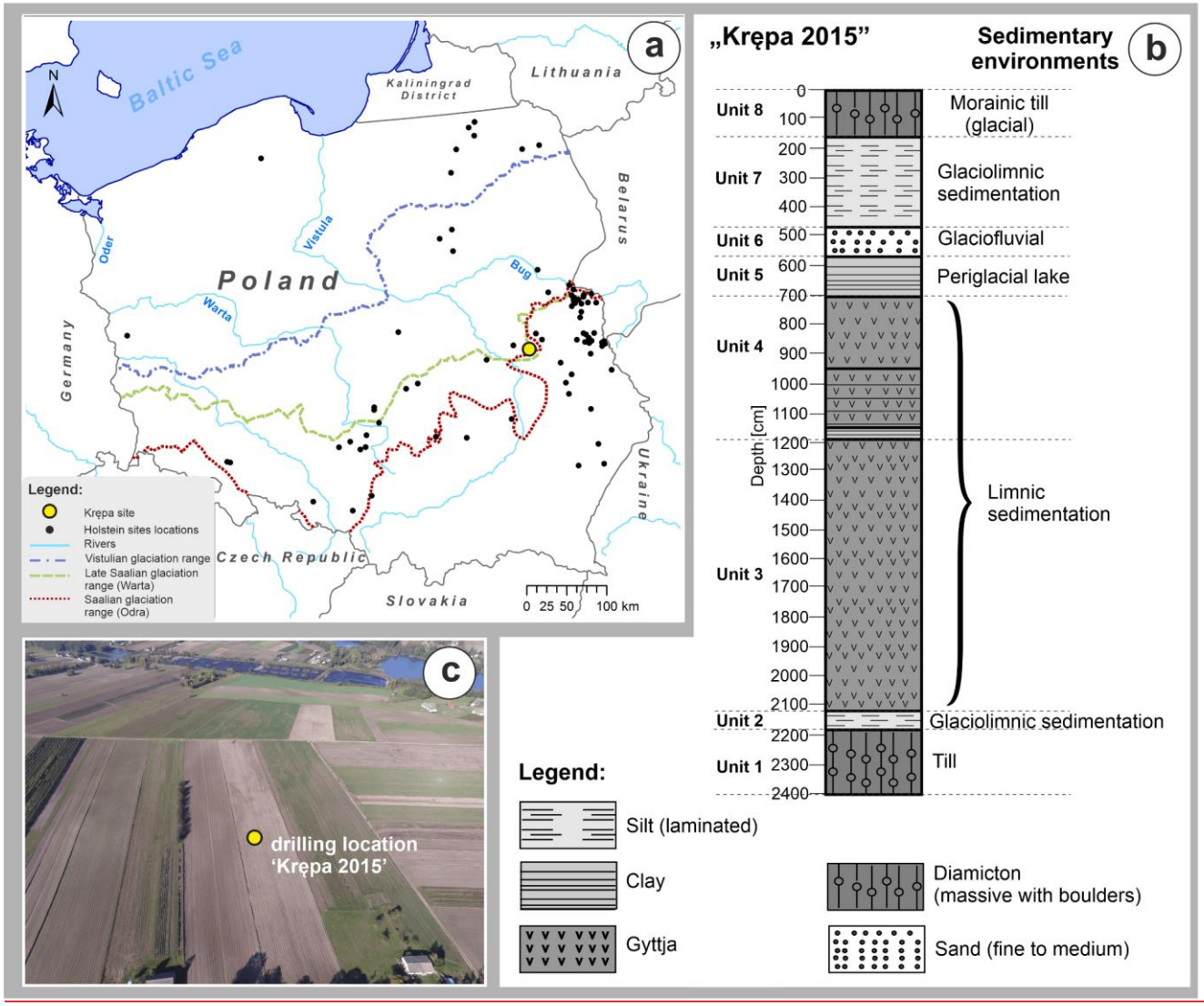



**Figure 1:** ~~Selected Holsteinian sites location in Poland with different glaciation ranges, Krępa site is highlighted with a big yellow dot (a). Glaciation ranges based on Żarski et al. (2024), Pochocka-Szwarc et al. (2024), Marks (2023). Krępa site lithological profile from 2015 (b) and (c) location of drilling (foto M. Zarski).~~ (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. Zarski).

## 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~~Part of it~~ 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~~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 ~~located~~ 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~~the co-occurrence~~ of first~~pollen from~~ *Picea-Alnus* and then *Carpinus*~~-~~ and Abies ~~trees~~, as well as by a significant proportion of *Taxus* ~~pollen~~, 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~~s~~ 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~~studies based~~ 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~~the northern part of~~ 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, ~~and~~ temperatures were milder and precipitation rates were higher, also reflected by the appearance of stenothermal plant species (Nitychoruk et al., 2005).

## ~~2.3 Study area~~

~~The Krępa site (51°37'53.2''N, 22°18'38.1''E, 146 m amsl.) is located in SE Poland, near Kock, approximately 120 km southeast of Warsaw. 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). The profile analysed in this paper is situated 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 drilled in 2015 using a Geoprobe drilling device (Górecki, 2023).

## 2.4 Lithological description of the Krępa sediment succession and palaeoenvironmental interpretation

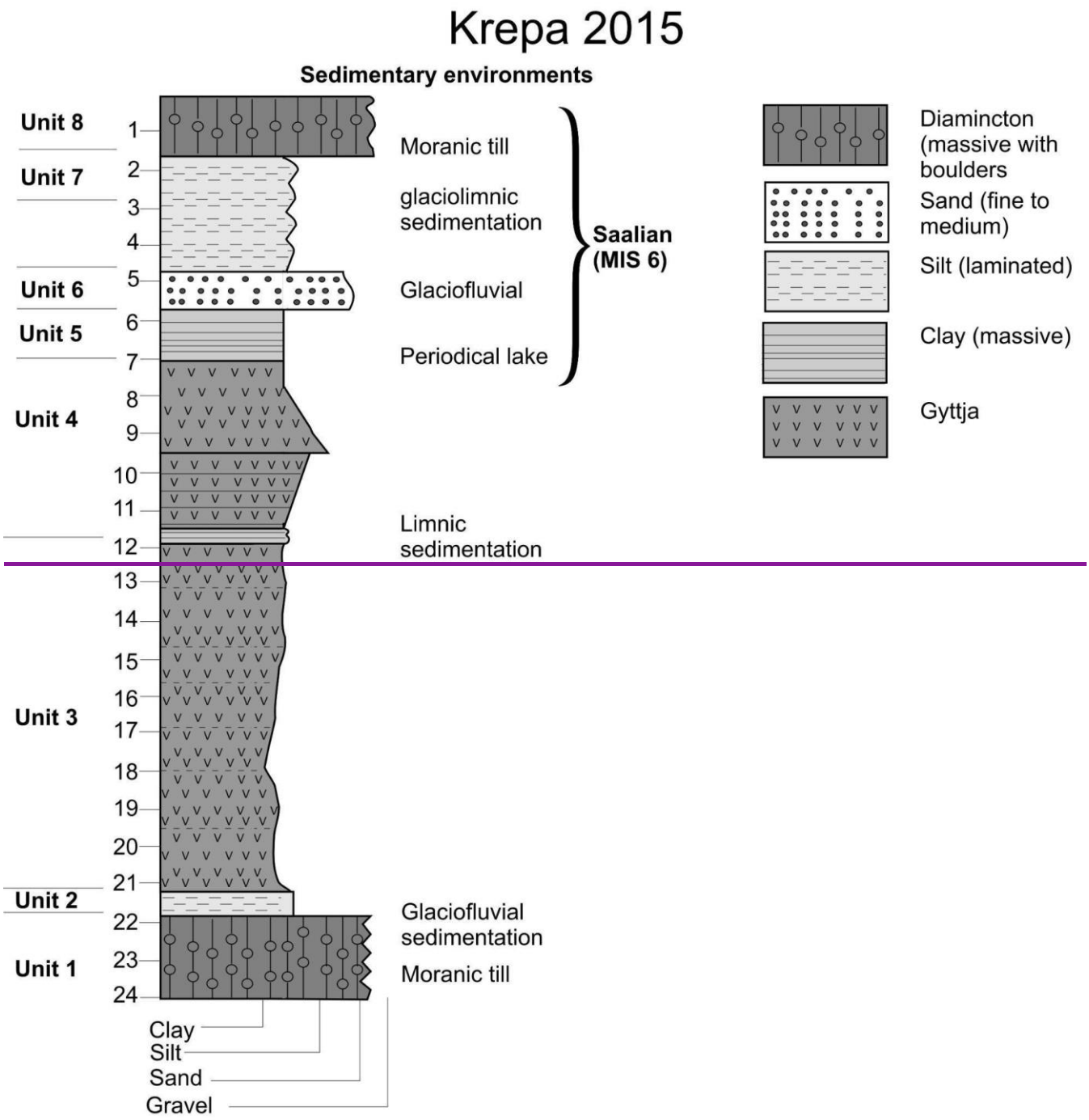
The basal part of of the 23.8 m long sediment core recovered from the Krępa sediment succession (Fig. 2) consists of a 2 m thick layer of massive, light greyish brown sandy clays with a large number of Scandinavian rock fragments (unit 1), which is interpreted as glacial till. As indicated by its stratigraphic position and its petrographic characteristics (Drozd and Trzepla, 2007), this till was accumulated during the Elsterian glaciation (or Sanian 2 glaciation in Poland), which is considered to correspond to MIS 12. Directly above the till, a 0.6 m thick layer of rhythmically 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 glacier. 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 11.87 and 7.6 m 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 related to the gradual shallowing of the lake, associated with its significant filling with sediments. At the same time, the systematic increase in mineral components in the sediments most probably reflects increased denudation and erosion in the catchment, likely related 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 10) ice sheet. Above this succession, the profile is capped by a 1.5 m thick layer of sandy moraine clay with Scandinavian rock fragments (unit 8) related to the Early Saalian glaciation.

In the collected 23.8 m long sediment core, there is a 2 m thick layer of massive, light gray-brown sandy clays with a large number of Scandinavian rock fragments at the base (unit 1), which is interpreted as glacial till (Fig. 12). Directly above, a 0.6 m thick layer of rhythmically laminated sandy silts and sandy clayey silts is found (unit 2), which gradually turns into a carbonate gyttja with small interlayers of carbonatic minerogenic gyttja (unit 3). Between 11.87 and 7.6 m core depth, non-carbonatic organic-minerogenic gyttjas with a generally increasing mineral content towards the top are found (unit 4). This gyttja sequence is overlain by a 1.9 m thick layer of massive clays (unit 5), which is followed by a 1.1 m thick layer of fine- to medium-grained sands (unit 6) and a 3.1 m thick layer of rhythmically laminated sandy silts (unit 7). The profile is capped by a 1.5 m thick layer of sandy moraine clay with Scandinavian rock fragments (unit 8).

The position of the lower glacial till (unit 1) and its petrographic characteristics (Drozd and Trzepla, 2007) indicate that it was accumulated during the Elsterian glaciation (or Sanian 2 glaciation in Poland), which is considered to correspond to MIS 12.

~~The sediments of unit 2 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 glacier. The glaciolimnic sediments gradually pass into limnic sediments (unit 3), which are interpreted to be deposited in the profundal of an already relatively deep lake. The limnic sediments of unit 4 are related to the gradual shallowing of the lake, associated with its significant filling with sediments. At the same time, the change towards colder climate conditions led to increased denudation and erosion in the catchment and a systematic increase in mineral components in the lake sediments. The unit 5 sediments probably represent accumulation in a periglacial lake, which was subsequently covered by proglacial sediments (units 6 and 7) of the transgressing Early Saalian (MIS 10) ice sheet and finally covered by its moraine clays (unit 8).~~

~~The origin of the sedimentary basin at Krępa is difficult to interpret. Most sites with deposits from the Holsteinian (Mazovian) Interglacial in this region of Poland are associated with tunnel valleys formed during the Elsterian (Sanian 2) glaciation (Żarski et al., 2005; Nitychoruk et al., 2006). However, these sites are usually located beyond the maximum extent of the Late Saalian glaciation (Drenthe Stage in Germany; Odra glaciation in Poland; MIS 6) and are thus subtly visible in the current terrain morphology. In the case of Krępa, the covering of these deposits by the Late Saalian (Odra) glacial advance has resulted in the complete obliteration of the post-Elsterian landscape. Based on the geological cross-section prepared by the authors of the Kock DGMP sheet (Drozd and Trzepla, 2007) and the distribution of interglacial deposits in the study area (Jesionkiewicz, 1982), it can only be inferred that this depression was a relatively extensive kettle hole, formed during the transgression and recession of the Elsterian (Sanian 2) ice sheet.~~




**~~Figure 2: Krępa site lithological profile.~~**

## 2.53 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.~~Palynological samples were prepared following the standard methodology outlined by Erdtman (1960), with modifications involving the use of HF acid (Berglund and Ralska-Jasiewiczowa, 1986). Prior to laboratory processing, a Lycopodium indicator 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. For most samples, counts were conducted up to 500 grains, including both arboreal (AP) and non-arboreal (NAP) plants. However, samples from glacial age sediments, which were low in palynomorphs concentrations, were counted up to 300 grains. Percentages were calculated based on the sum of pollen grains from trees, shrubs (AP), herbaceous plants, and dwarf shrubs (NAP).~~

~~The outcomes of the palynological analysis are depicted in a shortened~~ simplified pollen diagram (Fig. ~~2~~3), ~~divided into 14 Local Pollen Assemblage Zones (LPAZ). The formation of the lake can be traced back to the end of the Elsterian (Sanian 2) glaciation, although a hiatus in the pollen record is evident at 21.10–21.15 m, possibly encompassing the entirety of Pollen Period I (Betula and Betula–Pinus phases). The Holsteinian (Mazovian) commences~~ starts ~~with the Picea–Alnus phase of Pollen Period II. The upper segment of the succession, starting at 13.10 m, indicates multiple cold/warm oscillations, usually connected to the Early Saalian (Liviecian) Glaciation. More elaborate descriptions regarding pollen analysis results are provided in Górecki (2023).~~

## 2.4 Pollen-based climate reconstructions

Climate variables reconstructed using pollen data include mean annual air temperature ($T_{ann}$), annual precipitation sum (Pann), mean July air temperature ($T_{jul}$), and mean January air temperature ($T_{jan}$). 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~~6~~ Chironomidae analysis

Initially, 79 sediment samples of 1 $cm^3$, 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.~~30 Ssediment samples of 1 $cm^3$ were taken for chironomid analysis were taken at 5–40 cm intervals (sample volume approximately 1 $cm^3$).~~ 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~~sediment~~ was subsequently~~were~~ examined under a stereo ~~binocular~~ microscope (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 ~~by~~ 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~~7 Chironomid-based mean~~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 ~~(SNP TS,~~ (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~~lacustrine~~ sediments (unit 4 on Fig. 1). Samples that contained ~~significantly~~ 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.

~~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 because the test of the reconstruction showed acceptable results~~. 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~~5~~.

## 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 (~~or~~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~~glacier~~. 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 morainice tillclay 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 OlderLate Saalian glaciation (Drenthe Stage in Germany; Odra glaciation in Poland; MIS 6) and thus subtly visible in the present surfaceterrain morphology. In the case of Krępa, the covering of these deposits by the OlderLate 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 transgression and recession of the Elsterian ice sheet.

### 3.21 Regional and local vVegetation changes during the end of Holsteinian Iinterglacial and the Early Saalian Glacial at Krępa site

~~**Table 1: Description of local pollen assemblage zones (LPAZ) and distinguished in the sediments from the 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~~phase~~ is characteris~~z~~ed 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~~in~~ 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~~phase~~ 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~~creating~~ 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~~From~~ 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~~the phase~~. Open communities began to dominate the landscape (NAP <40 %), and woody vegetation was reduced to scattered~~loose~~ 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 ~~is visible~~ as a sudden increase in the proportion of pollen from temperate taxa. Following the dominance of herbaceous vegetation, ~~the~~ *Betula-Larix* forests re-established in ~~reentered~~ 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~~Trace number of~~ 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~~amounts~~ of Chironomidae head capsules~~Chironomidae~~ (approximately 15~~ head capsules~~ per sample). Dominance of *Chironomus anthracinus*-type (25 %) and Corynocera ambigua~~ type~~ (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* ~~type~~ (24 %) and high contents of *Chironomus anthracinus*-type. **Disappearance of *Glyptotendipes pallens*-type and ~~the~~ appearance of *Glyptotendipes~~appearance 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~~-type (15 %)~~ 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~~section of the~~ 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~~0~~ individuals per sample). Dominant species are *Corynocera ambigua*~~-type~~ (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~~individuals~~. 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~~-type~~ 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. L~~This zone is characteriszed by a l~~ow abundance of Chironomidae. Only two individuals of *Chironomus plumosus*-type were recorded~~ in the sediment~~.

| LPAZ | Depth | Main features of Local Pollen Assemblage Zones (LPAZ) | Main features of significant in the chironomid record |
|---|---|---|---|
| KR-1 | 2120-2180 | 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. |
| KR-2 | 2027.5-2110 | 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. |

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|---|---|---|---|
| **KR-3** | **1957.5-2027.5** | 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. |
| **KR-4** | **1892.5-2027.5** | 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. |

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|---|---|---|---|
| **KR-5 OHO** | **1855-1892.5** | 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. |
| **KR-6** | **1697.5-1855** | 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 phase is characterized 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. |

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| **KR-7**<br><br>**YHO** | **1647.5-1697.5** | 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. |
| **KR-8** | **1497,5-1647.5** | As in 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 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. |

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| **KR-9** | **1362.5-1497.5** | 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 in 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 phase ends with the decline of *Carpinus* and *Corylus* and the reappearance of *Picea*. | No Chironomidae. |
| **KR-10** | **1312.5-1362.5** | 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 %), creating 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. |

| | | | |
|---|---|---|---|
| KR 11a | 1257,5 1312.5 | From 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 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 the phase. Open communities began to dominate the landscape (NAP <40 %), and woody vegetation was reduced to loose birch larch tree stands that occured 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 favour soil erosion and redeposition of older material, which in the palynological record is visible as a sudden increase in the proportion of pollen from temperate taxa. Following the dominance of herbaceous vegetation, the *Betula Larix* forests reentered the area. The zone ends with a sudden increase in the percentage of *Pinus* pollen. | No Chironomidae. |
| KR 11b | 1222.5 1257.5 | *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. |

| | | | |
|---|---|---|---|
| KR-11c | 1187.5–1222.5 | 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. |
| KR-12a | 1122.5–1187.5 | At the beginning of the zone, the development of *Pinus* forests with an admixture of *Picea* (up to 6 %) is observed. Trace numberamounts of NAP suggest verysuggest 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 amounts of Chironomidae (approximately 15 head capsules per sample). Dominance of *Chironomus anthracinus* type (25 %) and *Corynocera ambigua* type (16 %). |
| KR-12b | 1072.5–1122.5 | 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 type* (24 %) and high contents of *Chironomus anthracinus* type. The number of *Glyptotendipes pallens* type and *Glyptotendipes severini* type. |

| | | | |
|---|---|---|---|
| KR-12c | 1022.5-1072.5 | 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 type* (15 %) and *Glyptotendipes pallens* type (13 %). |
| KR-13a | 967.5-1022.5 | Initially, there was a significant opening in the vegetation, and herbaceous plants and shrubs dominated the landscape. In the middle section of the 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 450 individuals per sample). Dominant species are *Corynocera ambigua type* (approx. 29 %) and *Chironomus anthracinus* type (18 %). |

| | | | |
|---|---|---|---|
| **KR-13b** | **877.5-967.5** | 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 individuals. 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* type is also abundant. |
| **KR-14** | **765-877.5** | 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. | This zone is characterized by a low abundance of Chironomidae. Only two individuals of *Chironomus plumosus* type were recorded in the sediment. |

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### 3.~~3~~2 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 ~~was prepared~~ follow~~s~~ing the pollen zonation because (1) ~~Local Pollen Assemblages Zones (LPAZ) as these~~it reflects~~reflect~~ climat~~e~~ic change~~s~~ better than the chironomid assemblages and (2)~~.~~

However, the low number of Chironomidae head capsules and as well as the small species diversity prevented the made it impossible to statistically robust determination of determine 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 Chironomidae preserved. The first individuals occur in LPAZ KR-4 (1892.5-2027.5 cm) and LPAZ KR-7 (1647.5-1697.5 cm). In these zones, eurytopic *Chironomus anthracinus*-type in a poor state of preservation is observed (Fig. 34). There are no remains of Chironomidae in the following LPAZ belonging to the Holsteinian Interglacial and the first single remains of head capsules of *Chironomus plumosus*-type are recorded again in LPAZ KR-11c (1187.5-1222.,5 cm), 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 (1122.5-1187.5 cm) is characterised by a eurytopic conditions with low abundance amounts of chironomid head capsules Chironomidae. Assemblages could indicate a wide range deterioration of environmental conditions (e.g. *Chironomus anthracinus*-type is a profundal species that is, tolerant to a suboptimal condition and wide thermal spectrum (Brooks et al., 2007; Luoto et al., 2019) and and or colder conditions as *Corynocera ambigua* type) 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 *Corynocera ambigua* type *and*, species like *Glyptotendipes pallens*-type and *Glyptotendipes severini*-type, which are often associated with algae and diatoms or mine leaves, i.e. *Glyptotendipes pallens* type and *Glyptotendipes severini* type, which are often associated with algae and diatoms or mine leaves (Tarkowska-Kukuryk, 2014). LPAZ KR-12c (1022.5-1072.5 cm) is characterised by species highly resistant to difficult environmental conditions, such asi.ea. *Chironomus anthracinus*-type, which is typical for nutrient-rich conditions with wide environmental tolerances (Saether, 1979; Self et al., 2011), *Corynocera ambigua* type, which has a broad has wide thermal tolerance (Brodersen & Lindegaard 1999a and *Glyptotendipes pallens*-type, which can better tolerate harsh better winter conditions and lives fing in different types wide range of substrates (Moller Pillot, 2013; Čerba et al., 2022). The next LPAZ KR-13a (967.5-1022.,5 cm) is a phase with mainly cold-adapted species such as *Corynocera ambigua* type. During LPAZ KR-13b (877.5-967.5 cm) the number of chironomid head capsules Chironomidae gradually increased with indicators of progressive eutrophication (e.g. *Chironomus plumosus*-type and *Dicrotendipes nervosus*-type (Iwakuma and Yasuno, 1981) and cold oligotrophic species but post-eutrophic environments (such as *Corynocera ambigua* type) (Brooks et al., 2007) still occurring alsomore frequently. During LPAZ KR-14 (765-877.5 cm) the numberamount 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* type could also be the result of large changes in oxygen concentration, reduced production of benthic algae or changes in the structure of the sediment (Brodersen and Lindegaard, 1999b).

In general, the chironomid assemblages preserved in the Krępa sediments are dominated by the two species *Corynocera ambigua type* and *Chironomus anthracinus* type. *Corynocera ambigua type* 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 aArctic 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

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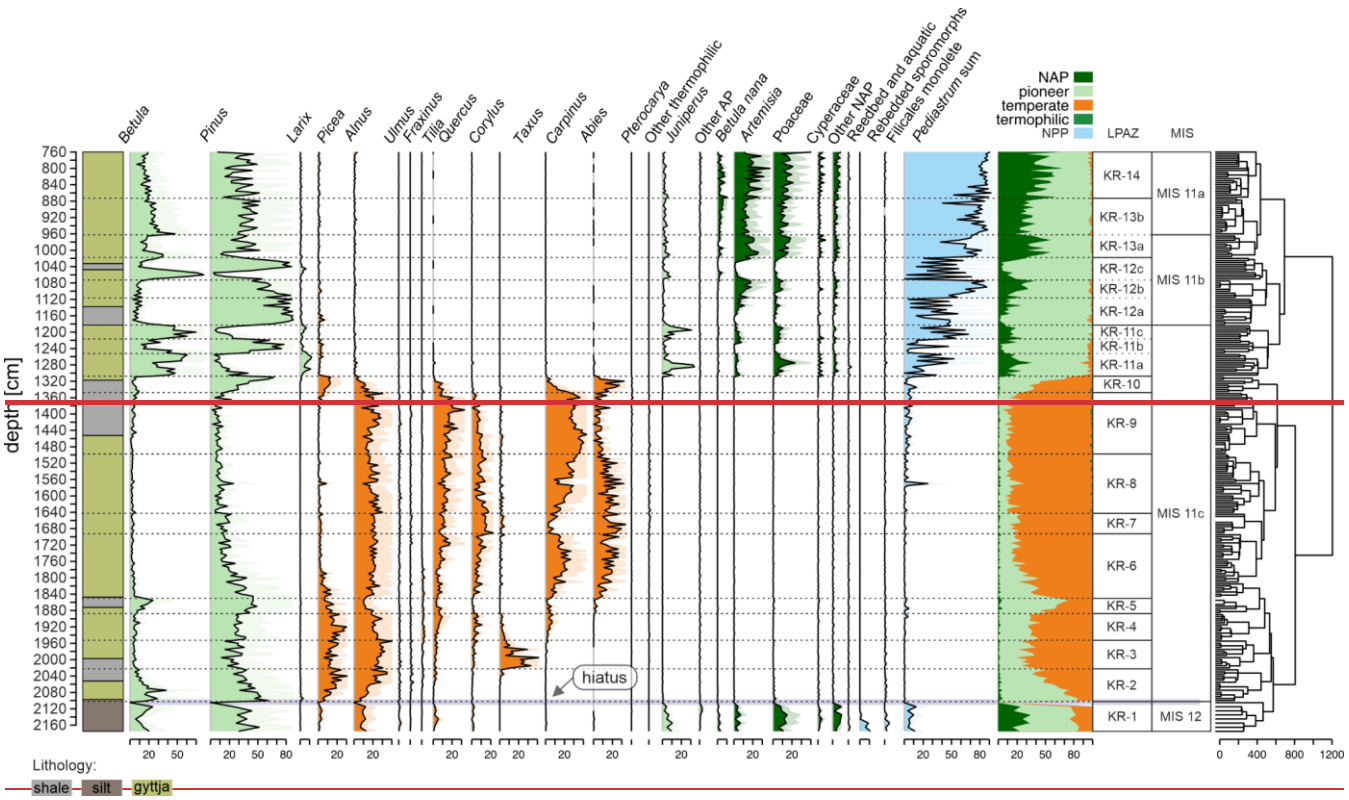
The occurrence of tThis species has been recorded during cold episodes or glacial periods, at sites in England (Bedford et al., 2004), Norway (Velle et al., 2005), Poland (Płóciennik et al., 2015), and the Baltic region (Hofmann and Winn, 2000). However, *Corynocera ambigua type*, cannot be considered a merely cold species. Some authors believe that it's 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; Gandouin et al., 2016; Ilyashuk et al., 2022). Luoto and Sarmaja-Korjonen (2011) claim that this is how the species adapts to existing climatic conditions. The locally observed decline in *Corynocera ambigua type* 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 the lakes and. This species is capable of surviving approximately 2--4 months of oxygen deficiency in the water (Hamburger et al., 1994). It is a species that easily occupiesinhabits niches that are inaccessible to other species due to difficult conditions. 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 Iit prefers softer 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 type* are species found in stratified lakes (e.g., Saether, 1979; Heiri, 2004). As we can see, both species are relativelycan be called resistant to unfavourable environmental conditions, thus having. They have a fairly wide range of conditions in which they can occur, today..


Betula
Pinus
Larix
Picea
Alnus
Ulmus
Fraxinus
Tilia
Quercus
Corylus
Taxus
Carpinus
Abies
Pterocarya
Other thermophilic
Juniperus
Other AP
Betula nana
Artemisia
Poaceae
Cyperaceae
Other NAP
Reedbed and aquatic
Rebedded sporomorphs
Filicales monolete
Pediastrum sum
NAP
pioneer
temperate
termophilic
NPP
LPAZ
MIS
depth [cm]
KR-14
KR-13b
KR-13a
KR-12c
KR-12b
KR-12a
KR-11c
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KR-8
KR-7
KR-6
KR-5
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KR-3
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KR-1
MIS 11a
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hiatus
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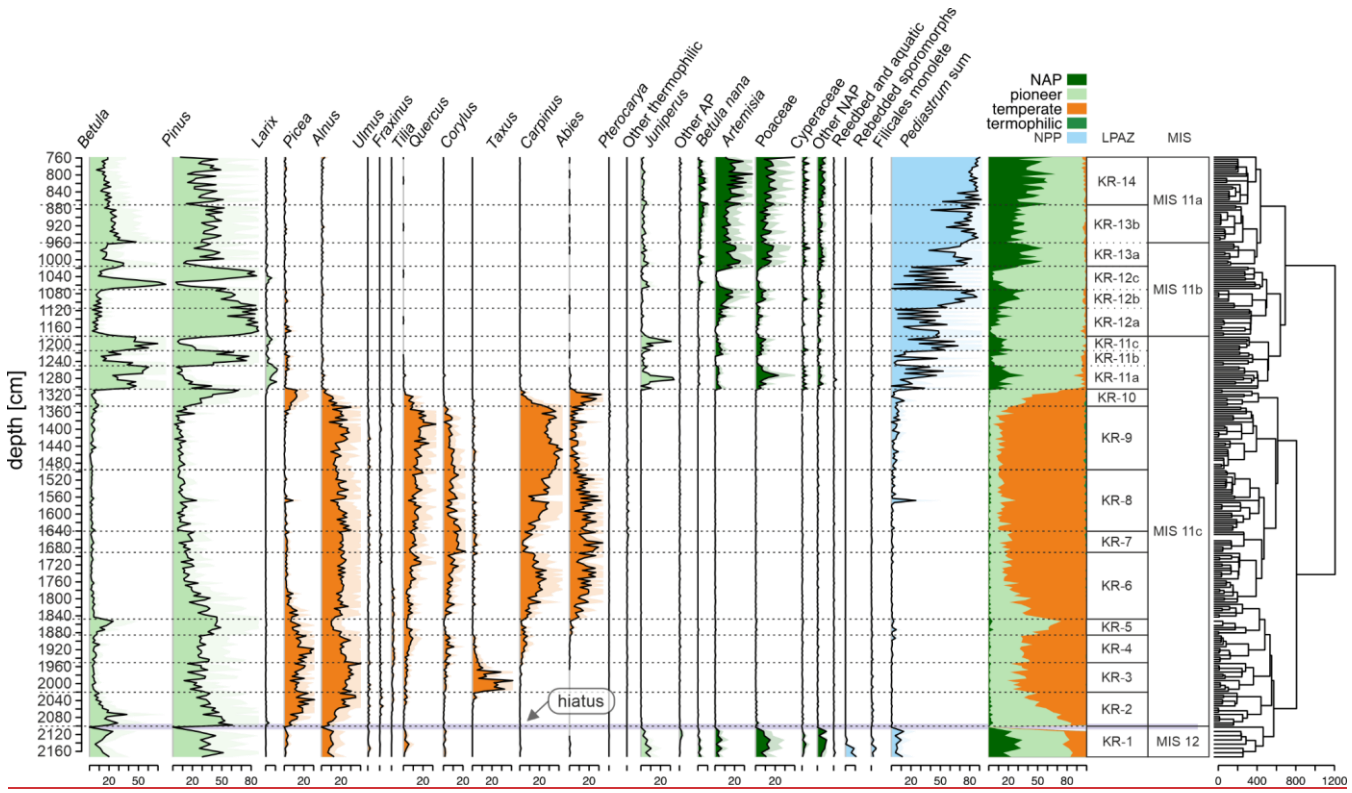



**Figure 23: Percentage diagram of selected pollen, spore, and algal taxa form the Krępa 2015 sediment site core on depth scale (cm) with zonation of the diagram.**

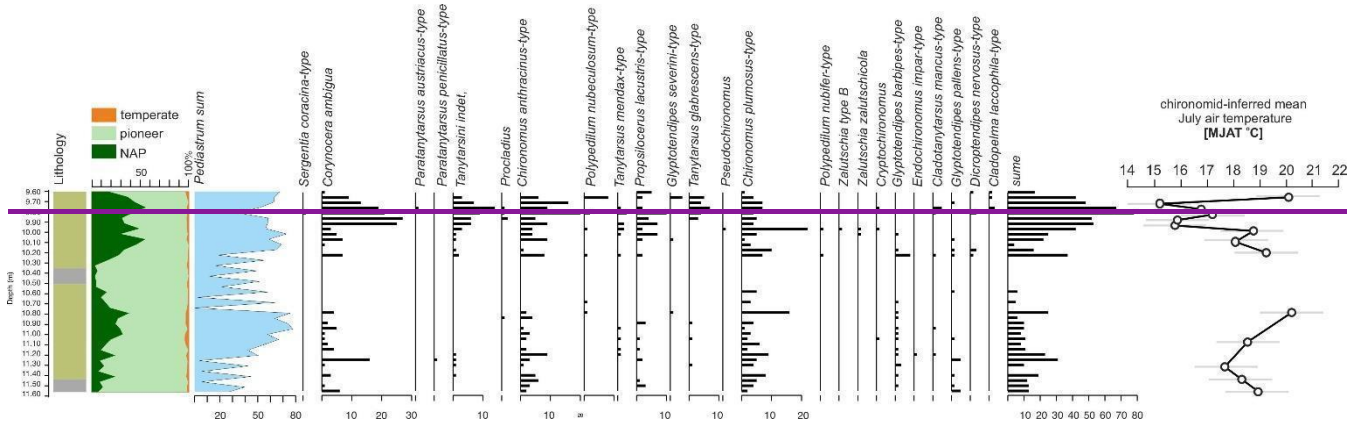
### 3.43 Summer July air temperature reconstruction based on Chironomidae assemblages from the Krępa site

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 stadial (Table 12). In LPAZ KR-12a (1122.5-1187.5 cm), 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 (1072.5-1122.5 cm). Summer temperatures remained at this level throughout in LPAZ KR-12c (1022.5-1072.5 cm) before significantly dropping to 15-17 °C in the middle of LPAZ KR-13a (967.5-1022.5 cm). Only at the end of LPAZ KR-13a (967.5-1022,5 cm), which is equivalent to the transition to the following interstadial that most likely corresponds to MIS 11a interstadial, summer temperatures markedly increased again to about 20 °C.

**Table 2~~1~~: ~~Chironomid-based summer a~~Air temperature reconstruction from Chironomidae preserved in the Krępa sediments~~site~~ with reconstructed mean July air temperature ($T_{jul\text{-}Ch}$~~jul~~), error of the estimated $T_{jul\text{-}Ch}$~~jul~~, minimum dissimilarity between the chironomid assemblage in the Krępa sediments ~~core and~~ training set samples (MinDC), principal component analysis values (PCA) and corresponding LPAZ**

| Core depth (cm) | $T_{jul\text{-}Ch}$ | error of est. ($T_{jul\text{-}Ch}$) | 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~~TS~~ reconstruction, 10~~3~~ samples with good modern analogues remain below the 5 % percentile threshold (minDC), while 3~~2~~ samples with average modern analogues have values above the 5 % percentile threshold ~~(68.5053 < minDC > 9.7531).~~ (6.08105 < minDC > 9.82830). PCA values range between ~ –1.92 and 6.59 (Tab. 1).



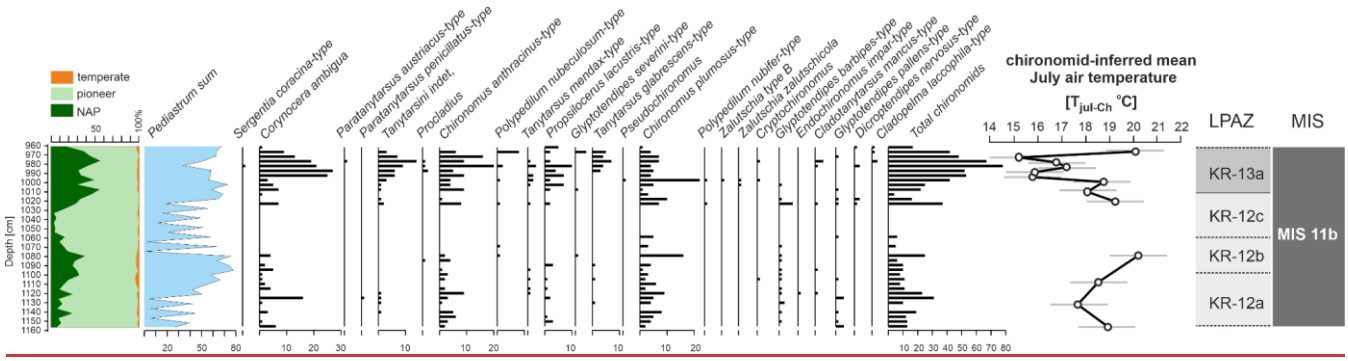



**Figure 3~~3~~4: Chironomid-inferred mean July temperature reconstruction from Krępa ~~site~~ with stratigraphic diagram of the Chironomidae assemblages~~-~~. Caption: Chironomidae species are presented as counted numbers of specimens. Grey bars in the $T_{jul\text{-}Ch}$ curve indicate error range.**

## 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 $T_{jul}$ 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.

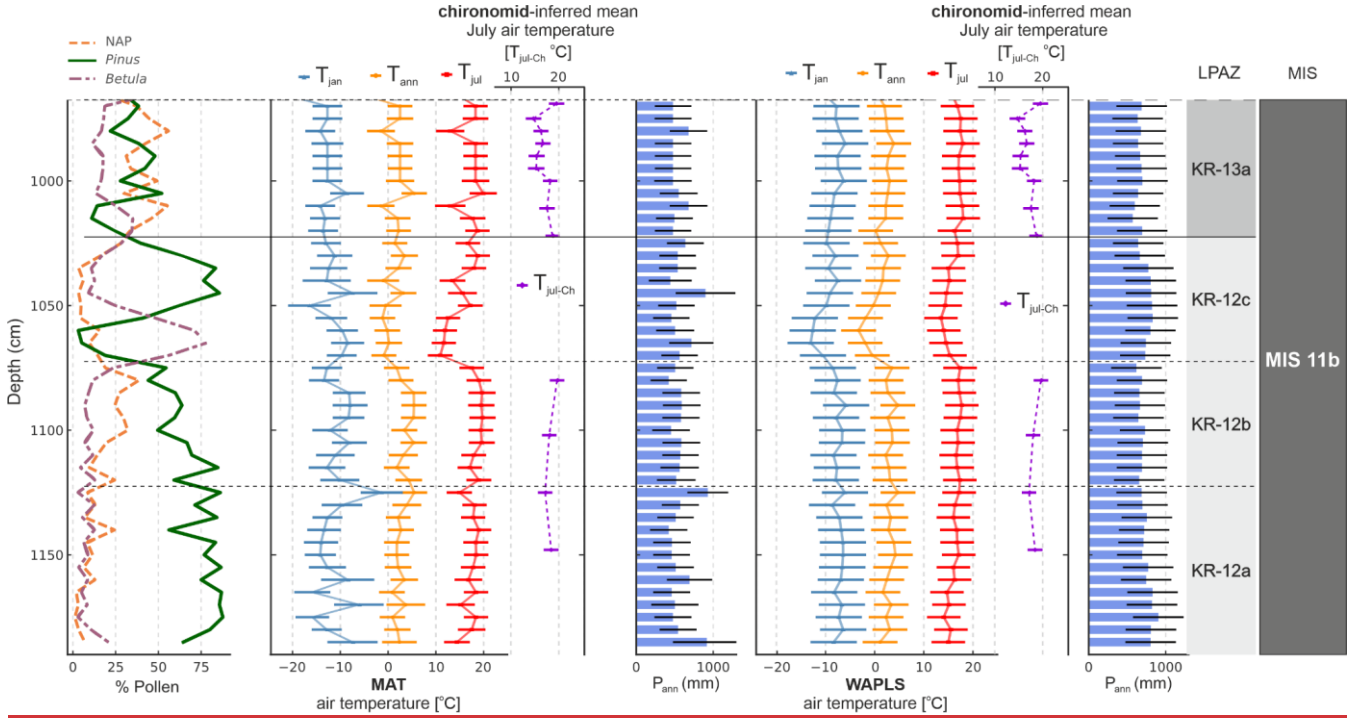



**Figure 4: Pollen-based reconstructions of mean July air temperature ($T_{jul}$), mean annual temperature ($T_{ann}$), mean January air temperature ($T_{jan}$), and annual precipitation sum ($P_{ann}$) for the Krępa site using MAT and WA-PLS. Error bars indicate the standard error of prediction (SEP). The chironomid-based $T_{jul-Ch}$ 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, ~~They~~ 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~~, because~~ they can extend the duration of the larval stage depending on environmental conditions (Butler, 1982). Because~~Thanks to the ability~~ of the excellent preservation of their larvae's head capsules ~~to preserve~~ in ~~the~~ lake and peat bog sediments for several hundreds of thousands of years, the analysis of their subfossil remains offers the~~it is~~ possibility~~le~~ to reconstruct ~~the diversity of the~~ environmental and climatic changes in the past~~ centuries.~~., ~~On the basis of Chironomidae, it is possible to~~ quantitatively reconstructions of the average July air ~~palaeo~~temperature~~ quantitatively,~~ and the trophic state~~y~~ of the inhabited water body~~,~~ as well as ~~and qualitatively~~ the type and dynamics of the lake, the water pH, and microhabitats. Furthermore, t~~T~~raining sets ~~were~~ are also ~~created~~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~~ (Krzeminski and Jarzembowski, 1999). The~~ processes taking place on Earth in the past were~~had~~ the same ~~course~~ as today (Krzeminski and Jarzembowski, 1999). This, for example, allows~~ makes it possible~~ to reconstruct ~~the~~ temperature based on fossil~~the~~ Chironomidae *assemblages by assuming*~~. In palaeoreconstructions, it is assumed~~ that a given species ~~from the Chironomidae family~~ still has the same habitat requirements as thousands or hundreds of thousands ~~of~~ years ago. The oldest recorded c~~C~~hironomid remains date back to the Late Triassic, i.e. ~200~~202 ±~~ 1 Ma BP (Krzeminski and Jarzembowski, 1999). Data from the MIS 11 Kręp~~a~~ sediments indicate~~sediments and preliminary observations from the Holstein Interglacial site of Ossówka (Fig. 1), indicate~~ a large~~big~~ difference in the number and state of preservation of the chironomid remains compared to Holocene sites. ~~The worst condition of the remains was in the sediments from the Ossówka site.~~ In general, ~~a~~~~A number of~~ at least 50 individuals per sample are ~~is~~ required for robust~~to create a~~ reconstructions of the average July temperature. As~~With a~~ smaller numbers~~amount~~ of identified head capsules considerably increase the~~increase, the~~ error range of the air temperature reconstruction~~ is larger, therefore the higher the number of counts, the more stable the result. With a small number of head capsules~~, it is commonly recommended to combine~~smooth the reconstruction of temperatures down the core, i.e. to combine~~ adjacent samples in case of low head capsule amounts (Heiri and Lotter, 2001). To~~In order to~~ enable~~be able to~~ selection of ~~subsequent~~ sites that could potentially yield chironomid-based ~~have the potential to reconstruct the~~ palaeoenvironmental reconstructions, it is therefore critical to~~worth~~ analyse~~ing~~ the factors that could limit the degree of preservation ~~of the remains~~ or cause the disappearance or decrease in the number of individuals. ~~Paleolake Krępa is a site that provides reliable and credible reconstructions in the late Vistulian. However, the question remains why the older sediment does not allow to obtain quantitative and qualitative results from the analysis of subfossil Chironomidae. In order to get closer to the answer, we analyse situations that are rarely discussed in the literature, i.e. the absence, disappearance or sudden decline of HC amount~~Chironomidae in the sediment.~~ .~~The most difficult conditions in which various species of Chironomidae occur has also been analysed. The aim is to determine the conditions that could differ from those still accepted today by the Chironomidae community.~~

Chironomidae inhabit all moist or aquatic habitats from moist wood to the ocean, between the tropics and~~ranging from the tropic climate zone to~~ the Arctic~~ climate zone~~. The high specialisation of individual species is thereby decisive for their~~of Chironomidae decided about such a~~ common occurrence and their ability to survive even under difficult environmental conditions. Among the features that allow~~ed~~ the family to succeed are: a short life cycle (in some cases only 8 days) (Reyes-Maldonado et al., 2021), osmoregulation that enables~~ing~~ survival in high~~ of high~~ salinity ~~of the~~ waters ~~body~~ (Kokkinn, 1986) or parthenogenesis that implies a ~~giving~~ 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~~ and the ability to repair the genome, which reduces the accumulation of harmful mutations~~ (Gusev et al., 2010; Cornette et al., 2015). Some species ~~of Chironomidae~~ are able to change ~~the~~ food resources ~~they use~~ depending on the~~ir~~ 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, ~~and~~ thus being characterised by a larger biodiversity~~larger more biodiversity~~ of Chironomidae (Allen et al., 1999; Heino, 2000; Tarr et al., 2005).~~,~~ and (2) are~~lakes~~~~and they 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~~Isolated, highly remote habitats from each other reduce species diversity in a single lake and disperse species between lakes~~ (Roberts, 2003).~~Large lakes like Krępa have a greater variety of habitats and thus more diverse communities of Chironomidae (Allen et al., 1999; Heino, 2000; Tarr et al., 2005), attract a more migratory population (J. Baber et al., 2004; Tarr et al., 2005) and they are more resilient to extreme droughts and other extreme events. Isolated, highly remote habitats reduce species diversity and dispersal (Roberts, 2003).~~

Despite the specialisation of chironomids~~Chironomidae~~, 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~~.~~ e~~E~~ach life stage ~~of the Chironomidae~~ 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~~have their~~ temperature maxima and minima, beyond which the given processes no longer take place. M~~In sub-zero temperatures, when the tank freezes, m~~ost groups can tolerate low sub-zero temperatures;~~.~~ t~~T~~he 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 ~~the~~ highest in the Orthocladinae family and ~~the~~ 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).

~~Some species stop eating and empty their intestines for the winter. There are larvae in which feeding continues, and the temperature only affects the occurrence of pupation. There are species (e.g. *Einfeldia synchrona* type) that burrow deeper in winter, penetrating deeper layers of silt. Early developmental stages of larvae often do not occur in winter. Another protective mechanism against freezing is the production of cocoons or sealing the tube (Danks, 1971).~~

~~Another factor strongly limiting the number of midges~~Chironomidae ~~is low - acidic pH. Below 6.0, most Chironomidae taxa are eliminated and replaced by Chaboridae and Ceratpogonidae (Henriksen et al., 1982; Walker et al., 1985; Walker, 2001; Brooks et al., 2007). Only a few species can withstand pH as low as 1.4, such as *Chironomus sulfurosus* type, *Chironomus acerbiphilus* type or *Polypedilum tamanigrum* type (Takagi et al., 2005; Doi et al., 2007).~~

Another important~~The~~ factor causing the decline of Chironomidae~~the~~ population~~s~~ is the lack of oxygen in the water, although this cannot be directly captured by~~. However, it is not possible to see this in~~ palaeoreconstruction~~s~~. Instead, low-oxygen conditions are in general only ~~The only thing that can~~ indicate~~d by the abundant~~ occurrence ~~of in the palaeo-record are remains and a large accumulation~~ organic matter ~~in the sediments~~. Such~~An~~ increase~~s~~ in organic matter commonly~~can~~ increase ~~the amount of~~ bacterial respiration~~,~~ and cause in consequence an~~ing~~ oxygen deficiency in the profundal of water bodies~~deep zone~~ (Charlton, 1980; Matzinger et al., 2010; Müller et al., 2012). ~~One of the species resistant to oxygen deficiency is, for example, *Sergentia coracina* type, which disappears after the concentration decreases to the level of 2.7 mg L-1 (Quinlan and Smol, 2001) and <4 mg L-1 (Luoto and Salonen, 2010). Oxygen deficiency can also be caused by freezing of the lake, as a result of which it is cut off from atmospheric oxygen (Pechlaner, 1966; Welch, 1991). Also, freezing can reduce the amount of calcite and the manganese to iron ratio, which may indicate an increase in decomposition processes at the bottom of the water body (Koinig et al., 2003). These changes may be caused by bathymetrymorphological factors (Aeschbach-Hertig et al., 1999) and thermal stratification (Jankowski et al., 2006) or the supply of biogenic elements: nitrogen and phosphorus (Rabalais et al., 2010; Frossard et al., 2013; Belle et al., 2016).~~

~~The abundance of midges~~Chironomidae ~~and their dispersal is limited by the poor ability to select a flight site and lay eggs. The Chironomidae larvae~~larva ~~only has the ability to disperse around the lake bottom and select the substrate for life. This dispersal is often done passively by water currents, by phototaxis or by the ability to feed on plankton. Chironomidae larvae have the ability to rheotaxis, which allows for quick and effective colonisation of environments (Davies, 1976).~~

Another factor limiting the preservation of chironomid ~~behaviour of Chironomidae~~ head capsules in ~~the~~ sediment~~s~~ are mechanical factors that cause damage to the head capsule~~s~~. For example, Tanypodinae remains are, due to their large size, ~~are~~ 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. ~~It is also debated how resistant the head capsule arising from the periodic shedding of the Chironomidae exoskeleton produced by ecdysis and the larvae that are buried and tanning in the sediment (Walker, 1987).~~ The preservation of~~Only~~ remains from the 3rd and 4th larval stages only~~are preserved in the sediments. This~~ is most likely related~~due~~ to the increased amount of chitin in these developmental stages, ~~which~~ make~~ings~~ ~~the~~ remains of these stages more resistant to ~~further~~ disintegration. ~~The capsules preserved in the sediment come from the habitats of living larvae (Iovino, 1975).~~ The remains of Chironomidae may also not be preserved if~~in the sediment because of~~there ~~was a low~~ accumulation rate is low and remains of species~~, while those~~ from ~~the~~ shore habitats could be poorly preserved. However, ~~most~~ studies confirm a~~the~~ 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 ~~being~~can be overrepresented compared to bivoltine species, however, it is difficult to determine whether changes in species composition correspond with voltinism (Tokeshi, 1995).

~~The physicochemical parameters~~properties of water are also a factor causing changes in chironomid communities. For example, a reduction in the number of chironomids may be caused by floods and heavy rainfall. Floods cause for example pollution, surface runoff, lowering of pH and/or instability and rolling of the substrate (Teristiandi, 2021). A decrease in the water level also leads to the disappearance of chironomid larvae ~~with subsequent~~with a subsequent changes in the groupings from lacustrine to semi-terrestrial and terrestrial communities (Płóciennik et al., 2015, 2020), and d~~D~~roughts may cause the ~~vanishing~~extinction of larvae (Buck, 1965; Berglund and Digerfeldt, 1970; Delettre, 1988; Jackson and Mclachlan, 1991; Rohrig et al., 2004). The chemical ~~parameters~~properties of water, such as increased concentrations of aluminium and other metals (Bitusik and Kubovcik, 2000), or Fe, NH4+ compounds also have an impact on chironomid communities (De Haas et al., 2006). A less significant impact is also reported for interspecific and intraspecific competition and predation (Davis et al., 2003; Roberts, 2003) or fish predation (Goyke and Hershey, 1992; Rieradevall and Roca, 1995; Mousavi et al., 2003; Milardi et al., 2016; Sayer et al., 2016).

The main factor influencing the preservation of Chironomidae~~the~~ remains is the content of CaCO3~~CaCO3 in the soil and the bottom of the water body~~, especially in moderately~~medium~~ 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 mineralis~~z~~ation occurs, the better the preservation of the remains (Briggs and Kear, 1993; Park, 1995). ~~Moist and anaerobic environments such as ditches, peat bogs or lakes in cold climate or desert conditions are more favourable for the preservation of chitinous remains (Speight, 1974; Huchet, 2014).This might partly explain the highest abundance of chironomid head capsules during the cool summer period at Krępa (975-995 cm depth) and lower abundance during warmer summer periods. Clay sediments favour better preservation than hydrated sediments or aquatic environments. Clay has tanning properties, catalyses the cross linking of proteins and also protects the remains from bacterial degradation.Moist and anaerobic environments such as ditches, peat bogs or waters at cold or desert conditions are more favourable (Speight, 1974; Huchet, 2014). Clay is a better environment for preserving remains than water. Clay has tanning characteristicsproperties, catalyses the cross linking of proteins. It also protects the remains from bacterial degradation. Kaolinites are a component conducive to the preservation of remains, they can facilitate preservation and accelerate mineralis~~z~~ation. Mineralis~~z~~ation is also favoured by the fine grain size of the sludge, the solubility of its components in organic acids with hypoxia or low dissolved oxygen, and the content of minerals: Fe, Al or Cr (Naimark et al., 2016). The main factors of decay are physical factors (such as pressure) or biological factors including bacteria and fungi (Speight, 1974; Huchet, 2014).~~

~~In our preliminary tests, we did not use chemicals and we soaked the samples for a long time to eliminate as much mechanical damage to the head capsules as possible during the sieving of the samples. Nevertheless, from some samplessites, whole head capsules have not been preserved, which could have been caused by high pressure and compression of the sediment. A small number of head capsules may be a difficulty at the stage of material. This necessitates summing up the samples and increasing~~

~~the volume of the analyzsed samples (some of the samples were even 20 cm3 in volume). Difficulties arising at the preparation stage also include the lack of continuity in the occurrence of Chironomidae and their low frequency in the sediment.~~

~~The~~ Further factors~~Ffactors~~ reducing the abundance of chironomids are~~:~~ extreme temperatures, low nutrient levels~~, adverse geomorphology, or following large storm events~~, acidic waters~~, pH, or~~ high Se concentrations (Del Wayne et al., 2018; Mousavi, 2002) ~~Gresens et al., 2007;~~. ~~T~~The content of hydrogen sulphide during holomixis~~, above 0.3 ppm, may also contribute to the death of Chironomidae. They~~Chironomidae do not occur, as well as ~~during~~ paludification of~~in~~ 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, ~~C~~chitin usually does not accumulate in anaerobic sediments because it is more easily broken down by ~~Fibro~~bacteria~~. Chitin was~~ effectively mineraliz~~z~~singed it into CH4 and CO2 (Wörner and Pester, 2019). ~~In the researched core, we have interruptions in the preservation of the head capsules. The sediment indicates that the lake was functioningfunctionaingl, but Chironomidae head capsules are not recorded. Based on the literature and our results, we are currently only able to exclude factors that do not affect the degree of preservation of the Chironomidae heads. In fact, in some periods, no parts of Chironomidae or chitinous insect parts or subfossilsmacroremains were visible in the samples, suggesting a lack of preservation of the remains. One of the hypotheses could be that chitin was mineralizsed from the head capsule and changed the contain of carbon in the sediment. It is especially possible with the lack of cellulose remains of plants too. However, further extended research on Pleistocene sediments is needed to discover which environmental factor caused the lack of capsules.~~

~~Based on our species, it is difficult to determine the factors that limited them.~~ Chironomid~~These are~~ species found in the Krępa sediments ~~core~~ have a~~with 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. ~~Additionally, in science it is customary not to describe a zero result. Such a result is often omitted as irrelevant to the study or a fragment of the analysis is excluded. In the context of ecology, however, it seems very important.~~ As there are obviously only very~~Based on the above descriptions, we can conclude that there are~~ few habitats where no invertebrates occur~~,~~ the absence of chironomid remains during most of the Holsteinian Interglacial might be best explained by ~~The history of our sediment indicates their absence or lack of record.~~ 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~~this phenomenon requires~~ further research as well as a~~and~~ comparison of~~ng~~ our results with other lake sediments that lack~~sites with disappearing~~ chitinous remains.

### 4.1.2 Chironomid-inferred reconstructions from the Krępa site in relation to pollen-based reconstructions~~Summer temperature and ecological reconstructions based on cChironomids from the Krępa site in relation to environmental change~~

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~~July~~ 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~~before increasing again~~ to about 20 °C at the top of LPAZ KR-13a~~,~~ possibly reflect~~sing~~ 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).~~These data indicate that summer temperature maximum during the post-Holsteinian period was even slightly higher than indicated in the Polish training set (17–20°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~~those~~ periods differ - MIS 11 was~~is~~ characterised by two insolation maxima, ~~whereas~~ while there was only~~is~~ one (though~~but~~ more distinct) during the Holocene~~latter period~~ (Rohling et al., 2010). In fact, summer temperature increase during MIS 11b might be explained by increasing insolation ~~rate~~ at that~~the~~ time.

In general, Chironomidae remains in the Krępa sediments ~~core~~ occur mostly during cool periods while they are absent during warm periods. For example, in the interglacial part of the sediment record~~profile~~ isolated remains were~~can~~ only found~~only be found~~ in LPAZ KR-4, which~~ that~~ precedes the OHO, and in LPAZ KR-7, which~~ that~~ corresponds to the YHO. In contrast,~~The most abundant~~ Chironomidae were most abundant in~~record is present in the part relating to~~ LPAZ KR-12, which~~.~~ ~~This zone~~ is thought to roughly correspond to MIS 11b, ~~which is considered~~ the first cold~~er~~ phase after the Holsteinian Interglacial~~of MIS 11~~ (Imbrie et al., 1984; Fawcett et al., 2011).~~ encompassing the transition into the glacial period that corresponds to MIS 10~~. ~~The pollen record during LPAZ KR-12a suggests the presence of a *Pinus* dominated forest, possibly still with a small admixture of *Picea*, which might indicate more humid conditions, but not necessarily a warmer climate (Caudullo et al., 2016).~~ ~~CIn the pollen record, cold periods like LPAZ KR-12b and KR-13a are characterizsed by rapid increases in NAP, which suggests the decline of forests. The *Pediastrum* remains, especially abundant during these cold phases, were identified as *P. kawraiskyi*, a species which, according to Jankovská and Komárek (2000), usually dominates the algal communities found in the cool phases of the Pleistocene, Late Glacial, and Early Holocene in Europe (Jankovská and Komárek, 2000). The Krępa palaeolake during LPAZ KR-12b was possibly an oligotrophic lake surrounded by open vegetation. Considering the dominance of herbs and dwarf shrubs in the pollen spectrum, the limiting factor for the development of forest communities was more likely connected to low winter temperatures as summer temperatures were still relatively high.~~

~~LPAZ KR-12c begins with the formation of pioneer *Betula-Larix* forests. Initially, the forests were sparse and shrub-tundra communities were still present in the area as indicated by *Juniperus* and *Betula nana* pollen. In the following, v~~Vegetation ~~gradually changed into dense *Pinus* dominated forests~~ over time~~. Chironomidae are absent during this interval, in agreement~~

~~with our observation that their presence is rather restricted to colder periods. They only re-appear during the final stage of MIS 11b, which is represented by LPAZ KR-13a. The apparently rather gradual cooling during LPAZ KR-13a possibly still enabled the presence of sparse *Betula* forests at the beginning of the phase. This is in agreement with reconstructed summer temperatures of about 19°C, similar to the end of LPAZ KR-12b. The following rapid cooling is reflected by the dominance of NAP in LPAZ KR-13a after the decline of *Betula*. Summer temperatures during this period reached only 15°C, but the limiting factor for vegetation development were most likely~~still remained the winter temperatures~~, which we can conclude from pollen analysis. The re-increase in chironomid-based summer temperatures at~~At the end of LPAZ KR-13a, another increase in temperature is observed, which might reflect~~be connected to the warming at the onset of the following interstadial, ~~corresponding~~being equivalent to MIS 11a. ~~The presence of Betula and Pinus pollen during MIS 11a is most likely related to long-distance transport (Hjelmroos, 1991; Jankovská, 2006) rather than reflecting local tree populations. Consequently, the pollen record cannot be regarded as a reliable indicator of temperature changes during this interval.As the pollen record during stadials is mostly controlled by wind-pollinated overproducers such as Poaceae and the long-distance transport of tree pollen (mostly *Pinus*), it is unfortunately not possible to directly connect temperature changes to the occurrence of specific plant taxa.~~ ~~Most~~To date, studies using~~based on climate reconstruction based on~~ subfossil Chironomidae to reconstruct past climate conditions mainly focused on ~~concern~~ the Weichselian Late Glacial and the Holocene (Gandouin et al., 2016; Nazarova et al., 2018; Druzhinina et al., 2020)~~. This results in a lack of similar time ranges of reconstructions, the results of which could be compared with those from the Krępa site.In general, the results from Krępa are really difficult to compare because chironomid-based temperature reconstructions from Europe are so far mostly restricted to 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~~but so far~~ none for the MIS 11 complex. In general~~However~~, chironomid~~these~~ records from other sites and time intervals are characterised by a higher abundance and species diversity of Chironomidae, while at Krępa Chironomidae~~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~~of~~ the Eemian Interglacial, when the site was surrounded by wet grass-sedge shrub tundra~~, while Chironomidae were absent during the warm~~ 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 ~~available~~ for the post-Holsteinian, a general comparison of temperature levels during this interval seems feasible. For example, pollen analyses on marine sediments from the~~It is worth mentioning that a few palaeotemperature reconstructions based on proxies has been conducted, e.g. in SW Europe -~~ Iberian margin ~~(Oliveira et al., 2016). Pollen analysis from this site~~ show~~s~~ similar climatic and ecological patterns for MIS 11b as observed at~~in~~ Krępa namely repeated~~site –~~ forest decline events. These were paralleled by reductions in sea surface temperatures, although ~~and relatively high~~ temperature~~s~~ 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)~~ levels~~. 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~~This also seems to be confirmed by~~ palynological data from ~~the SE Europe site –~~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).~~Convergence of data from different parts of the continent increases potential plausibility of palaereconstruction from Krępa.~~

## 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.

~~The reconstruction from the available section has mainly good modern analogues, which means that Chironomidae are a good proxy for temperature reconstruction also for the Pleistocene epoch. They are an environmental indicator. There is a great need for further research to better understand the factors limiting the functioning and preservation of head capsulesChironomidae in the Pleistocene. Up t~~To date, the vast majority of ~~palaeoenvironmental~~ 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 Holocen~~eian~~. 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.

~~Further study of chironomidsChironomidae from the Pleistocene will enable tracing climate changes without human influence. This will allow learning about the natural processes of global warming, the factors causing them, and the variability and specialisation of species.~~

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.~~To summarisze our results, the subfossil remains occur with higher concentrationabundantly only in non-calcareous gyttja – while investigating Holocene sites, it can be found in most lake sediment types. In contrast to Holocene sediment records, which are usually characterised by a high abundance and diversity of Chironomidae (Engels et al., 2020), the Holsteinian Interglacial sediments from Krępa reveal only a low number of individualsChironomidae, while they are more abundant/better preserved during the transition into the following glacial period.~~

**Financial support**

The research was funded by the National Science Centre project, "Novel multi-proxy approaches for synchronisz~~z~~ation of European palaeoclimate records from the Holstein interglacial". Project no. 2019/34/E/ST10/00275.

**Authors contribution**

TP ~~analyszed the cChironomid data,~~ proposed the idea of the main text, ~~constructed the manuscript,~~ and contributed to the figures. TP~~,~~ ~~and~~ AGr and AG wrote the original draft version of the manuscript. BK performed the c~~C~~hironomid-inferred summer temperature reconstruction. AG performed the pollen-inferred climate reconstructions. MŻ collected and described

the core in the field. ~~TP, AGr,~~ AG, ~~AH, SL,~~ and MS analy~~sz~~ed the pollen ~~and chironomid~~ data. ~~TP, AGr and MS analysed the chironomid data.~~ TP, AGr, AG, MB~~,~~ ~~and~~ MS did the visuali~~sz~~ations (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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