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Insight into the vegetation development of the Karkonosze Mountains (southwestern Poland) during the Late Vistulian and Holocene, based on data from glacial lakes

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ABSTRACT. New palaeoecological records from two glacial lakes (the Mały Staw – 1183 m a.s.l. and the Wielki Staw – 1225 m a.s.l.) from the Polish Western Sudetes were obtained with the aim of better understanding the long-term vegetation development, the relationship between postglacial migration patterns, climate changes and human interference in mountainous areas, as well as to verify the local survival of some cold-adapted species during the Holocene maximum warming.

Vegetation changes were reconstructed using pollen, spores and macrofossils. Several major stages of plant cover evolution over the last 12 000 years were identified. The end of the Late Vistulian (~12 100–11 700 cal BP) was documented for the first time in lake sediments from the region. During this period, the local vegetation was characterized by cold alpine meadows and patches of communities with shrubs (*Betula nana*, *Alnus viridis*, *Salix*, *Juniperus*, *Ephedra*) and trees growing at some distance from the lakes. In the Early Holocene, the expansion of boreal forests, consisting of *Betula*, *Pinus sylvestris*, as well as continental *Larix* and *Pinus cembra*, reached an altitude of ~1180 m a.s.l. An important discovery was the presence of *Larix* macrofossils in both studied profiles, which together with pollen evidence, confirmed its local persistence from the Early Holocene to the Middle Ages. It was also demonstrtaed that *Betula nana*, *Selaginella selaginoides*, *Huperzia selago* most probably persisted in the area from the Younger Dryas to at least the Middle Ages or even to the modern times, surviving through the Holocene climatic optimum.

The increase in grassland representatives from ~4100 cal BP and the appearance of the cultivated plants (*Triticum* type pollen) from ~3300 cal BP, was due to the long-distance transport of pollen reflecting the development of agriculture and settlement outside the Karkonosze Mountains. It was not until the 10th century AD that the environment underwent a stronger anthropogenic transformation. Growing economic activities (e.g. metallurgy, mining of non-ferrous metal ores, glass production, forest industry) that developed, especially from the 12th century onwards required the supply of wood raw material. The development of agriculture in the region promoted the expansion of meadows and pastures and the greatest taxonomic diversity of herbaceous plants was recorded between the 13th and 15th centuries.

KEYWORDS: glacial lakes, vegetation history, pollen analysis, macrofossils, Holocene, *Larix*, Sudetes

INTRODUCTION

The Karkonosze Mountains (the Czech name: Krkonoše Mts; other name: the Giant Mts), are part of the Sudetes (Fig. 1A, B) and, at the same time, represent the Hercynian Mountains in Central Europe, where the migration routes of plant taxa from different directions (mostly originating in the Alps or the Carpathians) intersect. Mráz and Ronikier (2016),

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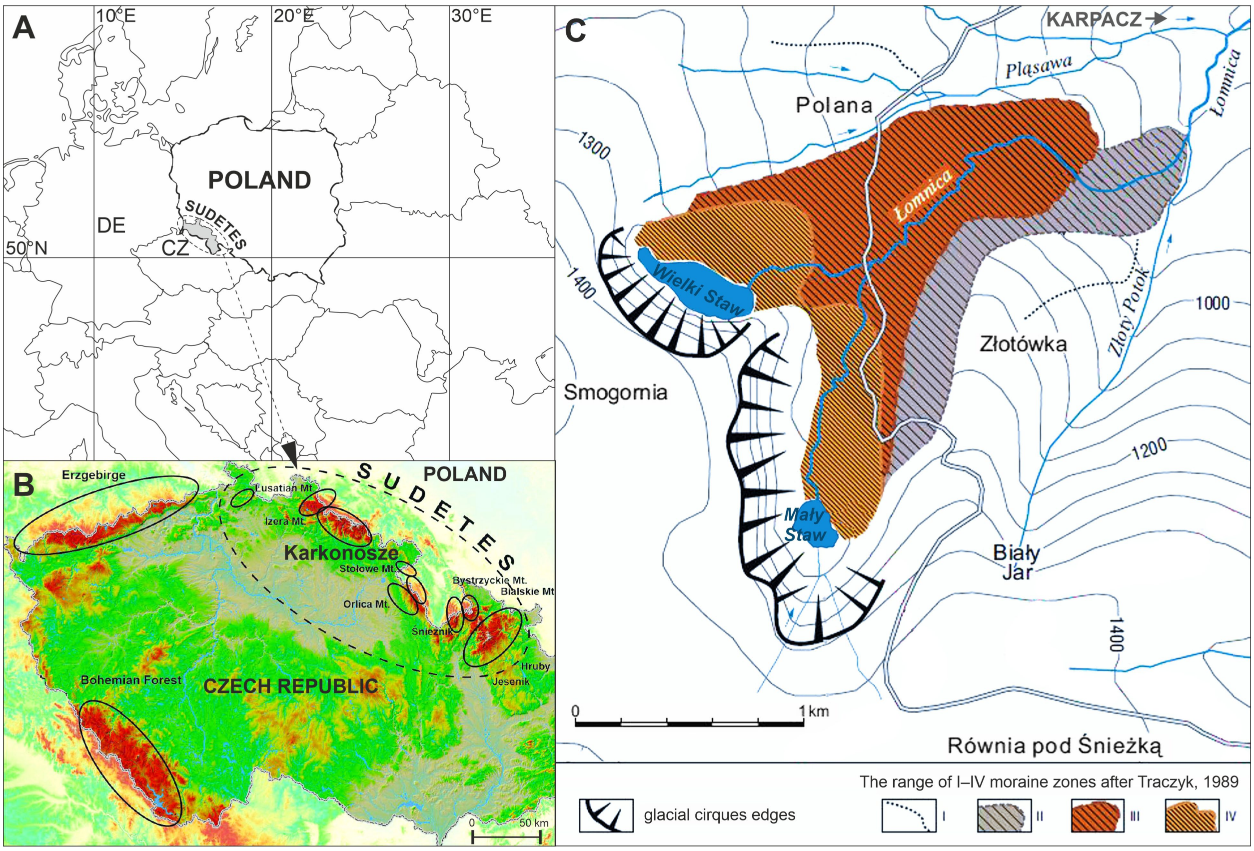

Figure 1. Location of the study area; **A**. Location of the Sudetes in Central Europe; **B**. Distribution of the Sudeten montane ranges, including the Karkonosze, about the Erzgebrige and Bohemian Forest ranges (acc. to Urbaniak and Kwiatkowski, 2023, simplified); **C**. Location of lakes Mały Staw and Wielki Staw in the Łomnica Valley (acc. to Traczyk and Woronko, 2010, simplified)

summarising the state of research, pointed out that because the mountain biota of the Western Carpathians and that of the Sudetes had a physical relationship during glacial periods, and the Sudetes were strongly affected during glaciations, the existing populations there often originated from the Carpathians. Therefore, provides an opportunity to address questions related to the biogeography of this part of Europe. In addition, the Karkonosze Mts are characterized by the occurrence of the large forest-free areas throughout the Holocene which represent the only alpine islands between the Scandes, the Alps and the Western Carpathians, northernmost in Central Europe (Jenik, 1998; Treml et al., 2006). This implies their crucial importance for reconstructing the post glacial history of e.g. alpine grasslands, as well as for verifying the status of taxa as glacial relicts. More recently, Urbaniak and Kwiatkowski (2023) summarized the current state of knowledge and pointed out the great potential of the Hercynian Mts area for evolutionary research. Palaeobotanical studies of sediment deposited in glacial lakes and peat bogs provide an important data supporting the phyto- and phylogeographic research. They allow to reconstruct the spatial-temporal changes of vegetation cover from the end of the last glacial up to the modern times. Among other things, they provide arguments for a better understanding of the natural and anthropogenic processes that shaped past vegetation and distribution ranges of plants. Palaeobotanical data document the timing and directions of re-colonisation of the area by woody taxa after deglaciation. Also of interest are the changes in the course of the treeline ecotone, forming the lower limit of the alpine area, which is generally dependent on climate but in the Late Holocene shaped also by human impacts, such as pasturing or intentional burning. In the Sudetes, the first possible human impacts were recorded in the Iron Age, but transformation started mostly during the High Medieval period (since AD 1300) (e.g. Treml and Banaš, 2000; Treml et al., 2006, 2008; Novák et al., 2010).

As the glacial mountain lakes are not common either in the area of the Karkonosze Mts or in all the Sudetes Mts, it is important to study these valuable sources of palaeoenvironmental information. Madeyska (1999) and Jankovská

(2007a) summarized the beginnings of palynological research in the Karkonosze Mts. The current knowledge concerning the issues mentioned above in the Polish Sudetes is highly incomplete. It is based mainly on the several Holocene palynological records from, e.g. Zieleniec peat bog (Madeyska, 1989, 2005), Wielki Staw Lake (Malkiewicz et al., 2016), Izerskie Bagno (Popowski, 2005), Śnieżka peatland (Fiałkiewicz-Kozieł et al., 2023), Polanica-Zdrój (Kuszel, 1988), four peatbogs from Stołowe Mts (Glina et al., 2017) and eight sites (e.g. Hala Izerska, Bagnisko) mentioned in the study of Baranowska-Kącka and Malkiewicz (2003) and also Baranowska-Kącka (2003). The small number of radiocarbon dating and generally low temporal resolution of palynological studies, as well as limited access to carpological data are the main factors limiting detailed reconstructions and supra-regional comparisons. Much more numerous are pollen records from the Czech part of the Sudetes stored in the Czech Palynological Database – PALYCZ (Kuneš et al., 2009; https://botany.natur.cuni.cz/palycz/data/). They include nearly forty sites from the three regions: the Western Sudetes (9 localities, e.g. Labský důl valley; Jankovská, 2004a, 2007b, Pančická louka mire; Hüttemann and Bortenschlager, 1987; Speranza, 2000; Speranza et al., 2000), the Bromovsko (16 localities; e.g. several sites from the Adršpašsko-teplické skály cliffs; Kuneš et al., 2007) and the Eastern Sudetes (11 localities, e.g. Vozka Skřítek, Pstruží potok, Rejvíz and Lomnice from the Hrubý Jeseník Mts; Dudová et al., 2010, 2013, 2014, 2018).

In terms of palaeoecological knowledge, there is a significant lack in Polish Sudetes compared to other mountain regions in Western and Central Europe, including not only the Alps (e.g. Garcés-Pastor et al., 2022; van Vugt et al., 2022), but also the Polish Carpathians (e.g. Ralska-Jasiewiczowa, 1980; Obidowicz, 1996, 2003; Margielewski, 2006; Buczkó et al., 2009; Obidowicz et al., 2013; Wacnik et al., 2016; Kołaczek et al., 2020, 2021), especially as regards the Late Vistulian (Vistula glaciation; Weichselian glaciation) and Early Holocene.

Here, we present combined palaeobotanical records (pollen, spores and plant macrofossil) from the new site, the Mały Staw Lake, as well as new additional data from the Wielki Staw Lake. In the case of the first site, previous palaeoecological studies have focused on fossil diatom and Cladocera assemblages, which have recorded the impact of variable climate conditions, as well as the recent anthropogenic activity on trophy and geochemistry of the lakes (Szeroczyńska, 1984, 1993, 1998a, b; Szeroczyńska and Zawisza, 2007; Sienkiewicz, 2005, 2016; Vrba et al., 2008). The second site was previously palynologically studied by M. Malkiewicz et al. (2016).

The main objectives of the study were: (i) to obtain new data on vegetation changes in the Karkonosze Mts, especially to fill the gap concerning the Late Vistulian and the transition to the Holocene; (ii) to determine the timing of immigration of forest-forming trees in the post-glacial compared to the other ranges of Sudetes; (iii) to identify human impacts on vegetation, including changes in the taxonomic richness of subalpine grasslands; (iv) to document the post-glacial history of selected cold climate adopted plants, such as *Larix*, *Pinus cembra*, *Betula nana*, *Alnus viridis*, *Selaginella selaginoides* and *Huperzia selago*, and to verify its ability to survive locally during maximum warming in the Holocene.

DESCRIPTION OF THE STUDIED REGION

GEOLOGY AND GEOMORPHOLOGY

The Polish Sudetes on the NE margin of the Bohemian Massif province comprise a complex mosaic of pre-Permian basement units, traditionally included in the Hercynids (Variscides). The Hercynian (Variscan) orogeny which spanned most of Central and South-Eastern Europe was a period of intense rock-forming movements that occurred during the Palaeozoic era, between the Late Silurian and the end of the Permian. Subsequently, the folded Hercynian mountains were eroded and during the Alpine orogeny were lifted a second time, as the so-called "log mountains". In Central Europe, the system of mountains that emerged includes e.g. the Black Forest, the Thuringian Forest, the Harz and the Bohemian Massif: with the highest part called Sudetes, the Erzgebirge (Krušné hory) and the Bohemian Forest (Šumava) (e.g. Żelaźniewicz, 1987; Aleksandrowski et al., 2000; Treml et al., 2006; Urbaniak and Kwiatkowski, 2023; Kaiser et al., 2023). They are located quite far from much larger and much higher mountain ranges, such as the Alps or Carpathians, but they also strongly differ from them in the shapes of their vegetation zones. A fragmentarily developed alpine zone occurs only in the Karkonosze Mts (Urbaniak and Kwiatkowski, 2023). The mentioned range being a part of the Western Sudetes is also the highest part of the entire Sudetes (Fig. 1B) with the highest peak Śnieżka Mt. (1602 m a.s.l.; Mazurski, 2003). The Polish part of the Karkonosze Mts has an area of only ~177 km^2, while the Czech part is much larger and covers 440 km^2. In the Czech part the highest peaks are Lučni hora Mt. (1555 m a.s.l.) and Studnični hora Mt. (1554 m a.s.l.; Kondracki, 1994, 2001).

The Polish Sudetes lie almost entirely in the Oder basin, and only a small part of the area belongs to the Elbe basin (Walczak, 1972; Kondracki, 2001). High precipitation, poorly permeable ground and steep slopes cause rapid water runoff, especially during spring snowmelt and summer rains (Czerwiński and Mazurski, 1992). The characteristic of the Karkonosze Mts is the soil zonality, conditioned by climate and morphology. Between ~900 and 1200 m a.s.l. podzolized muck soils (Histic Podzols) occur and muck-gley soils on slopes ~1100–1300 m a.s.l. (Pelišek, 1974; Adamczyk et al., 1985; Kabała, 2011; Kabała et al., 2013).

CLIMATE

The geographical location of the Sudetes causes a relatively cool and very humid mountain-type climate, with a strong influence on atmospheric masses of Atlantic origin. Based on the layer-level climate diversity index, the following can be distinguished: a moderately warm layer (below 600 m a.s.l., with an average annual temperature above 6°C), with weak dynamic activity of the air, strong spatial differentiation of temperature and precipitation; moderately cold floor (600–960 m a.s.l., with an average annual temperature of 6–4°C), frequent winds that come from the south-west and take on the character of foehns with heavy rainfall; cold floor (960–1320 m a.s.l., with an average temperature of 4–2°C), with rainfall exceeding 1200 mm per year, as well as very favourable conditions for the accumulation and maintenance of snow cover (70 to 180 days a year). The highest floor is a very cold floor, above 1320 m a.s.l., with an annual temperature below 2°C. The average annual temperature of the upper parts of the Karkonosze ranges between 0°C and +1°C. The amount of atmospheric precipitation reaches 1500 mm/year (Hess, 1968; Hess et al., 1980). On Śnieżka Mt. (1603 m a.s.l.), the growing season lasts on average 116 days (Dubicka and Głowicki, 2000).

PLANT COVER

The Karkonosze Mts according to the geobotanical classification belongs to the Central European Mountain Province and the Hercynian-Sudetic Subprovince. They are located in the Western Sudetes District and the Jizera-Karkonoski Sub-District covering the Jizera Mts, the Karkonosze Mts and the Kaczawskie Mts (Pawłowski and Zarzycki, 1977). This division was slightly modified by J.M. Matuszkiewicz (1993). The richness of the Karkonosze flora is reflected in the occurrence of species from various geographical regions in a small area, including glacial relics and endemics. These include *Sorbus sudetica*, *Pimpinella saxifraga* subsp. *rupestris*, *Campanula bohemica*, *Pedicularis sudetica*, *Saxifraga moschata* subsp. *bazaltica*, or *Galium sudeticum* (Krahulec, 2006). The list of publications by Polish and Czech scientists containing valuable information on both forest and shrub communities in the discussed area is very rich, however, in this study the main source of data are the publications of A. and W. Matuszkiewicz (1975), J. Fabiszewski (1985), J.M. Matuszkiewicz (2001) and Danielewicz et al. (2013). The current vegetation there has a zonal system. The lowest vegetation level is the foothills of the sub-montane zone, reaching up to ~500 m a.s.l., dominated by meadows and arable areas. Natural vegetation here was almost destroyed. Fragments of previously dominant oak-hornbeam forests – presumably *Galio-Carpinetum* and *Luzulo-Quercetum* communities – occur on Chojnik Mt. Small fragments of riverside mountain alder forests have been preserved along the streams. In the lower montane forest zone (500–1000 m a.s.l.), natural vegetation was replaced by spruce and larch monocultures and logging communities. Previously, the landscape here was dominated by the *Luzulo-Fagetum* community, acidic mountain beech forest. In the river valleys fragments of the fertile Sudetes beech forest *Dentario enneaphylli-Fagetum* community are preserved. In the higher parts of the lower montane zone a similar to natural lower montane fir-spruce forests *Abieeti-Piceetum* community can be found. The upper montane forest zone (1000–1250 m a.s.l.) is almost entirely covered with upper montane Sudeten spruce forest *Calamagrostio villosae-Piceetum* community. In addition to forests, there are also meadow communities. Many legally protected species can be observed there, including *Arnica montana*, *Carlina acaulis*, *Convallaria maialis*, *Crocus* sp., *Gentiana asclepiadea*, *Primula elatior* and *Streptopus amplexifolius*. The so-called upper forest limit runs at an altitude of ~1200 m a.s.l., and above it, there is the subalpine zone (1250–1450 m a.s.l.). According to Treml and Banaš (2000), the maximum elevation of the alpine timberline rans at 1370 m a.s.l. The most common community is thickets of *Pinetum mugo sudeticum*. In more fertile habitats, in well-watered areas, there are also thickets of stunted trees and deciduous shrubs with *Prunus padus* subsp. *borealis*, *Sorbus aucuparia* subsp. *glabrata*, *Betula pubescens* subsp. *carpatica* and *Ribes petraeum*. In the vicinity of springs, streams and lakes, often on peat bogs, there are clusters of *Salix lapponum*, also having an endemic and relic character. Moreover, in the subalpine zone, significant areas are covered by herb and grass communities. In the ridge parts of the Karkonosze Mts large areas are covered with *Nardus stricta*, which forms the *Carici-Nardetum* matgrass-meadows. Particularly noteworthy are the raised peat bogs, most of which are concentrated in the upper montane zone and in the lower part of the dwarf pine forest, covering ~85 ha (Tołpa, 1985). The alpine zone (1450–1602 m a.s.l.) was developed only fragmentarily on Śnieżka Mt., the ridge of Czarny Grzbiet Mt., in Śnieżne Kotły and in the highest parts of Wielki Szyszak Mt. The vegetation is of the nature of low treeless rocky grasslands and mountain rush *Carici-Festucetum airoidis*.

DESCRIPTION OF STUDIED SITES

The studied cirque lakes developed in niches deepened by the glacier flowing down the Łomnica valley (Piasecki, 1958; Traczyk and Woronko, 2010; Szarłowicz et al., 2018). Traczyk and Woronko's research (2010) confirmed previous hypotheses (Traczyk, 1989), that the valley was glaciated at least twice in the Pleistocene. At the maximum stage of glacier development, the length of the glacial tongue reached 3.5 km and the front ended at ~900–850 m a.s.l. In addition to glacial cirques also moraines were formed (Fig. 1C). It is assumed that moraine zone II was formed during the Wartanian (Odranian) glaciation (MIS 6) and moraine zones III and IV in the older and younger phases of the Vistulian (MIS 5d-2) glaciations (Traczyk and Woronko, 2010). In the case of the Mały Staw Lake, Piasecki (1958) described two phases in its development: the formation of a basin as a result of erosive glacial activity, subsequent glacier retreat and weathering of bedrock, and next refilling of the basin with ice, firn or snow. The substrate for the water basin is granite rubble impermeable to water, as it is sealed with fine material washed from the slopes. The sedimentation history of lakes was the subject of previous research (e.g. Piasecki, 1958; Wicik, 1984a, b, 1986; Szarłowicz et al., 2018 and further literature therein).

The Mały Staw Lake (50°44′57″N, 15°42′03″E) fills the largest of the glacial cauldrons in the Polish part of the Karkonosze Mts (Fig. 1C). It is located at an altitude of 1183 m a.s.l., in the upper part of the upper montane forest zone, its length is 253 m and its width is 140 m. The lake area is ~3 ha and its maximum depth is ~7 m. The glacial cauldron, whose walls rise to approximately 200 m, is filled with the Wielki Staw Lake (50°45′30″N, 15°41′40″E). This largest lake in the Karkonosze Mts lies at an altitude of 1225 m a.s.l. and has an area of 8.32 ha (length 646 m and width 138 m) and is ~25 m deep (Wicik, 1984a; Szeroczyńska, 1993; Malkiewicz et al., 2016; Szarłowicz et al., 2018).

MATERIALS AND METHODS

FIELD WORKS

The material for the palaeoecological studies was obtained in 1982 by Dr. B. Wicik and Dr. K. Więckowski of the University of Warsaw, Institute of Geography. Sediment profiles, from both the Mały Staw and Wielki Staw Lakes, were collected with a core-piston probe (constructed by K. Więckowski), during the winter season. The sampling site in both cases was selected based on a bathymetric plan (Komar, 1978). The bathymetry of the studied lakes was published e.g. by Sienkiewicz (2016) and recently by Szarłowicz et al. (2018).

The thickness of the Maly Staw Lake core is 900 cm. The coring site was selected in the central-eastern part of the lake. Lithology is described (after Wicik, 1984a, 1986) as follows: the upper 15 cm of sediment semi-liquid algal gyttja dark brown; 15–857 cm clay-detritus gyttja with interbeddings at the depths: 745–747.5 cm light-grey clay, 747.5–751 cm dark-grey organic-mineral matter, 751–751.2 cm fine-grained sand, 751.2–752 cm dark-grey organic-mineral matter, 752–757.5 cm fine-grained sand with organic detritus; 857–880 cm clay with sand; 880–900 cm sand with gravel. Additionally, at the depth of 330–720 cm, admixture of sand, gravel and plant macrofossils is present.

The thickness of the Wielki Staw Lake core (Fig. 1C) is 1100 cm. It was taken at 18.5 m below the water table. Lithology is described (after Więckowski, 2009) as follows: mineral sediments classified as clay-detritus gyttja prevail in the whole profile. At the bottom (the depth of 840–920 cm) coarse-grained sand is present. According to Malkiewicz et al. (2016), the sediment is generally rich in organic matter and the typical feature of the core is a variable micro-stratification with thin layers containing medium-coarse sand.

LABORATORY PREPARATION

Pollen analysis

Samples of 1 cm^3 in volume were taken for palynological studies discontinuously from the sediment cores. A total of 59 samples in intervals of 10–20 cm were taken from the sediment profile of the Mały Staw Lake. This site has not been investigated before. From the Wielki Staw Lake, 23 samples were selected for expert examination at 50 cm intervals. This is a completely new series of samples taken from this profile. Another series of samples was independently studied by M. Malkiewicz. The results obtained from the Wielki Staw Lake in the current study should be seen as complementary to an earlier one, which included 33 samples from the same profile, albeit from different depths (Malkiewicz et al., 2016).

To remove silica, the sediment samples were kept in boiling 40% hydrofluoric acid for 24 h. Subsequently, a modified Erdtman acetolysis method was implemented (Berglund and Ralska-Jasiewiczowa, 1986). The chemical treatment resulted in an extract of pollen grains, spores and non-pollen palynomorphs for taxonomic analysis. To determine the concentration of plant microremains in the samples, one tablet containing a known number of spores of the indicator *Lycopodium clavatum* was added to each sample before acetolysis (Stockmarr, 1971). Palynological examinations were performed by analyzing the plant microremains present on the surfaces of at least 2 slides, using a light microscope (at magnifications of ×400 and ×1000). Specialized keys and atlases (e.g. Punt, 1976; Moore et al., 1991; Reille, 1992, 1995, 1998; Beug, 2004) and a collection of comparative palynological permanent slides from the National Biodiversity Collection of Recent and Fossil Organisms at W. Szafer Institute of Botany of the Polish Academy of Sciences (KRAM herbarium) were used in the identification of sporomorphs. The percentages of individual taxa were calculated in relation the total sum consisting of the sums of pollen counts of trees and shrubs [AP], and those of dwarf shrubs and terrestrial herbaceous plants [NAP]; [AP + NAP = 100%]. The mean value of the total counts of AP is ~500 per sample while the total sum of AP + NAP is between 620 and 1530 per sample. When calculating the percentages of local taxa (aquatic plants, marsh plants, and cryptogams), the total sum was, each time, increased by the number of counts of the respective taxon [AP + NAP + local taxon =100%]. The results of the analyses are presented in the form of pollen percentage diagrams plotted in the POLPAL programme on the metrical scale. The delimitation of Local Pollen Assemblage Zones [L PAZ] was based on significant differences in taxonomic composition and percentage values of the most abundant and characteristic taxa. The ConSLink analysis was used to verify the accuracy of the delimitation of selected pollen zone boundaries. The results of the analysis were illustrated in the form of percentage pollen diagrams drawn on chronological scale and diagrams of pollen concentration plotted using the POLPAL software (Walanus and Nalepka, 1999, 2003). The estimation of changes in palynological richness was based on rarefaction analysis E (T minimal pollen sum) calculated using the application RAREF included in POLPAL (Nalepka and Walanus, 2003; http://www.adamwalanus.pl/Polpal.html; Figs 2–6, 8).

Macrofossil analyses

For the analysis of macroscopic plant remains, small amounts of sediment left over from other palaeoecological analyses were used. 74 samples from the Mały Staw Lake and 62 samples from the profile of the Wielki Staw Lake ranging from 1 to 10 cm^3 were analyzed. First, the sediment was boiled in a 10% KOH solution, it was flushed on sieves with a mesh diameter of 0.2 mm, and the plant residues were placed in a mixture of glycerin, water and ethyl alcohol (with a ratio 1:1:1), with a small addition of thymol, and then determined under the microscope. Specialized keys and atlases (Beijerinck, 1947; Katz et al., 1965; Nilsson and Hjelmquist, 1967; Berggren, 1969; Cappers et al., 2006), as well as the carpological collection of the W. Szafer Institute of Botany, PAS, Kraków, Poland were used to identify plant macrofossils. The results of the analyses (qualitative and quantitative composition of plant remains in the samples) are presented in the form of diagrams made in POLPAL.

CHRONOLOGY

From the Mały Staw Lake two radiocarbon dates were obtained using the conventional technique (Wicik, 1986). From the Wielki Staw Lake three radiocarbon dates were obtained using the AMS technique (Malkiewicz et al., 2016) and an additional two using the conventional technique (Wicik, 1986). For both pollen profiles depth-age models were constructed (Fig. 2; Table 1), using POLPAL Depth/Age (https://adamwalanus.pl/polpal_depth_age.html; https://adamwalanus.pl/2015/depthage.html), based on the IntCal20 calibration curve (Reimer et al., 2020). Although the studied lakes are nearby and their location differs in terms of altitude by several dozen meters, the models were made independently. Due to the small number of datings, precise chronology of pollen records is still lacking and the proposed chronology, especially for the Mały Staw Lake, should be treated with great caution, only as an approximation. Unless otherwise indicated in the article, calibrated ages BP are used. All dates were calibrated using CALIB 8.2 /http://calib.org/calib/calib.html.

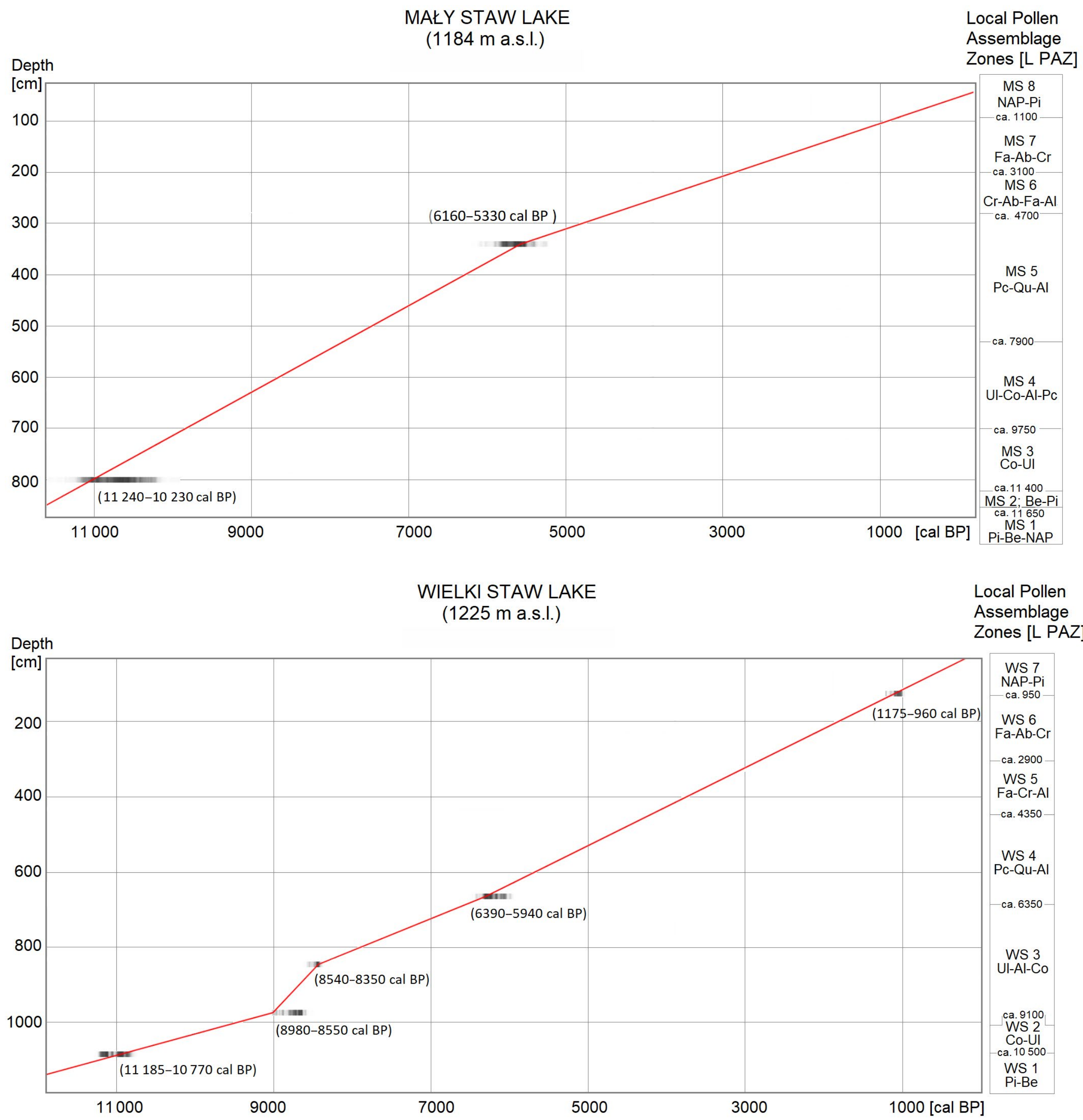

Figure 2. The Mały Staw and Wielki Staw Lakes. Age-depth models: Pi – *Pinus*, Be – *Betula*, NAP – Non Arboreal Pollen, Co – *Corylus*, Ul – *Ulmus*, Al – *Alnus*, Pc – *Picea*, Qu – *Quercus*, Fa – *Fagus*, Cr – *Carpinus*, Ab – *Abies*

Table 1. Radiocarbon dates from the Mały Staw and Wielki Staw Lakes

Site name	Depth (cm)	Lab. code	Radiocarbon age ^{14}C BP uncalibrated	Calibrated age cal BP; probability 95.4%	Median probability; cal BP	Type of material	References
Mały Staw Lake	340	Hv 11977	4983 ± 140	6160–5330	5732	Bulk	Wicik, 1986
	800	Hv 11978	9450 ± 210	10 230–11 240	10 740	Bulk	Wicik, 1986
Wielki Staw Lake	120–140	Poz-53653	1130 ± 35	1175–960	1024	Plant remains	Malkiewicz et al., 2016
	670	N/A	5400 ± 90	6390–5940	6180	Bulk	Wicik, 1986
	840–860	Poz-53654	7620 ± 50	8540–8350	8410	Plant remains	Malkiewicz et al., 2016
	980	N/A	7880 ± 50	8980–8550	8700	Bulk	Wicik, 1986
	1080–1100	Poz-53655	9630 ± 50	11 185–10 770	10 960	Bulk; gyttja	Malkiewicz et al., 2016

RESULTS

The local pollen assemblage zones (L PAZ) delineated in the diagrams (Table 2; Figs 3–6), as well as the comparison of palaeoecological records (Fig. 8) from both sites allowed us to describe the eight stages of vegetation development in the area. Pollen data provided the basis for characterizing the 12 millennia of vegetation history, particularly in the higher landscape zone of the Karkonosze Mts and identifying signs of climate and past human impact. In the profiles from the Mały Staw Lake 142 (Fig. 3), and in the Wielki Staw Lake 110 morphological types of pollen and spores were recognized (Fig. 5). The obtained results are presented in Table 2. The palynological results were complemented by the taxonomic identifications of macroscopic plant remains confirming the local growth of taxa. These were limited to only 12 taxa, partly due to the small size of the sample. In addition, Wicik's (1996) data on wood finds in the bottom sediments of the Mały Staw Lake were also included (Fig. 3).

DISSCUSION

ORIGINS OF LAKES AND SEDIMENT ACCUMULATION

The cirque lakes developed in niches after the glacier finally retreated and most of the snow and ice in them was melted. The Mały Staw Lake developed at the end of the Younger Dryas. This is consistent, among other things, with the results of an earlier study by Engel et al. (2007, 2008, 2010), which pointed to the Late Pleistocene as the period when the Karkonosze glaciers began to melt and to a period around 11 700–10 800 cal BP when the cirque lakes were largely free of glacial ice. The oldest part of the accumulated sediment (~12 100–11 650 cal. BP) contained clays with sand interbeds and gravel, eroded and transported downslope. In the case of the Wielki Staw Lake, bottom sediments were accumulated during the Eoholocene (~11 180–10 770 cal BP; Malkiewicz et al., 2016) and were composed of coarse-grained sand.

In a similar period in the upper Labe Valley (Labský důl site; 1039 m a.s.l.) sedimentary conditions also changed, and the sediment sequence dated to ~12 400–10 800 cal BP represented the accumulation in proglacial lake, formed at the margins of retreating cirque glacier. The presence of sandy layers was interpreted there as a result of sedimentary input associated with glacier oscillations. Furthermore, Engel et al. (2010) pointed out a coincidence of oscillations in the magnetic susceptibility record in the Krkonoše Mts and major advances of glaciers in the Alps. Also, Wicik (1984a) linked changes in the intensity of sediment accumulation and the cyclic occurrence of sand layers in the Mały Staw Lake to short-term climatic oscillations. The studies of fossil Cladocera from the mentioned lake showed a predominance of Arctic low-temperature tolerant species in the bottom sediment (Szeroczyńska, 1984, 1993, 1998a, b; Szeroczyńska and Zawisza, 2007). Similarly diatoms revealed that deposition took place under cold climatic conditions when the lake was poor in nutrients (Sienkiewicz, 2005, 2016).

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Phase I [L PAZ MS 1 *Pinus-Betula*-NAP; ~12 100–11 650 cal BP; Fig. 7]

The landscape around the Mały Staw Lake was open, with a mosaic of habitats and extensive areas covered by patches of treeless tundra and cold alpine grasslands developed on rocky ground. The vegetation cover was not dense. In the dry microhabitats, in rock crevices grew e.g. representatives of Poaceae, *Artemisia*, Chenopodiaceae, *Armeria maritima*, *Pleurospermum austriacum*, *Gypsophilla fastigiata*, *Helianthemum canum*, *Saxifraga oppositifolia*, Caryophyllaceae, *Aster* and *Botrychium* (Fig. 3; Table 2). On damp surfaces Cyperaceae, *Filipendula*, *Rumex acetosa*, *Urtica*, *Potentilla*, *Polygonum bistorta*, and *Sphagnum* occurred.

At lower elevations, there were patches with shrubs associated with cool temperate to Arctic habitats with: *Alnus viridis*, *Salix*, *Betula nana* growing in moist depressions, as well as *Juniperus*, *Populus* cf. *tremula*, *Ephedra dystachia* and *E. fragilis* in dry habitats.

The data also revealed a high proportion of tree pollen due to the 'high montains effect' of long-distance transport, similarly like in the case of e.g. Labský důl site (Jankovská, 2004a, 2007b) or the Plešné Lake (Jankovská, 2006). It is important to remember that 'pollen production decreases quantitatively with increasing

Table 2. Description of results of palynological and carpological studies from the Mały Staw and Wielki Staw Lakes

Site name	Mały Staw Lake		Wielki Staw Lake	
No. of pollen phase	L PAZ name, No.; depth; age	Description of results	L PAZ name, No.; depth; age	Description of results
Phase I	MS 1; *Pinus-Betula*-NAP; 900–855 cm; ~12 100–11 650 cal BP	Predominance of AP. Characteristic high proportion of *Pinus diploxylon* type pollen (incl. *P. sylvestris* and *P. mugo*) (up to 50.5%) and *Pinus haploxylon* type (up to 12.2%), most probably representing *P. cembra*. Besides *Betula* (up to 30%), a continuous curve of pollen of *Betula nana* type (up to 4.4%), *Salix* (up to 2.2%) and *Juniperus* (up to 1.4%). A few pollen records of *Ephedra distachya* and *E. fragilis* types. Continuous curve of *Alnus* and *Alnus viridis* (<1%). Significant frequency of NAP (mean value 23%). The highest percentages *Artemisia* (5.1%), Chenopodiaceae (1.4%), Cyperaceae (3.3%), *Urtica* (2.3%), Poaceae (10.9%) and *Filipendula* (1%). Occurrence of cold climate indicators of: *Armeria maritima*, *Gypsophila fastigiata* type, *Helianthemum canum* type, *Saxifraga oppositifolia*, *Polygonum bistorta* type and *Pleurospermum austriacum*. Absence of plant macroremains in sediments.		
Phase II	MS 2; *Betula-Pinus*; 855–825 cm; ~11 650–11 400 cal BP	Significant increase in AP percentages. Codominance of *Betula* (up to 51.5%) and *Pinus diploxylon* type (up to 43.5%; maximum values throughout the profile). Decreasing *Pinus haploxylon* type, *Betula nana* type and *Juniperus* (less than 1%). Infrequent *Alnus* and *Alnus viridis* pollen. Continuous curve of *Ulmus* (up to 2.1%), *Salix* (up to 1.4%), as well as *Picea*, *Quercus* and *Corylus* (<1%). Single pollen of *Larix* and *Ephedra*. A significantly lower proportion of Poaceae (up to 3.3%), Cyperaceae (up to 1.5%) and *Artemisia* (up to 1.7%). Slightly higher values of *Filipendula* and Cichorioideae pollen. Significant increase in the frequency of fern spores (Filicales monolete up to 15%). Presence of macrofossils of *Betula* cf. *pubescens*, and herbaceous taxa.	WS 1; *Pinus-Betula*; 1100–1075 cm; ~11 100–10 500 cal BP	Single pollen spectrum with high frequency of *Pinus diploxylon* type (46%) and *Betula* (38.5%). Presence of *Betula nana* type (1.3%), *Salix* (1%), *Juniperus* (0.3%), as well as *Populus* and *Pinus haploxylon* type pollen (0.1%). Among NAP the highest values of Poaceae (2.2%), *Artemisia* (2%), and *Urtica* (1%). Cryptogams represented by spores of Filicales monolete (11.2%), *Selaginella selaginoides*, *Huperzia selago* and *Botrychium*. The sediment does not contain plant macroremains.
Phase III	MS 3; *Corylus-Ulmus*; 825–710 cm; ~11 400–9750 cal BP	Distinguishing the rapid upward trend and the highest frequency of *Corylus* pollen in the profile (up to 45%). Sharp reduction of *Betula* (from 32% to 8%) and gradual decline of *Pinus diploxylon* type (from 31% to 19.5%). Final decline of *Pinus haploxylon* type and *Juniperus*. *Populus* in the lower part of the zone. Reduction of *Alnus viridis* (up to 0.9%), *Salix* (up to 0.5%) and *Betula nana* type (up to 0.9%). Gradual increase of *Ulmus* (up to 7.6%), *Quercus* (up to 2.9%) and *Tilia* (up to 2.2%). Continuous curve of *Fraxinus*, *Alnus* and almost constant occurrence of *Picea* pollen (<1%). Regular records of *Vaccinium* type pollen. Among NAP the most abundant pollen of Apiaceae (up to 1.7%), *Humulus* type (up to 1.5%), Cichorioideae (up to 1.7%), *Rumex acetosella* type (up to 1.7%), Cyperaceae (up to 1.3%) and Poaceae (up to 5%). The high proportion of Filicales monolete spores (up to 40%). A continuous curve of *Huperzia selago* spores. Among macroremains, only herbaceous plants identified.	WS 2; *Corylus-Ulmus*; 1075–975 cm; ~10 500–9100 cal BP	A sharp increase of *Corylus avellana* pollen reaching the highest values in the profile (46%). A strong decrease in *Pinus diploxylon* type pollen (from 39.5% to 24.5%) and *Betula* (from 14% to 8.5%). Slight increase in the frequency of *Ulmus* (up to 5%), *Quercus* (up to 3.7%), *Alnus* (up to 2.4%), *Tilia* (up to 1.4%), and *Picea* (up to 1.3%). Presence of *Betula nana* pollen type and *Juniperus*. Slight decrease in NAP. The significant proportion of Poaceae (up to 4.3%). Presence of *Selaginella selaginoides* and *Huperzia selago* spores. Plant macroremains not found.

Table 2. Continued

Site name	Mały Staw Lake		Wielki Staw Lake	
No. of pollen phase	L PAZ name, No.; depth; age	Description of results	L PAZ name, No.; depth; age	Description of results
Phase IV	MS 4; *Ulmus-Corylus-Alnus-Picea*; 710–450 cm; ~9750–7900 cal BP	The highest values of *Ulmus* (up to 9.3%), *Quercus* (up to 8.5%) and *Tilia* (up to 3.6%). Significant increase in pollen frequency of *Picea* (up to 12%) and *Alnus* (up to 12.5%). Percentage values of *Pinus* and *Betula* with no significant change. High but decreasing frequency of *Corylus* (from 36% to 22%). Single pollen grains of *Larix* and *Alnus viridis*. Beginning of a continuous curve of *Fagus* (<1%). Regularly present pollen of *Acer*, *Hedera* and *Viscum*, as well as single counts of *Vitis*. The lowest NAP values in the profile. Continuous curves form among others: Poaceae (up to 6.8%), Apiaceae, Cichorioideae, *Artemisia*, *Chamaenerion angustifolium*, *Rumex acetosella* type and Cyperaceae. Macroremains of *Larix* sp., *Rubus* cf. *idaeus*, Ericaceae, *Vaccinium* sp. and *Carex* sp. identified.	WS 3; *Ulmus-Alnus-Corylus*; 975–675 cm; ~9100–6350 cal BP	A high value of *Corylus* (up to 30%), a gradual increase and maximum values of *Ulmus* (up to 8%). Pollen percentages of *Alnus* (up to 13.5%), *Picea* (up to 8%), *Quercus* (up to 5.6%), *Tilia* (up to 3.2%) and *Fraxinus* (up to 2%). Continuous curve of *Fagus sylvatica* (<1%). Single pollen grains of *Hedera helix* and *Viscum album*. Among NAP continuous curves form e.g. Poaceae (up to 2.7%), *Urtica* (up to 1%), *Artemisia* (up to 1.2%), as well as Cichorioideae, Apiaceae, *Aster* type, *Polygonum bistorta* type, and *Rumex acetosella* type. Increase in frequency of cryptogams. Presence of macrofossils of *Pinus sylvestris* and *Fagus sylvatica*.
Phase V	MS 5; *Picea-Quercus-Alnus*; 450–290 cm; ~7900–4700 cal BP	The beginning of the zone marked by slight decreases in *Pinus diploxylon* type and *Corylus* pollen values. Increase of *Picea* and beginning of continuous *Carpinus* curve (up to 5%). Low pollen frequencies of *Pinus* (up to 19%), *Betula* (up to 6.5%) and *Salix* (up to 1%). Characteristic systematic decrease of *Ulmus* (from 5.5% to 1.7%), *Corylus* (from 24% to 8.5%), significant values of *Quercus* (up to 7%) and *Tilia* (up to 3.7%). The highest values of *Picea* (up to 17%) and *Alnus* (up to 13.5%). An upward trend in *Fagus* (up to 7.5%). In the upper part of the zone regular presence of *Abies alba* pollen (up to 1.7%). Several counts of *Hedera helix*, *Juglans* and *Viscum* pollen grains. Almost continuous curve of *Betula nana* type. Among NAP continuous presence of e.g. Apiaceae (up to 3.4%), *Artemisia*, *Aster* type, *Filipendula*, Cichorioideae, *Polygonum bistorta* type, *Potentilla* type, *Urtica* and *Rumex acetosella* type, Poaceae (up to 7%) and *Plantago lanceolata*. Higher pollen counts of lake shore zone plants. Still high values of the Filicales monolete spores (up to 56%). Macroremains of *Larix* sp., *Juniperus communis* and *Pinus sylvestris* present.	WS 4; *Picea-Quercus-Alnus*; 675–475 cm; ~6350–4350 cal BP	Values of *Corylus avellana* (up to 22.5%) and *Alnus* (up to 13.5%) remain high. The highest percentages of *Picea* (up to 16.5%), *Quercus* (up to 11.6%) and *Tilia* (up to 3.2%). A gradual increase in the proportion of *Fagus* (up to 4.1%), *Carpinus* (up to 2.3%) and *Abies* (1.1%). Regularly noted *Salix* pollen. Decreasing trend of *Ulmus* (up to 2.9%). A slight upward trend in NAP values. Significant frequency of Poaceae (up to 4.7%). Continuous pollen curve of *Plantago lanceolata*. Regularly noted pollen of e.g. Cichorioideae, *Plantago media* type, *Potentilla* type, *Ranunculus*, *Urtica*, *Humulus* and *Rumex acetosella* type. In the upper part of the zone increase in frequency of Filicales monolete spores (up to 27%). Presence of *Selaginella selaginoides*, *Huperzia selago*, *Botrychium*, *Pteridium aquilinum* and *Sphagnum*. Occurrence of macroscopic remains of *Pinus sylvestris*.
Phase VI	MS 6; *Carpinus-Abies-Fagus-Alnus*; 290–210 cm; ~4700–3100 cal BP	The rapid increase and high percentages of *Abies alba* (up to 6.3%), *Carpinus* (up to 6.2%), *Alnus* (up to 17%) and *Fagus* (up to 11%). The decreasing trend in *Picea* (up to 8%), *Corylus* (from 15% to 7%), *Ulmus* (up to 2.6%) and *Quercus* (up to 5%). The lowest in the profile frequency of *Pinus diploxylon* type (up to 15.5%). Regular pollen records of *Betula nana* type. Increase in frequency and taxonomic diversity of NAP. Continuous curves of e.g. Poaceae (up to 11.5%), Cichorioideae, *Plantago lanceolata*, *Aster* type, *Thalictrum*, *Artemisia*, and *Potentilla* type. High values of Filicales monolete (up to 41%) and *Sphagnum* (up to 2.3%) spores. The presence of wood of *Picea*/*Larix* and *Pinus sylvestris* needles.	WS 5; *Fagus-Abies-Carpinus-Alnus*; 475–330 cm; ~4350–2900 cal BP	Significant decrease of *Corylus* (up to 13.5%), *Ulmus* (up to 1.3%), *Quercus* (up to 3.4%), *Tilia* (up to 1.2%) and *Picea* (up to 7.1%) pollen values. The highest frequency of *Alnus* pollen (up to 15.5%), along with *Carpinus* (7.1%), *Abies* (10.5%) and *Fagus* (up to 10%). Regular presence of *Juniperus* and *Viscum* pollen. Fairly stable proportion of NAP (~20%), consisting mainly of Poaceae (up to 6%), *Artemisia* (up to 1.6%), *Humulus* type (up to 0.9%), *Aster* type and *Plantago lanceolata*. High and stable proportion of cryptogams. Absence of plant macroremains.

Table 2. Continued

Site name	Mały Staw Lake		Wielki Staw Lake	
No. of pollen phase	L PAZ name, No.; depth; age	Description of results	L PAZ name, No.; depth; age	Description of results
Phase VII	MS 7; *Fagus-Abies-Carpinus*; 210–95 cm; ~3100–1100 cal BP	Systematic decline in AP share (up to 70%). Characteristic highest value of *Fagus* (up to 13.5%). Significant frequency of *Alnus* (up to 15%), *Abies alba* (up to 6.3%), *Carpinus* (up to 4.4%), *Picea abies* (up to 8%) and *Quercus* pollen (up to 3.9%). Decrease in *Corylus* (from 15% to 5.4%). Very low frequency of *Ulmus* and *Tilia* (both up to 1%). Continuous curve of *Acer*. Regular counts of *Juglans* pollen. A marked increase in Poaceae pollen (from 5.2% to 16.5%). Values of other NAP unchanged or slightly higher, e.g. *Rumex acetosella* type (up to 2.0%), *Polygonum bistorta* type (up to 1.2%), Cichorioideae (up to 2.4%). Regular presence of *Plantago major* and *P. media*. Single pollen of cultivated plants such as *Triticum* type. Macroremains of *Pinus sylvestris* noted.	WS 6; *Fagus-Abies-Carpinus*; 325–125 cm; ~2900–950 cal BP	Stable, high proportions of AP (average 80%). High frequency of *Fagus* (up to 11%), *Abies* (up to 10%), *Carpinus* (up to 6.7%), *Pinus diploxylon* type (up to 17.5%) and *Alnus* (up to 15%). Increase of *Betula* (up to 12%) and *Quercus* (up to 7.5%). Low pollen values of *Corylus* (up to 7.3%). Among NAP the highest frequency of Poaceae (up to 8.5%), as well as *Rumex acetosella* type (up to 1.2%), *Plantago lanceolata*, *Polygonum bistorta* type, *Potentilla* type, *Artemisia* (up to 1.6%) and *Urtica*. First pollen of *Triticum* type and *Secale cereale*. More diverse macroscopic remains representing: *Pinus sylvestris*, *Pinus cembra*, *Betula* sp., *Picea abies* and *Abies alba*.
Phase VIII	MS 8; NAP-*Pinus*; 95–5 cm ~1100–50 cal BP	Strong decline of AP (to 58% in the upper part of the zone). The sharp reduction in abundance of *Fagus* (up to 9%) and *Carpinus* (up to 2.8%). Stable frequency of *Alnus* (up to 10.5%), *Quercus* (up to 3.8%), *Tilia* (up to 1.9%), *Picea* (up to 7%), and *Betula* (up to 9.5%). A slight increase of *Pinus diploxylon* type pollen (up to 18.5%) and *Corylus* (up to 9.5%). Stable values of *Vaccinium* type (up to 1.4%), *Calluna*, and sporadic presence of *Empetrum*. Prominent frequency of NAP, represented by abundant pollen of Poaceae (up to 24%). Continuous curves of cultivated plants: *Triticum* type and *Secale cereale*. Presence of *Fagopyrum* pollen and *Centaurea cyanus* (crop weed). Significant frequency of *Plantago lanceolata* (up to 1.6%), *Rumex acetosella* type (up to 3%), *Artemisia* (up to 2.4%), *Potentilla* type (up to 1.2%), Cichorioideae (up to 3%), *Urtica* (up to 2.3%) and Apiaceae (up to 1.8%). The presence of *Urtica dioica* seed.	WS 7; NAP-*Pinus*; 125–5 cm; ~950–50 cal BP	The marked decrease in the proportion of AP (up to 56% in the uppermost part), particularly of *Carpinus* (up to 1.7%), *Abies* (up to 5%), *Fagus* (up to 6.9%), *Alnus* (up to 8.9%) and *Betula* (up to 8%). Stable frequency of *Pinus diploxylon* type (up to 18.5%), *Picea* (up to 7.1%), *Quercus* (up to 5.2%) and *Corylus* (up to 7.2%). Single pollen grains of *Juglans* and *Vitis*. Increasing trends of *Vaccinium* type (up to 1.5%) and *Calluna* (up to 1.5%). A rapid growth in NAP, particularly of Poaceae (from 15.0% to 23.0%). High values of *Plantago lanceolata* (up to 2%), *Artemisia* (up to 1.6%), *Humulus* type (up to 1.4%), and *Rumex acetosella* type (up to 2.7%). Continuous curve of cultivated plants: *Triticum* type (up to 1.2%) and *Secale cereale* pollen (up to 1.9%). The highest counts of Filicales monolete spores (up to 37.5%). Occurrence of macroremains of *Pinus sylvestris* and *Larix* sp.

elevation (…). This fact combined with the regionality of the pollen dispersal at high elevation leads to a distortion of the near timberline pollen assemblages in terms of the local vegetation represented' (Markgraf, 1980: p. 127). We assume that the source of tree pollen in the Younger Dryas environment was patches of low-density boreal forests already developed probably in the Sudetes foothills. They were composed of *Pinus sylvestris* (*Pinus* subgenus *Pinus* pollen type = *Pinus diploxylon*; including *P. sylvestris* and *P. mugo*), *Pinus cembra* (*Pinus* subgenus *strobus* pollen type = *Pinus haploxylon*; including *P. cembra*; Moore et al., 1991) and *Betula*, with low edaphic requirements. Taking into account that pollen values of *Pinus cembra*, ~12%, are considered evidence of its local growth (Wegmüller, 1977; Obidowicz, 2013), we interpret our results as a presence of *P. cembra* at least in the wide surroundings of Mały Staw Lake. In the case of *P. sylvestris*, a pollen value of 50% is assumed to be the minimum amount of pollen confirming its dominance in local forests while values of *Betula* pollen, >25%, indicate the local presence of birch forests (Huntley and Birks, 1983; Latałowa et al., 2004; Ralska-Jasiewiczowa et al., 2004). In the case of the studied site, the mean percentage values were generally lower, therefore, we assume that areas covered by loose pine-birch forest communities occurred in the lower mountain locations. In the Younger Dryas the alpine timberline in the Krkonoše Mts, according to Treml et al. (2006), ran at an altitude of about 500–600 m a.s.l. Similar taxonomical composition of pollen spectra in the Younger Dryas is known also from the Western Carpathians, e.g. the Tatra Mts. (Zielony Staw, 1671 m a.s.l.; Czarny Staw, 1621 m a.s.l.; Żabie Oko, 1390 m a.s.l.; Obidowicz, 1996), and the Beskid Makowski Range (Kotoń mire, 740 m a.s.l.; Margielewski et al., 2003). Analyzing the altitudinal distribution of the palynological sites, it can be seen that the representation of *Pinus sylvestris* was visibly higher at lower altitudes (Siódmowo, 507 m a.s.l., Klaklowo, ~500 m a.s.l., Beskid Średni Range; Margielewski, 2006), which supports the presence of pine-dominated boreal forests there. The results from the Plešné Lake (the Bohemian Forest; Jankovská, 2006) provided a similar picture at the vegetation of the end of the glaciation. Based on the data from the Komořanské jezero Lake (NW Bohemia), Jankovská and Pokorný (2013) suggested that it was likely that the forest-tundra communities became mountain tundra on the summit plateau of the Krušné hory Mts while České středohoří hills were probably covered by open steppe with a scattered occurrence of *Pinus sylvestris*.

Phase II [L PAZ MS 2 *Betula-Pinus*; ~11 650–11 400 cal BP & L PAZ WS 1 *Pinus-Betula*; ~11 100–10 500 cal BP; Fig. 7]

At the beginning of the Holocene the landscape at ~1200 m a.s.l. remained mostly open. Poorly developed initial soils on the slopes favoured the development of grasslands and tall herb communities with Poaceae, *Artemisia*, *Helianthemum*, and Chenopodiaceae. In places with higher humidity, Cyperaceae, *Filipendula*, *Thalictrum*, *Urtica dioica*, as well as cryptogams grew. The presence of macrofossils of herbaceous plants (between 11 650 and 11 000 cal BP; Fig. 3) in the sediments of the Mały Staw Lake suggests the development of a denser plant cover in the catchment which has likely provided better stabilization of the substrate and thus a change in the sediment composition to a less mineral type. In a shore zone, small patches of reed and marsh vegetation with *Typha latifolia*, *T. angustifolia*, *Menyanthes trifoliata*, *Equisetum* and *Sphagnum* have developed. It is probable that also *Juniperus*, *Ribes*, *Betula nana* and *Alnus viridis* shrubs grew not far from the lake taking advantage of the mosaic of microhabitats. In response to climate warming (e.g. Björck et al., 1998; Bond et al., 2001; Starkel et al., 2013; Rasmussen et al., 2014), there was an intensive development of loose birch and pine forests. Around 11 650 cal BP *Betula* cf. *pubescens* occurred near the Mały Staw Lake (as confirmed by macrofossils; Fig. 3). The exceptionally high frequency of birch pollen ~11 650–11 400 cal BP (reaching 50% of total sum) confirms fast expansion and development of birch dominated forests in the region probably also in the upper landscape zone (Figs 3, 4). Such a high proportion of birch has not yet been observed in either the Sudetes Mts (Madeyska, 1989; Jankovská, 2004a, 2007b) or the Western Carpathians (Granoszewski et al., 2013). Although this was characteristic in e.g. Central and Northern Poland (Huntley and Birks, 1983; Ralska-Jasiewiczowa et al., 2004). At the Labský důl site (1039 m a.s.l.), such a distinct birch phase was not found, but a long-lasting persistence of pine-dominated forests (Engel et al., 2010). Nevertheless, similar changes in pollen assemblages were recorded also at the Plešné Lake site in the Šumava Mts (1105 m a.s.l.; Jankovská, 2006). In the case of the Komořanské jezero Lake (a submontane basin in the Krušné hory Mts), the higher birch values coincided with the same beginning of lake sedimentation (Jankovská and Pokorný, 2013).

From ~11 300 cal BP birch was reduced and pine (possibly also *Pinus mugo*) gained in importance as a component of mixed forests, where infrequent *Larix*, *Pinus cembra*, *Sorbus*, *Populus* cf. *tremula* and *Salix* were also present. From ~11 180 cal BP the limnic sedimentation started in the Wielki Staw Lake (1225 m a.s.l.; Figs 5, 6; Malkiewicz et al., 2016).

Phase III [L PAZ MS 3 *Corylus-Ulmus*; ~11 400–9750 cal BP & L PAZ WS 2 *Corylus-Ulmus*; ~10 500–9100 cal BP; Fig. 7];

The montane grasslands still covered vast areas of the upper montane zone, where also abundant cryptogams occurred: Filicales (unidentified ferns), *Polypodium vulgare*, *Dryopteris filix-mas*, *Huperzia selago*, *Sphagnum* and *Selaginella selaginoides* in the Wielki Staw Lake area (Fig. 5). Several shrub taxa, such as *Alnus viridis*, *Salix*, *Betula nana*, and probably the mountain pine *Pinus mugo* may also have occurred there. We have no evidence of trees in the vicinity of the studied lakes. Moreover, data from the Krkonoše Mts (Czech part) indicated that ~10 400–9800 cal BP alpine timberline ascended to ~1000 m a.s.l. (Treml et al., 2006, 2008). A distinctive feature of phase III was the rapid expansion of deciduous mesophytic trees. *Ulmus*, probably *U. glabra*, encroached on wet habitats from ~11 500 cal BP, as suggested by the increase in concentration of its pollen (Figs 3, 4). No earlier than ~11 300 cal BP *Corylus avellana* expanded its range into more fertile habitats, especially in the lower montane zone and foothills. Birch and pine were unable to down out either hazel seedlings or saplings in these habitats. A phase of high percentages of hazel (greater than 25%) around 10 900–9200 cal BP (Fig. 3; Malkiewicz et al., 2016) indicated the development of communities with at least co-dominant hazel (Huntley and Birks, 1983; Tallantire, 2002; Miotk-Szpiganowicz et al., 2004). Analogous records were obtained in other parts of the Sudetes, including the Bystrzyckie Mts (Zieleniec peat bog; Madeyska, 1989, 2005) and the Hrubý Jeseník Massif (~10 800 cal BP; Dudová et al., 2010, 2013), as well as the Vernéřovice (Rybničkova and Rybniček, 1996). In the Polish Carpathians, where currently the highest hazel stands were recorded in the Tatra Mts at 1335 m a.s.l., in the Gorce Mts at 1220 m a.s.l. and in the western Bieszczady at 1210 m a.s.l. (Gostyńska-Jakuszewska and Zieliński, 1976 and further literature therein), the beginning of an analogous phase was recorded later, between ~9500 and ~7800 cal BP (Obidowicz et al., 2013).

In the Mały Staw Lake, the mineral layers deposited around 10 600–10 500 cal BP (at a depth of 757–745 cm) and the accompanying decrease in pollen concentration, indicates increased erosion. During a similar period, temperature drops of 0.8°C (Heiri and Lotter, 2003) or even 1°C (Larocque-Tobler et al., 2010) have been reported in the Alps, occurring around 10 700–10 500 and 10 700–10 300 cal BP, respectively. The cooler and wetter period (called the Boreal oscillation) defined at 10 450–10 250 cal BP partially overlaps with the higher lake level phase of 10 300–10 000 cal BP (Magny, 2004). Previously, Wicik (1984a) suggested the weakening of the sedimentation rate at a depth of 757–745 cm resulted from the harsh climatic conditions of the Younger Dryas. However, our study proved that this episode was much younger and preceded climate warming (Starkel et al., 2013). In deciduous forests of the lower montane forest zone *Hedera helix* and *Viscum album* regularly occurred from 10 300 cal BP, confirming favorable climate conditions (Iversen, 1944).

Phase IV [L PAZ MS 4 *Ulmus-Alnus-Picea-Corylus*; ~9750–7900 cal BP & L PAZ WS 3 *Ulmus-Corylus*; ~9100–6350 cal BP; Fig. 7]

The direct vicinity of the studied lakes stayed mostly open, though it was already in the range of *Larix* and *Pinus sylvestris* (documented by macroremains; Figs 3, 5; see also Wicik, 1996). This is consistent with data from the Krkonoše Mts (the Czech part) showing that after ~8100 cal BP the alpine timberline ran at an altitude of ~1320 m a.s.l. (Treml et al., 2006, 2008). Possibly shrubs of *Rubus idaeus*, *Salix* sp., *Alnus viridis* and *Betula nana* occurred there, as well as clumps of Ericales: *Vaccinium*, *Calluna* and *Empetrum*. *Betula nana* became more common between ~7800 and 5300 cal BP near the Mały Staw Lake. Among the cryptogams: ferns of unspecified genus, *Huperzia selago*, *Selaginella selaginoides* and *Sphagnum* were identified as spores, and numerous sporangia of Filicales indicated its presence on the lake shores. In the Wielki Staw Lake *Isoëtes lacustris* was a component of the underwater vegetation. Our study confirmed the occurrence of only single spores (~8600 cal BP; Fig. 5), while earlier results by M. Malkiewicz et al. (2016) documented its numerous occurrences in this lake from the climatic optimum to the present. In our opinion, a likely explanation for this discrepancy between records was the use of an overly aggressive chemical procedure to prepare the samples in our study, which may have destroyed these delicate spores. The omission of spores in our analysis is unlikely. Today, the Wielki Staw Lake is the only high-mountain lake with *Isoëtes lacustris* in Poland (Dynowski et al., 2024). The analyses of Cladocera from the Mały Staw Lake revealed the dominance of species that prefers higher temperatures (Szeroczyńska, 1993).

In the Polish Karkonosze forests the spruce appearance at ~10 300 cal BP was delayed compared to the Polish Western Carpathians, where migration dates back to ~10 800 cal BP

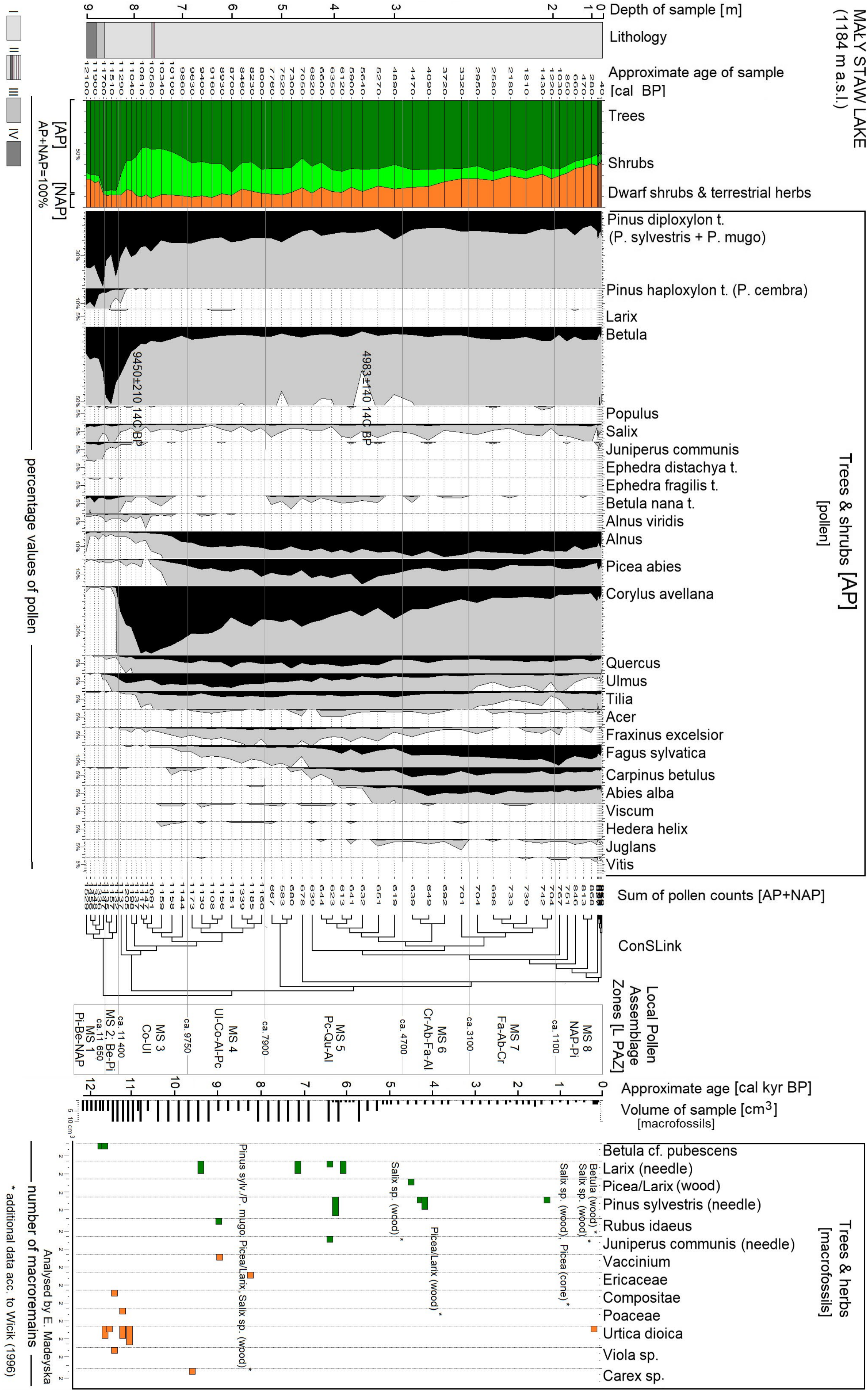
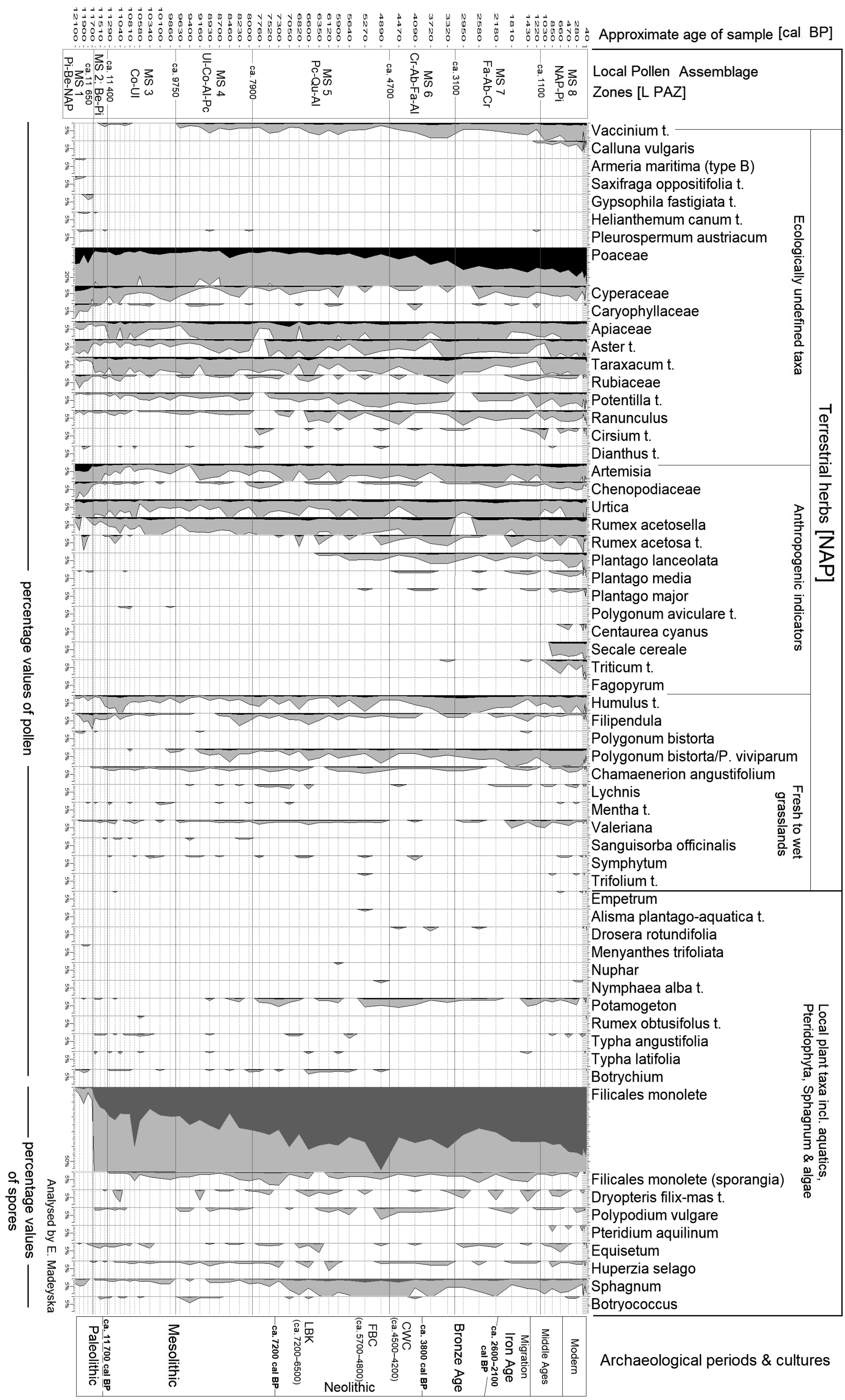


Figure 3. The Mały Staw Lake. Simplified percentage pollen and spores diagram, as well as plant macroremains record. I – gyttja; II – organic and mineral intercalations; III – gyttja with sand; IV – sand with gravel. For further explanations see Fig. 2



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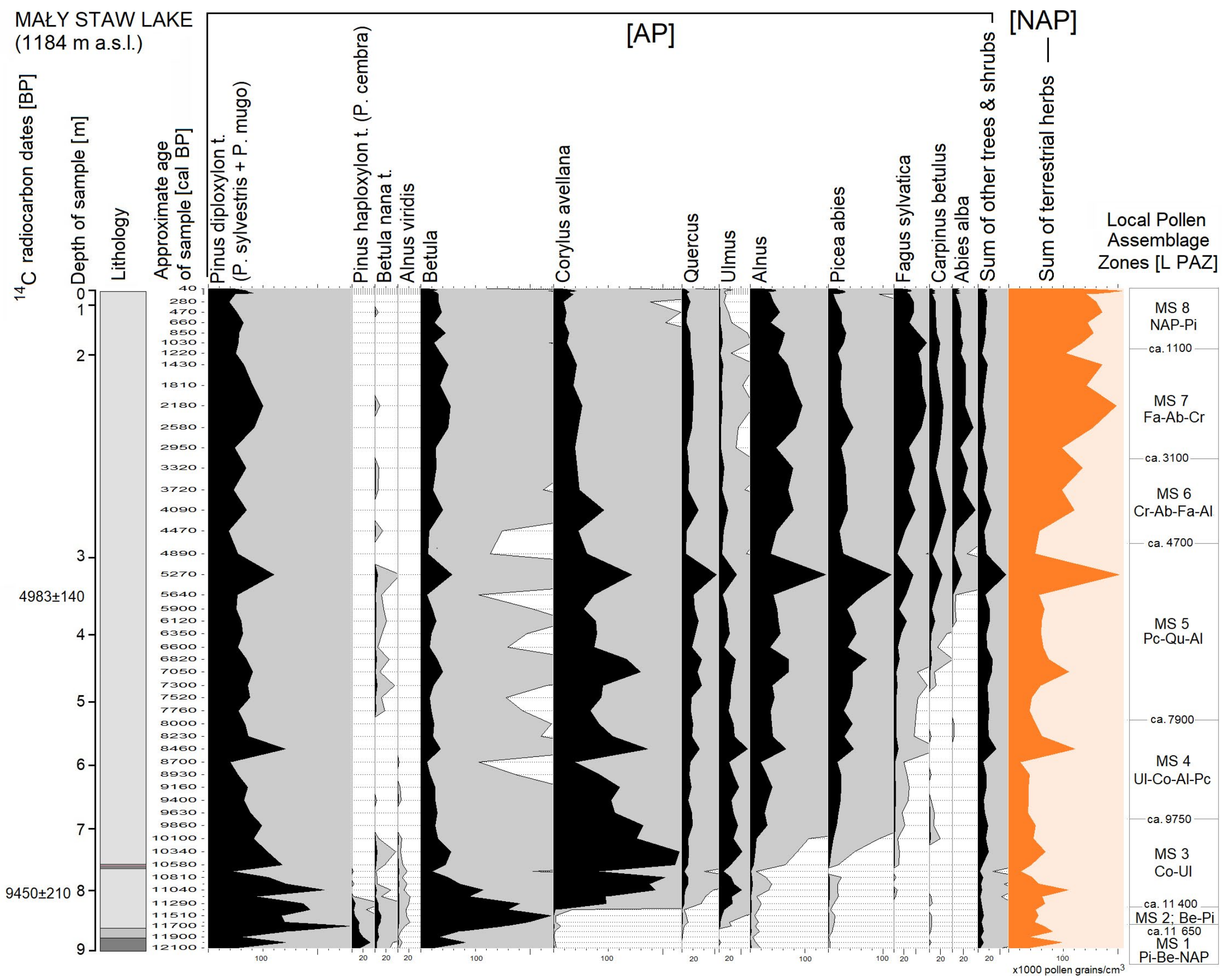


Figure 4. The Mały Staw Lake. Diagram showing changes in pollen concentration of selected taxa. For further explanations see Fig. 2

(Obidowicz et al., 2004b, 2013), but occurred earlier than in the Erzgebirge (see Fig. 1B), where *Picea* expansion occurred ~9000 cal BP (Kaiser et al., 2023). If we take into account that the 2% spruce pollen threshold tracks the range expansion (Latałowa and van der Knaap, 2006; Lisitsyna et al., 2011), the observed pollen shares of ~12% (Fig. 3) support its important role in the forests from ~9400 cal BP. Also, in the Slovak Tatra Mts (Popradské pleso Lake; 1513 m a.s.l.) already before 9500 cal BP (date considered too young) spruce reached a high proportion in the forests (~15% of pollen; Rybničkova and Rybniček, 2006). The occurrence of spruce was documented ~9500–9000 cal BP in different Czech sites from the Sudetes (Engel et al., 2010; Dudová et al., 2010, 2013). According to Svobodová et al. (2001), its major expansion (> 5% pollen) took place ~9250 cal BP (= 8260 ± 70 uncal BP) or even ~9500 cal BP (Vočadlová et al., 2015). According to Latałowa and van der Knaap (2006), the spruce expansion over most of the Alps and Jura Mts took place in two waves 11 700–8900 cal BP and 6800–5700 cal BP, and the spruce expansion after 6800 cal BP occurred in several isolated hilly or mountainous areas, including the Harz Mts in central Germany.

Around 8600 cal BP in the Wielki Staw Lake the sharp decrease of pollen concentration and reduction of taxonomic diversity probably resulted from the slope erosion event marked as the sand layer in sediment. Analogous change of pollen concentration was also noted in the Mały Staw Lake at ~8700–8500 cal BP but the thicker sand interbeds were not observed (Fig. 8). It cannot be ruled out that these phenomena could be related to wider climate oscillations. The interval between 9000 and 8000 cal BP has been identified as one of the globally recorded rapid climate change events which may be interpreted as a partial return toward glacial conditions in the Northern Hemisphere (Mayewski et al., 2004). Also, in the Tatra Mts, some rare minerogenic inserts within the sequences of lacustrine sediments were dated at ~8600–6600 cal BP (Kotarba and Baumgart-Kotarba, 1997). According to Starkel et al. (2013) the period 9600–8400 cal. BP was recognized in Poland as a humid phase with the rise of lake levels and the high frequency of extreme events. It precedes the 8.2 ka event of climate cooling (e.g. Bond et al., 2001; Magny et al., 2003; Rasmussen et al., 2007).

At that time, the multi-species deciduous forests composed of oak, lime, elm, ash, maple and rich hazel in the undergrowth prevailed in the foothills and lower montane forest zone. Larger areas were also covered by alder forests similar to the current *Alnetum incanae*.

Phase V [L PAZ MS 5 *Picea-Quercus-Corylus*; ~7900–4700 cal BP & L PAZ WS 4 *Picea-Quercus-Tilia*; ~6350–4350 cal BP; Fig. 7]

On the shores of both lakes, there were patches of rushes and floating-leaved plant communities (Figs 3, 5). Changes observed in the Mały Staw Lake plankton composition during this period have been linked by Szeroczyńska (1993) to a gradual deterioration of edaphic conditions caused by climate change. Both lakes remained within the range of generally open vegetation with patches of *Pinus sylvestris*, *Larix*, and shrubs of *Juniperus*, *Sorbus* sp., *Salix* sp. (documented as macrofossils Figs 3, 5; see also Wicik, 1986). In addition, in the Wielki Staw Lake a fragment of the spruce trunk was found (Więckowski, 2009; Malkiewicz et al., 2016), confirming its growth in the immediate vicinity ~6300–6000 cal BP (Figs 3, 5). The spread of conifers was favoured by a wetter climate and the development of soils with humus horizons (Bennett and Willis, 1995). The rise of precipitation registered e.g. in fluvial records and the beginning of a humid period was dated to ~6400 cal BP in Poland (Starkel et al., 2013). The mosaic of habitats enables the development of the high-mountain grasslands together with dwarf shrubs (*Vaccinium*, *Calluna*) and *Betula nana* shrubs in the lake's surroundings. Jankovská (2007a) pointed out missing evidence for *Juniperus communis* occurrence in the Karkonosze Mts in the younger Holocene. Our study revealed its occurrence not only in the Younger Dryas and at the beginning of the Holocene (~12 100–11 000 cal BP), but during the Mesoholocene, as suggested by the discontinuous presence of pollen and a single needle of *J. communis* dated to ~6350 cal BP (Fig. 3).

During this phase, in the Mały Staw Lake the number of spruce in the upper montane forest zone increased gradually and became most frequent ~6800–5600 cal BP. In the case of the Wielki Staw Lake, the analogous phenomenon was delayed (~6100–4600 cal BP). Spruce forests, however, did not play as important a role as in the Labský důl Valley (Jankovská, 2007a) or in the Hrubý Jesenik Mts (Dudová et al., 2010). Forest composition changed also significantly due to the expansion of *Fagus*. It is accepted that 2% values of beech pollen (or even less; Björkman, 1996; Lisitsyna et al., 2011; Wacnik et al., 2016, 2017) indicate its scattered local presence while values >5% indicate a considerable presence in a region (Huntley and Birks, 1983; Ralska-Jasiewiczowa et al., 2004). It can be assumed that beech appeared sporadically as early as ~6800 cal BP, but was an admixture in local forests from ~6100 cal BP (Figs 3, 5). A single particle of *Fagus* wood, most probably redeposited, was identified in sediments from the Wielki Staw Lake dated to ~7800 cal BP. The fir *Abies alba* was the last new forest-forming tree species in the region, appearing ~5300 cal BP (the first increase in pollen concentration; Fig. 4). Current observations showed that >1% of pollen indicates the local presence of a few fir trees while >6% indicates the local development of fir forests (Pidek, 2013). According to Svobodová et al. (2001), the major expansion of *Abies* in Šumava occurred from ~6300 cal BP, that is much earlier than in the Krkonoše Mts (Labský důl Valley; ~4600 cal BP; Jankovská, 2004a). Analogous transformations of forest were observed in the Erzgebirge at ~6000 cal BP due to *Fagus* and ~4200 cal BP due to *Abies* migration (Kaiser et al., 2023).

In the multi-species deciduous forests found in the lower montane zone, the proportion of elm decreased in parallel with the expansion of spruce and alder. Hornbeam *Carpinus betulus* was also present in their composition from ~6100 cal BP.

An interesting phenomenon resulting from long-distance transport was a regular record of *Juglans regia* pollen from at least ~5300 cal BP (Mały Staw Lake; Fig. 3). Its source may even have been populations occurring in southern Europe. *Juglans* was present in Switzerland (~6850–4950 cal BP), Slovenia (~6370–6300 cal BP) and before that Italy (Pollegioni et al., 2017).

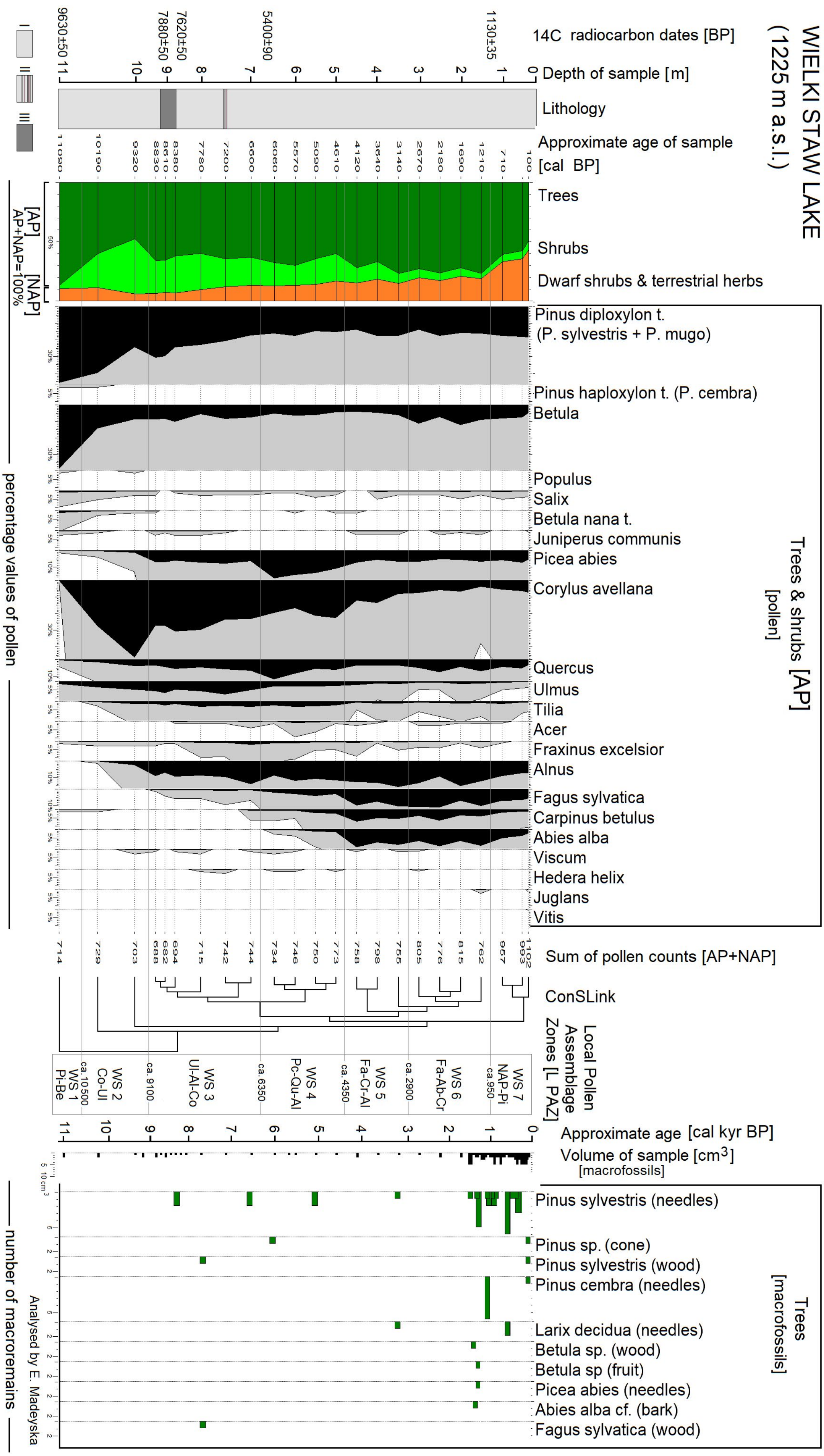
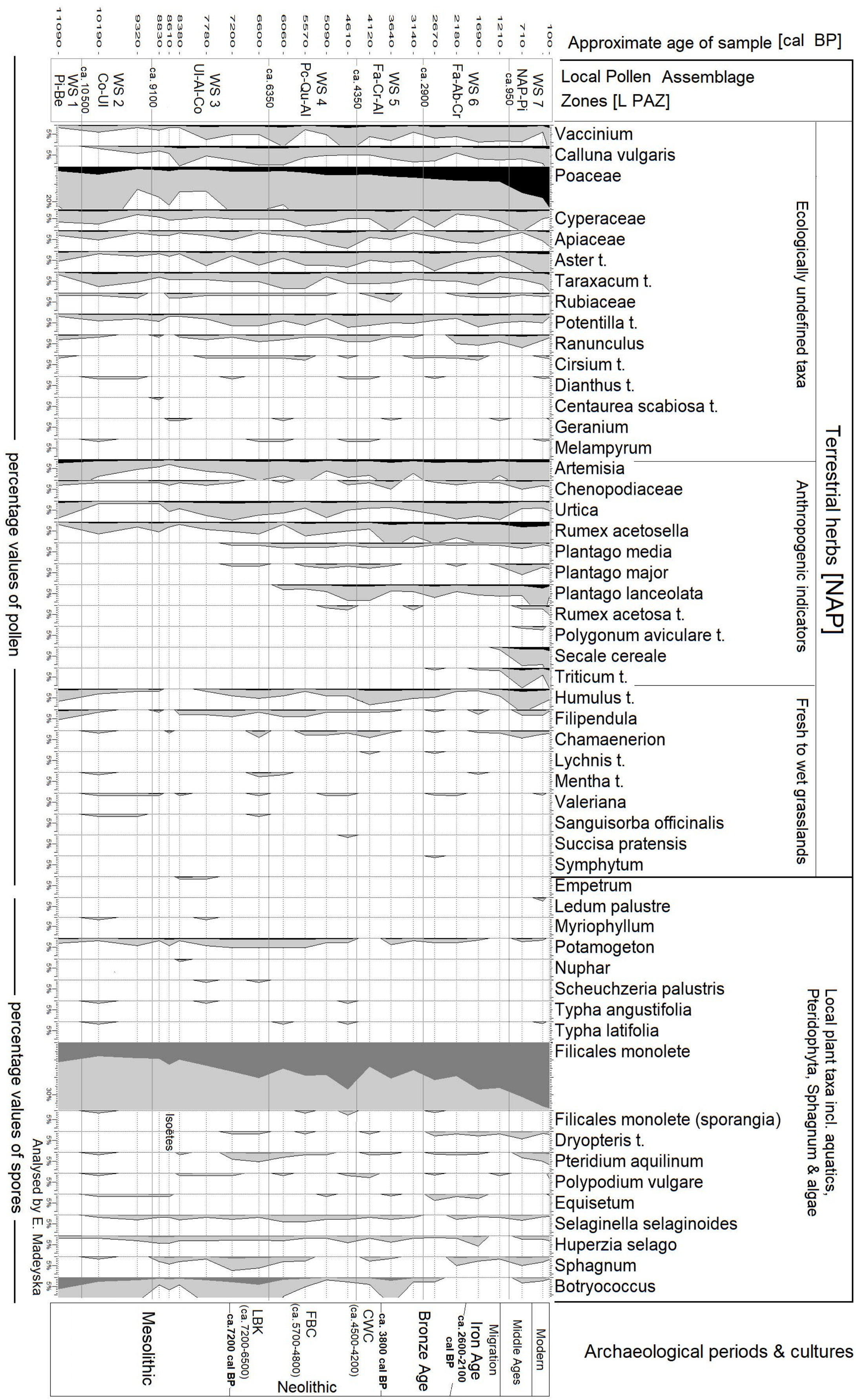


Figure 5. The Wielki Staw Lake. Simplified percentage pollen and spores diagram, as well as plant macroremains record. I – gyttja; II – sand intercalations; III – sand. For further explanations see Fig. 2



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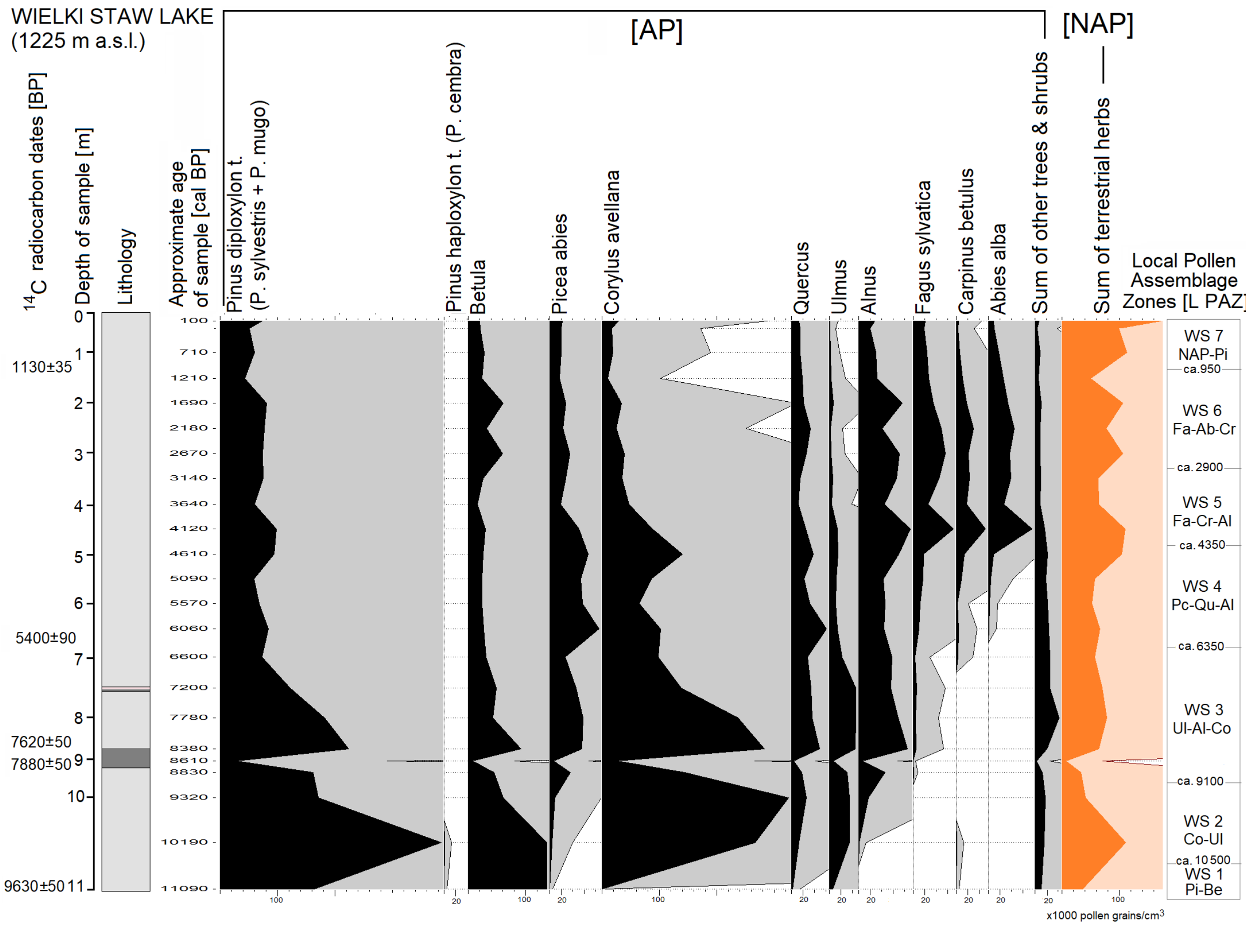

Figure 6. The Wielki Staw Lake. Diagram showing changes in pollen concentration of selected taxa. For further explanations see Fig. 2

Phase VI [L PAZ MS 6 *Carpinus-Abies-Fagus-Alnus*; ~4700–3100 cal BP & L PAZ WS 5 *Fagus-Carpinus-Alnus*; ~4350–2900 cal BP; Fig. 7]

Pinus sylvestris (possibly also *P. mugo*), *Picea* and *Larix* formed patches in an open environment (Figs 3, 5). In the Karkonosze Mts, further expansion of *Fagus* was observed between ~4600 and 4100 cal BP (Figs 3, 5; also Engel et al., 2010), slightly earlier than in the Eastern Sudetes (~3950 cal BP; Dudová et al., 2013). At the same time, the share of hornbeam and fir increased and played an important forest-forming role while the spruce stands were reduced. In the foothills and the lower montane forest zone, oak-lime-hornbeam forests with considerable admixture of hornbeam remained the basic type of communities. In the Krušné hory Mts the share of hornbeam was lower (Jankovská, 2006).

The area of alder woodland has expanded slightly since from about 4500 cal BP, which may have been related to climatic conditions. According to Wicik (1984a) in this time 'a series of extreme years in terms of thermal and humidity characteristics' occurred. It is consistent with the phase of the climate becoming strongly wet, recorded in the Carpathians (Margielewski, 1998; Bryndal et al., 2003; Starkel et al., 2013), which also brought increased fluvial activity in the upper Vistula (~4900–4400 cal BP).

Phase VII [L PAZ MS 7 *Fagus-Abies-Carpinus-Alnus*; ~3100–1100 cal BP & L PAZ WS 6 *Fagus-Abies-Carpinus*; ~2900–950 cal BP; Fig. 7]

In the vicinity of the lakes patches of *Pinus sylvestris* (and/or *P. mugo*), *P. cembra*, *Betula* and *Picea abies* occurred. The discovery of fir bark in the Wielki Staw Lake sediments confirmed its growth at an altitude of about 1220 m a.s.l. at ~1500 cal BP. It is in agreement with Hošek (1983), who indicated the occurrence of fir trees up to 1200 m a.s.l. At present fir is mostly distributed in the Karkonosze Mts up to 1000 m a.s.l. (Musil and Hamerník, 2007). Filipiak (2006) based on the current distribution of fir trees suggests, that in the past, *Abies alba* was widespread in the Sudetes at the altitude range 350–800 m a.s.l.

Thanks to the greater shade tolerance and wind resistance, fir and beech could effectively compete with spruce. The share of pioneer birch was slightly higher, as well as the representation of herbaceous plants.

Phase VIII [L PAZ MS 8 NAP-*Pinus*; ~1100–1 cal BP & L PAZ WS 7 NAP-*Pinus*; ~950–1 cal BP; Fig. 7]

The vicinity of the lakes was partly overgrown. It is confirmed by macrofossils of *Pinus sylvestris* (possibly *P. mugo*), *P. cembra* and *Larix decidua* found in the Wielki Staw Lake from the Middle Ages, as well as *P. sylvestris*, *Salix*. and *Picea* in the Mały Staw Lake (Wicik, 1986). The large patches covered with grasses, sedges and tall herbs indicated a largely open environment (Figs 3, 5).

The disturbances in the structure of forests and the general shrinking of their extent in the region have increased considerably since the Middle Ages. The Sudeten forests have suffered especially from human activity but also from natural catastrophes, e.g. formation of windfalls, snowfalls, an outbreak of insect pests and fungal diseases (Margas and Szymczak, 1969; Zimny, 1996; Pawlik, 2012). The cumulative effect of various environmental influences, especially human activities, was evident in our pollen records as a reduction in tree frequency. This concerned especially beech-fir forests, but also in the foothills oak-hornbeam and alder forests. It is also clearly marked in profiles from the Stołowe Mts from the 12th–14th centuries AD (Glina et al., 2017). At the end of the last century, the environment of the Western Sudetes suffered from intensive industrial activities around the so-called Black Triangle. Acid rain causes acidification of water and soils (Sienkiewicz et al., 2006) and affects the vegetation (e.g. Fiałkiewicz-Koziel et al., 2023).

EVIDENCE OF HUMAN ACTIVITY IN POLLEN RECORDS FROM POLISH KARKONOSZE MTS

High-mountain pollen sites associated with treeless or park-like subalpine vegetation on the summits collect data of extra local or regional origin also on human impact on the environment (e.g. Obidowicz, 1996; Rybníčková and Rybníček, 2006; Kozáková et al., 2021), which significantly limits the possibility to identify local anthropogenic impact undertaken on a small scale. This applies, according to Dudová et al. (2018), to the sites in the Jeseníky Mts, and also to the lakes in the Karkonosze Mts, where the transport of pollen grains by air currents (what is confirmed e.g. by the presence of *Juglans* pollen in the premedieval period) modified the obtained results in a way that is difficult to define.

At the outset, it should be also noted that the relatively low chronological resolution of the pollen data and the low precision of the depth-age model (especially from the Mały Staw Lake) significantly limits the possibility of correlating archaeological and palaeobotanical data. To assess this, other suitable sediments with better coverage of the last millennia (or existing sites in more detail) should be analyzed in the future.

The taxa classified as the secondary anthropogenic indicators, such as Poaceae, Chenopodiaceae, *Artemisia*, *Urtica*, *Rumex acetosella* and *Rumex acetosa* have been components of the vegetation since the Late Vistulian. However, increase in the frequency of herbaceous plants, the emergence of taxa with low pollen production and at least limited spatial distribution of pollen (such as *Polygonum aviculare*, *Trifolium*, *Plantago major*, *Centaurea cyanus*), including also primary anthropogenic indicators (cultivated taxa: *Triticum* type, *Secale cereale*, and *Fagopyrum*), are considered an argument pointing to the development of grasslands associated with grazing and agriculture (e.g. Behre, 1981; Kozáková et al., 2015, 2021).

In the case of the studied lakes, the onset of the continuous presence of *Plantago lanceolata* dates back to ~6300–6100 cal BP, and was accompanied by an increase in the taxonomic diversity of other herbs, but not in their frequency (Figs 3, 5). This phenomenon has been related to short-term disturbances of the plant cover caused by natural factors, particularly as the Karkonosze Mts remained beyond the range of settlement in the Early Neolithic. According to Kadrow (2019: p. 41) ‘the population of the oldest phase of the Linear Pottery culture (LBK; ~7200 cal BP; Fig. 3), which was formed south of the Carpathians and Sudetes, migrated relatively quickly to the loess areas located on the north side of those mountain ranges and settled there in enclave areas’. It is

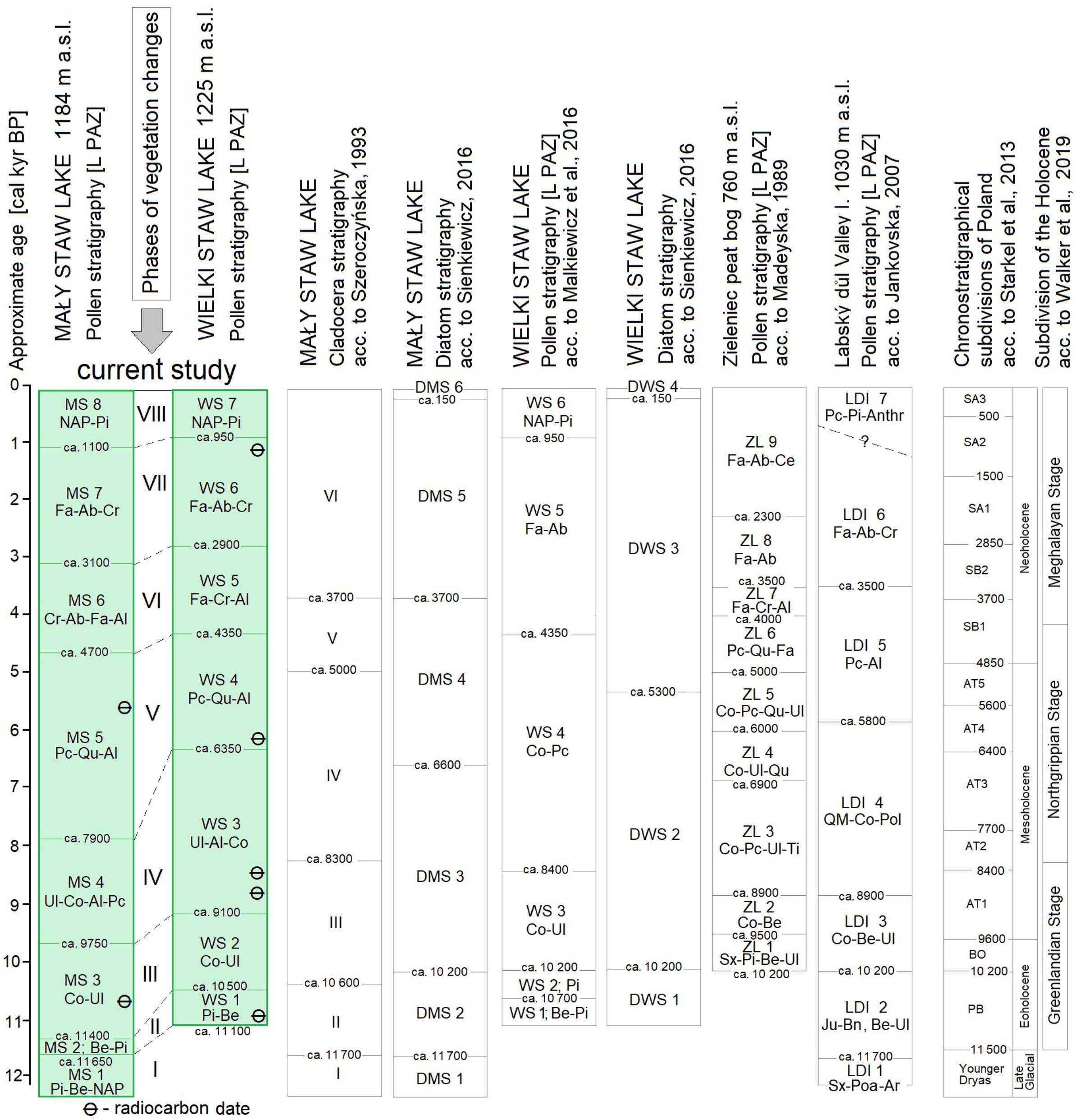

Figure 7. Correlation of the palynological stratigraphy of the studied sites with Cladocera and diatom stratigraphy, and with other pollen records from the Sudetes about Holocene chronostratigraphy. Ti – *Tilia*, Sx – *Salix*, Bn – *Betula nana*, Ju – *Juniperus*, Poa – Poaceae, QM – *Quercetum mixtum*, Ce – Cerealia, Pol – Polypodiaceae, Anthr – Anthropogenic taxa. For further explanations see Fig. 2

assumed that human activity first affected the belt of uplands stretching north of the Sudetes (e.g. Gedl, 1989; Kulczycka-Leciejewiczowa, 1993; Kozłowski and Nowak, 2019; Nowak et al., 2020). The increase in the number of archaeological sites occurred only during the settlement of the Funnel Beaker culture (TRB; ~5600–4800 cal BP; Kulczycka-Leciejewiczowa, 1993; Nowak, 2019; Nowak et al., 2020). Mainly fertile soils in the upper and middle Oder basin, as well as on the other side of the Sudetes on the Elbe River were exploited by humans. However, likely, that it was not until the pastoral people of the Corded Ware culture (CWC; ~4700–4200 cal BP; Włodarczak, 2009) moved deeper into the higher parts of the Sudetes and left archaeological traces of penetration also above 500 m a.s.l. (Kulczycka-Leciejewiczowa, 1993). In the Karkonosze Mts, slightly higher representation and taxonomic variability of herbaceous taxa, including secondary anthropogenic indicators, was observed ~5900 cal BP and ~5300 cal BP (Figs 3, 8). Then, the share of herbs increased visibly ~4100 cal BP suggesting the enlargement of grassland patches with Poaceae, *Plantago lanceolata*, *P. major*, *P. media*, *Urtica*, Chenopodiaceae, *Artemisia*, *Rumex acetosella* and

R. acetosa. These data reflected anthropogenic activity in areas outside the Karkonosze Mts (e.g. Kulczycka-Leciejewiczowa, 1993). An increase in the abundance of herbs from ~4800 cal BP was recorded in the Bystrzyckie Mts (Zieleniec peat bog; 760 m a.s.l.; Madeyska, 1989, 2005). The first direct indicators of crop cultivation (*Triticum* type pollen) were dated to ~3300 cal BP in the record of the Mały Staw Lake and to ~2600 cal BP in the Wielki Staw Lake (Figs 3, 5) during the development of the Late Bronze Age settlement north and south of the Sudetes. The further increase in grassland representatives and the fluctuations of taxonomic diversity was particularly pronounced in the Mały Staw Lake (see RAREF; Fig. 8) at ~3300 cal BP and ~2500 cal BP. In our opinion the mentioned human indicators reflected the regional phenomenon and resulted from the longer distance pollen transport. Archaeological sources indicated that the Early Únětice culture, developed between ~4200 cal BP and ~3900 cal BP, left faint traces indicating infrequent penetration of the Sudetes, and only the settlement of the Lusatian culture ~3400–2600 cal BP was more intense (Furmanek and Lasak, 2013). Although in the Lusatian Mts (the Western Sudetes) the first reliable indicators of human activities in pollen data appeared also in the Bronze Age. However, the pollen site there was located at an altitude of 400 m and well correlated with the archaeological evidence (Kozáková et al., 2015).

The archaeological finds from the pre-Roman and Roman Iron Age come mainly from the vicinity of Jelenia Góra, Walbrzych and Kłodzko. Most of them are linked to the Przeworsk culture (~2250–1450 cal BP), except a few from the Jelenia Góra surroundings, where the influence of the Luboszyce culture was noted (Błażejewski, 2006). The increased share of herbs in the Karkonosze Mts was marked by a very high concentration of pollen (Figs 4, 8). Single cereals pollen was also present at ~1430 cal BP. The observations from the Bystrzyckie Mts (Madeyska, 1989, 2005) showed the presence of cultivation indicators from that period (*Secale cereale* from ~1600 cal BP and *Centaurea cyanus* from ~2100 cal BP). In the highest regions of the Jeseníky Mts, pollen and charcoal data suggest the possible human interventions in the Iron Age (Novák et al., 2010; Dudová et al., 2018). Slightly younger were traces of human impact in the Czech part of the Karkonosze Mts (Černá hora peat bog; 1190 m a.s.l.) dated to ~1300 cal BP. The next increased anthropogenic influence going on until the present started ~800 cal BP when the presence of Cerealia and *Secale cereale* was indicative of sustained settlement and land use (Speranza et al., 2000).

In the case of our sites, the continuous curve of *Triticum* from ~1030 cal BP and that of *Secale cereale* pollen from ~850 cal BP in the Karkonosze Mts were associated with their transport from the arable fields located probably in short distances. In the 9th century AD, the Sudetes were on the border between various Central European political structures. In the Early Middle Ages (8th–10th century) hillforts were created in the Sudetes (Lisowska and Jaworski, 2021). They separated the Great Moravian State from its northern neighbours – Slavic tribes, inhabiting the area later known as Silesia (Wachowski, 1997; Buko, 2005; Moździoch, 2017). Archaeobotanical sources have confirmed that also millet *Panicum miliaceum* (whose pollen is indistinguishable from Poaceae) and rye became important crops in many places in Lower Silesia (SW Poland) from the 10th to the 12th century (Klichowska, 1956; Kosina, 1981; Kosina and Marek, 2021). This is consistent with Behre (1992) who indicated that rye was a major cereal in the High Middle Ages, especially in Germany and Central Europe. Ciok (1995) indicated that good conditions for agricultural activity in the Sudetes include areas lying below an altitude of 500–600 m a.s.l. The introduction of agriculture to the slopes of the Sudetes over the last several hundred years has led to a strong transformation of the environment and caused significant soil erosion, accumulation of diluvium, and a change in the drainage network (Latocha, 2005). *Vitis vinifera* and *Juglans regia*, registered in both studied pollen records, were, however, blown from some distance, but they have been cultivated e.g. in south-western Poland since the Middle Ages (Lityńska-Zając and Wasylikowa, 2005). The onset of long-term human impact and intense forest exploitation in the Sudetes dates back to around the 12–14th century (Valde-Nowak, 1999). Based on Pawlik (2012), it should be noted that in the 13th and 14th centuries AD planned colonization of the Sudetes was initiated. During that time the highest taxonomical diversity registered by pollen was observed (about

660–470 cal BP). In the modern time, mining of non-ferrous metal ores, copper and tin, developed, together with the activity of lime kilns for burning lime, ash and potash production (Peřina and Samek, 1958; Wilczkiewicz, 1982). There was also the development of metallurgy, related to, among others, the establishment of Szklarska Poręba and the start of glass production (Popowski, 2005). These forms of economic activity required a large amount of fuel and caused a significant reduction of forested areas, recorded in the pollen data as a strong fall of *Fagus* frequency and to a lesser extent also *Quercus*, *Carpinus* and *Abies*. Agricultural activity remained at a similar level until the 19th/20th century when slightly increased. In the 17th and 18th centuries sheep grazing emerged and was continued with varying intensity until the end of World War II (Peřina and Samek, 1958; Wilczkiewicz, 1982). It is indicated by the growing representation of taxa associated with pastures, such as Poaceae, *Aster*, *Taraxacum*, *Plantago lanceolata*, *Ranunculus*, *Potentilla*, *Juniperus* and taxa growing on disturbed, nitrogen-enriched substrate *Urtica*, *Artemisia* and Chenopodiaceae over the last three centuries in the pollen data from the Mały Staw Lake. Speranza et al. (2000) pointed at the maxima of deforestation in the 17th and 18th centuries recorded in the Černá hora site, supported by the local historical data. The Sudeten forests were affected by massive forest clearing in the 19th and 20th centuries. The dwarf montane pine in the 19th century was cut off on the peaks of the Karkonosze Mts, e.g. in the area of Równia pod Śnieżką (Wilczkiewicz, 1982). This event was not reflected in our pollen records (Figs 3, 5), nor is the mass extinction of spruce monocultures in the 1970s and 1980s, which occurred as a result of industrial emissions and damage of various origins (Mazurski, 2008).

NOTES ON THE POST-GLACIAL HISTORY OF *LARIX* AND OTHER COLD CLIMATE-ADOPTED SPECIES IN THE KARKONOSZE MTS

Larix decidua Mill.

European larch tree is native to the mountains of Central Europe, in the Alps and Carpathians, with disjunct lowland populations in Poland. This tree is very cold and wind tolerant with a cold hardiness limit of around –30°C (Da Ronch et al., 2016). *Larix decidua* is characteristic of the subalpine zone and the highest parts of the mountains of Central Europe. It may locally dominate their composition, but most often it grows together with *Pinus cembra* (Huntley and Birks, 1983). In the Tatra Mts, it forms patches of the *Cembro-Piceetum* association (Myczkowski, 1969). The typical European larch (*Larix decidua* subsp. *decidua*) occurs only in the Alps and the Tatra Mts, at the upper forest limit and in the upper part of the upper montane zone, while its Sudeten variety – *sudetica* – can be found in the lower mountain forest zone of the Eastern Sudetes (Boratyński, 1986). Important publications have appeared in recent years, summarizing available palaeoecological information about the history of *Larix* in certain areas of the Czech Republic and Slovakia (eastern part of Central Europe e.g. Jankovská and Pokorný, 2015; Wagner et al., 2015; Dudová and Szabó, 2022), including also data from the palynological database PALYCZ (Kuneš et al., 2008). Palaeobotanical data revealed that larch reached its maximum distribution in the Late Glacial and Early Holocene, but that its range shrank following climate warming. This also applies to Poland. Wagner et al. (2015) consider nuclear clusters distinguished based on genetic studies in the Alps and in the eastern Sudetes, the lowlands of Poland, the High Tatra Mts, and possibly also the south-eastern Carpathians as refugial areas from which European larch spread in the Late Glacial and Early Holocene. Palaeobotanical data showed that in Moravia and several parts of the Czech Republic, larch grew in mixed forests throughout most of the Holocene, while its disappearance in the Late Holocene could have been influenced by humans (Jankovská, 1998, 2007c; Jankovská and Pokorný, 2008, 2015). According to Dudová and Szabó (2022), *Larix* was present throughout the Early and Middle Holocene, disappeared from most of its sites (probably due to the closed canopy of climax forests) during its mid-late Holocene bottleneck, and then appeared again in the Iron Age (possibly thanks to human disturbances of vegetation). Up till now, the Jeseníký Mts were considered the only region of the Czech Massif where *Larix* survived throughout the Holocene (Dudová et al., 2013; Dudová and Szabó, 2022).

The distribution of fossil larch sites allows us to assume that its contemporary occurrence in some locations in Poland (Tatra Mts,

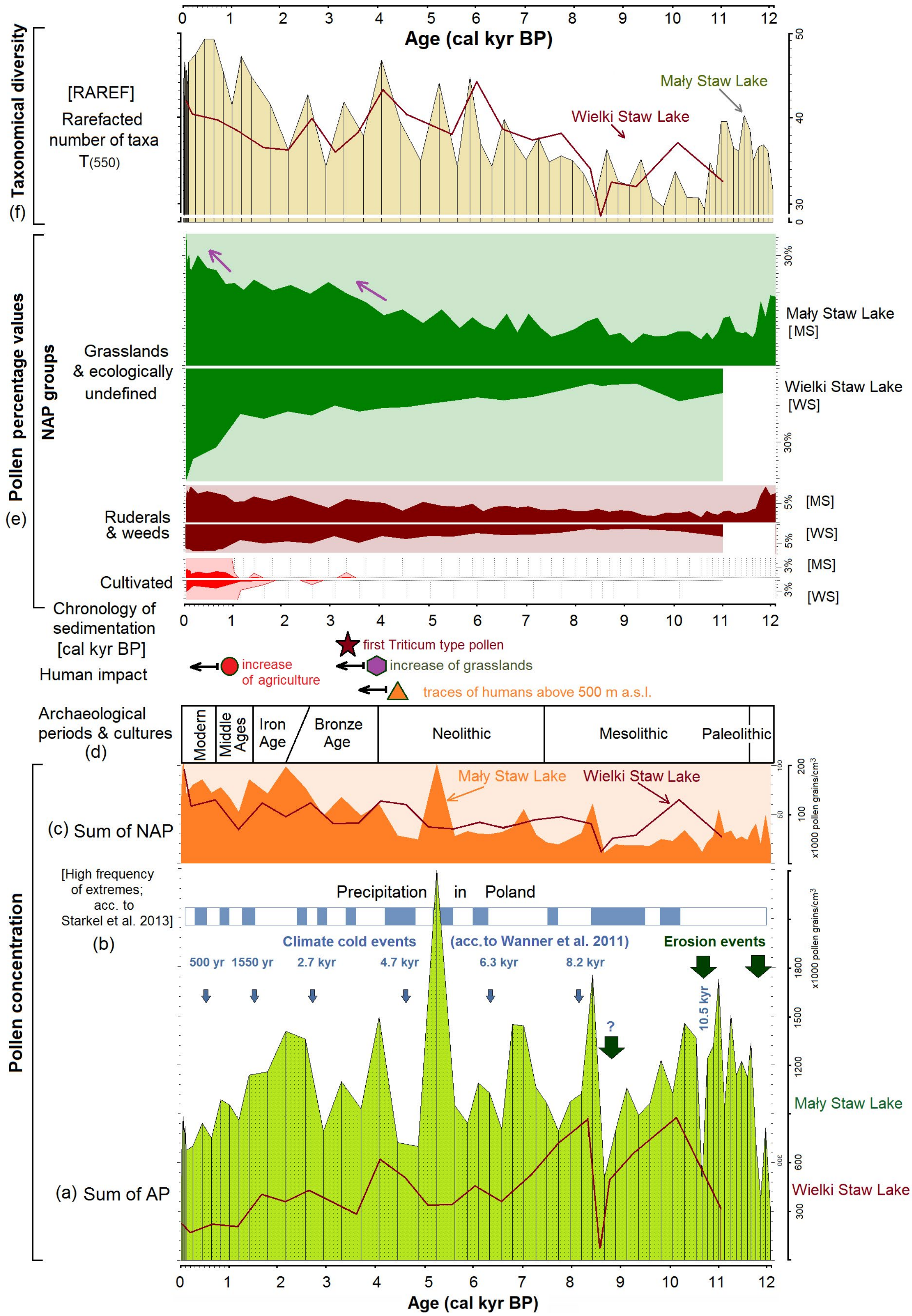

Figure 8. Diagram linking palynological data from the Mały Staw and Wielki Staw Lakes with archaeological and palaeoclimatic data – potential drivers of vegetation change. (a) concentration of arboreal pollen, (b) palaeoclimatic data: precipitation in Poland acc. to Starkel et al. (2013); cold climate events acc. to Wanner et al. (2011), (c) the concentration of non arboreal pollen, (d) archaeological division acc. to different authors cited in the text (e.g. Kulczyńska-Leciejewiczowa, 1993; Furmanek and Lasak, 2013; Nowak et al., 2020), (e) human impact; percentage values of NAP groups from the Wielki Staw and the Mały Staw Lakes, (f) pollen-based taxonomical diversity

Pieniny Mts, Beskid Niski Mts, Holy Cross Mts) is natural and continuous (Środoń, 1986; Starkel, 1988) from the glacial period, where the presence of *Larix* was confirmed throughout the Vistulian and in the Early Holocene (e.g. Środoń, 1986; Granoszewski, 2003; Wacnik et al., 2004; Madeyska, 2005; Szczepanek et al., 2013; Kołaczek et al., 2017). During the last glaciation and especially in the Early Vistulian interstadials (in the Brörup and Odderade), the share of larch in the forests was quite significant, as evidenced by numerous sites containing macrofossils and pollen grains (e.g. Środoń, 1986; Tobolski, 1991; Granoszewski, 2003; Krupiński, 2005; Malkiewicz, 2010; Kołaczek et al., 2012). Although the latter, due to their morphology and low possibility of being preserved in the sediment, are extremely difficult to register in pollen analysis (Dyakowska, 1936; Janssen, 1966; Huntley and Birks, 1983; Jankovská, 2007c; Pelánková and Chytrý, 2009; Sjögren et al., 2008a, b, 2010). For this reason, the presence of even single *Larix* pollen grains is considered evidence of the local presence of this tree. Even when larch dominates the composition of the surrounding forests, its value in the pollen diagram rarely exceeds 10% (Janssen, 1966; Huntley and Birks, 1983). An example may be research conducted in areas where larch is the only tree (forest tundra) and its pollen grains, despite the proximity of trees, occur sporadically (Jankovská, 1995, 1998; Panova et al., 2003; Jankovská et al., 2006). Data are very limited indicating the presence of larch in the Karkonosze Mts in the post-glacial period and, importantly, its macrofossils from the Holocene period have not yet been documented throughout the Sudetes. Our new data (combined pollen and macrofossils) are therefore particularly important, as they confirmed its occurrence in the Karkonosze Mts from ~11 500 to 6000 cal BP, then at ~3400 cal BP, and ~800–700 cal BP (Figs 3, 5). This corresponds well with the data from the Eastern Sudetes (Jeseníky Mts; Dudová and Szabó, 2022), proving that the Western Sudetes also helped the persistence of larch in the Holocene.

Pinus cembra L.

Another cold-resistant tree important for the vegetation history of the region for the end of the Vistula glaciation was Swiss stone pine. Nowadays, it is an endemic coniferous species growing in upper treeline ecotones of high elevations in the Alps and Carpathians (Casalegno et al., 2010; Caudullo and de Rigo, 2016; Zięba et al., 2019). In Poland, it occurs exclusively in the Tatra Mts, where grows on poor soils in the extreme conditions of cliff forests (at elevation 1300–1650 m a.s.l.) and is characteristic of the *Piceion abietis* alliance (Matuszkiewicz, JM., 2001). In the Alps it forms an association *Larici-Pinetum cembrae* with larch (Obidowicz et al., 2004a) and similarly to *Larix* it is very resistant to low temperatures down to −40°C. Swiss stone pine was one of the tree species that survived the Last Glacial Maximum in the Carpathians (Obidowicz et al., 2004a; Jankovská and Pokorný, 2008). However, it was frequently noted in the lowland Vistulian sites (e.g. Granoszewski, 2003; Kołaczek et al., 2012). The isopollen maps showed its main distribution limited to the southern part of Poland (Obidowicz et al., 2004a). This tree expanded into the Jasło-Sanok Depression (Harmata, 1989) and the Bieszczady Mts from ~15 600–13 900 cal BP (Ralska-Jasiewiczowa, 1980) and then spread toward the north and west. Our data confirmed that its range included also the Karkonosze Mts (Figs 3, 5) between ~12 000–11 200 cal BP in addition to the Carpathians (Ralska-Jasiewiczowa, 1980; Harmata, 1989; Ralska-Jasiewiczowa and Latałowa, 1996; Granoszewski et al., 2013; Schwörer et al., 2022). The possibility of its growth in the Czech part of the range in the Late Glacial and in the Early Holocene was previously pointed out by Jankovská (2007a). The finding of *Pinus cembra* needles in the Wielki Staw Lake dated to ~1130–930 cal BP confirmed its natural presence in the upper forest montane zone at that time. However, to verify the possibility that *P. cembra* survived throughout the Holocene in the Karkonosze Mts further research is needed.

Betula nana L.

The next taxon, dwarf birch representing shrub birches, regarded in Poland as a glacial relic, is currently widespread in the arctic regions. In the Northern Hemisphere, *B. nana* is a key component of arctic and alpine tundra and water-logged montane habitats (de Groot et al., 1997). At present it grows at only three isolated locations in Poland, in the Sudetes Mts (Izerskie mire; Izerskie Mts and Zieleniec peat bog; the Bystrzyckie Mts) and the Chełmno

Lake District (Linje mire; northern Poland). Aside from these locations, dwarf birch still grows in several places in the Alps and the Carpathians (Kruszelnicki and Fabiszewski, 2001). The occurrence of *B. nana* indicates that the maximum temperature of the coldest month was below 0°C and the minimum mean July temperature was around 7°C. (Kolstrup, 1980; Granoszewski, 2003; Isarin and Bohncke, 1999). Because its presence is related to low temperatures, it was more widespread during the Vistulian than it is today (Provan and Bennett, 2008). Ralska-Jasiewiczowa and Starkel (1988) suggested that dwarf birch disappeared in Poland in the Holocene climatic optimum (e.g. Essell et al., 2023), possibly due to the negative effects of the palaeoenvironmental conditions, such as an increase in temperature, very high precipitation and waterlogging of the substratum. Based on findings of *B. nana* pollen grains in the Karkonosze Mts from the Late Glacial and Early Holocene to at least the Atlantic period, Jankovská (2004b, 2007a) suggested that it cannot be excluded that it was growing there till historic times. However, there was a lack of objective evidence. Our studies filled this gap and revealed the discontinuous presence of dwarf birches in the Mały Staw Lake area from the Late Vistulian until modern times (~430 cal BP; Figs 3, 5). The results of molecular studies suggest that all Polish dwarf birch populations underwent a reduction in abundance during post-glacial and recently as a result of land reclamation (Jadwiszczak et al., 2012).

Alnus viridis (Chaix) DC. in Lam. et DC.

Green alder is distributed widely across the cooler parts of the Northern Hemisphere in the form of different subspecies. The subspecies *viridis* is found in different European montain ranges, mainly in the Alps and Carpathians at altitudes between 1600 m and 2300 m a.s.l. (Ball, 1993). It prefers moist and open areas, including avalanche tracks, edges of wet meadows, streambanks and/or other disturbed sites, which play an important role in primary successions (Mauri and Caudullo, 2016). In Poland, green alder reaches the north-western border of the Carpathian range. This shrub associated with the Eastern Carpathians grows in Poland in natural sites in humid gullies on the summits of the Western Bieszczady Mountains, as part of the *Pulmonario-Alnetum* association (Jasiewicz, 1965), above the upper forest limit (Skoczowski et al., 2021). Macrofossils and pollen of *Alnus viridis* were discovered, among others, in Late Glacial and Early Holocene materials from the Bieszczady Mts (Ralska-Jasiewiczowa, 1980). Our pollen data from the Mały Staw Lake confirmed its wider range beyond the Carpathian Mts, covering also the Karkonosze Mts in the Late Vistulian and the Early Holocene (from ~12 100 to ~8700 cal BP; Fig. 3). To our knowledge there are no traces so far in the younger Holocene outside the Carpathians.

Selaginella selaginoides (L.) P.Beauv. ex Schrank et Mart.

The open, humid environment in the subalpine zone of the Karkonosze Mts was conducive to a rich representation of cryptogams. One of them was club spikemoss, an arctic-alpine species whose range covers Northern Europe, Iceland, Greenland, the Alps, the Carpathians, the Rhodopes, the Dinaric Mountains and the Pyrenees Mts (Hultén and Fries, 1986). *Selaginella* grows in areas with a cold climate, with the temperature of the warmest month not exceeding +17°C (optimum mean temperature 10–14°C) and with a minimum mean July temperature of 7°C (Kolstrup, 1979). In Poland, it occurs only in the Western Carpathians (Zając and Zając, 2001) and in the higher parts of the Sudetes (Izerskie Mts and Karkonosze Mts). In recent years, in the Karkonosze Mts, it has been found only in three small localities in humid surfaces of post-glacial basins (Krukowski, 2000). It prefers grassy rock ledges, flat areas and stream banks (Pawłowski, 1956). It is a species characteristic of the *Festuco versicoloris-Seslerietum tatrae* association and also grows in associations of the *Caricetalia davallianae* order. Spores of *Selaginella selaginoides* are very often found in flora of various glacial periods, including those from the Vistulian, from areas that are currently beyond its range of occurrence, i.e. in the European Plain (Hultén and Fries, 1986). The isopollen maps of Poland registered it occurred throughout the country, in the period approx. 13 900–11 700 cal BP. The highest shares were noted ~11 700 cal BP in the Bieszczady Mts and the Małopolska Upland. *Selaginella* was displaced to mountains due to the warming progress and the expansion of forest communities, and its modern range was established between 11 700 cal BP and 10 800 cal BP (Granoszewski et al., 2004). According to Jankovská (2004a), findings of *Selaginella* spores were sporadic in Late Vistulian deposits of the Labský důl Valley. More numerous were found on the Pančava mire from the Early and Middle Holocene. An almost continuous occurrence of *Selaginella selaginoides* spores was reported by Madeyska (2005) and Malkiewicz et al. (2016) from the profile of the Wielki Staw Lake from the entire Holocene (Fig. 5). It is interesting that it was not found in the Mały Staw Lake where the possible reason was the lack of exposed, wet habitats near the lake, which would favour its development.

Huperzia selago (*Lycopodium selago*) (L.) Bernh. ex Schrank et Mart.

Northern firmoss is classified as a mountain plant, and at the same time, due to its wide range covering the boreal zone of Eurasia and North America, it is treated as an arctic-alpine species (Pawłowski, 1972; Piękoś-Mirkowa and Mirek, 2006). In Poland, it grows in all mountain ranges and also has numerous locations in the southern Polish uplands and Pomerania. In the Tatra Mts, it occurs from the lower montane forest zone to the highest peaks, and in the Sudetes it reaches an altitude of 1590 m a.s.l. It is mainly associated with spruce forests of the Vaccinio-Piceetea class (Piękoś-Mirkowa and Mirek, 2006). Our data confirmed observations by Malkiewicz et al. (2016), and documented the persistence of this species in the Karkonosze flora since the end of the glacial period throughout the Holocene.

CONCLUSIONS

The main results of the present paper can be summarized as follows:

1. The Late Vistulian and Early Holocene, so far the least understood periods in terms of vegetation history, were recorded in bottom sediments from the previously unexplored Mały Staw Lake. The initial vegetation in the upper mountain zone developed on a mosaic of habitats at ~1180 m a.s.l. and was characterized by the presence of patches of cold subalpine meadows with high taxonomic diversity (including steppe and tundra elements). At the beginning of the Holocene, open vegetation with dwarf birch, willow, green alder and juniper dominated, with at least a few birches appearing in the upper montane zone around the lake area, while the region was overgrown by loose boreal pine-birch forests with Swiss stone pine and larch.

2. The palaeobotanical record from the Wielki Staw Lake, the second study site located just 40 m higher, was about a millennium shorter. It began after the immigration of elm and hazel into the Karkonosze foothills (~11 100 cal BP). The immediate vicinity of this lake was probably treeless until about 8500 cal BP when the range of *Pinus sylvestris* (and/or *Pinus mugo*) extended above 1220 m a.s.l.

3. The study of plant macrofossils was crucial in confirming the local composition of plant cover. Combined micro- and macroremains studies confirmed the broader difference from what was thought the range of cold-adopted species e.g. *Larix decidua*, *Pinus cembra*, *Betula nana*, *Alnus viridis*, *Juniperus* in Poland which, at least in the Younger Dryas and the Early Holocene, extended also into Karkonosze Mts. The study also identified the status as glacial relicts of selected taxa (*B. nana*, *Selaginella selaginoides*, *Huperzia selago*).

4. Larch remains, discovered for the first time in the whole Sudetes in the form of macroremains, correspond well with the data from the Eastern Sudetes and confirm that also Western Sudetes favored the persistence of larch during its Mid-Late Holocene period of the greatest reduction of its range.

5. The discovery of *Pinus cembra* needles in the Wielki Staw Lake, dated to the Middle Ages, confirmed its natural presence in the upper montane forest zone during that period. However, further research is needed to verify the possibility that *P. cembra* survived in the Karkonosze Mts from the end of the glaciation throughout the Holocene.

6. The occurrence of macrofossils in lake sediments generally coincided with the Holocene climatic optimum and the period from ~500 cal BP. In the vicinity of the Wielki Staw Lake, the presence of woody taxa was most common around 8500–5100 cal BP and during the last 1500 years, while in the Mały Staw Lake area, it was most frequent between ~9300 and 4100 cal BP. This indicates changes in the upper forest limit over time.

7. Two episodes of increased erosion, a sharp decline in pollen concentration and a reduction

in taxonomic diversity recorded in sediments of both lakes ~10 600 cal BP and ~8700–8500 cal BP were possibly related to periods of climate oscillation during the Early Holocene.

8. The spread of *Picea* began ~10 300 cal BP and lagged behind that of the Western Carpathians. It reached its maximum extent in the upper mountain forest zone between 8000 and 4600 cal BP. The expansion of *Fagus sylvatica* began ~6800 cal BP, much earlier than *Abies alba*, which appeared around 5300 cal BP as the last forest-forming species to arrive in the Karkonosze Mts.

9. Two periods of grassland expansion have been identified. The first occurred during the Younger Dryas and Early Holocene when the development of cold subalpine grasslands was supported by the cold climate following glacial melt in the Łomnica Valley. The second was recorded in the Late Holocene, ~4100 cal BP, and reflects human influence in the wider region.

10. Cerealia pollen first appeared ~3300 cal BP in sediments from the Mały Staw Lake and ~2600 cal BP in the Wielki Staw Lake, indicating a chronological association with the Bronze Age. This presence most likely reflected remote settlement and agricultural activities carried out in the Sudetic foothills.

11. From the Middle Ages onwards, the relatively undisturbed vegetation was subject to continuous and strong human interference caused by various economic activities (i.e. metallurgy, non-ferrous metal ore mining, glass production, forest industry) requiring logging. Starting ~1000 cal BP onwards, the development of agriculture in the region favoured the expansion of meadows and pastures.

The studies are characterized by a relatively low resolution of analyses and dating, which strongly limits the possibility of drawing precise conclusions and making comparisons between sites. Nevertheless, the material from the Mały Staw Lake, in particular, revealed great potential for palaeoenvironmental research. Many interesting questions remain unresolved, such as the emergence of *Pinus mugo* and the development of subalpine communities dominated by this species. Future high-resolution interdisciplinary research is undoubtedly needed, including the development of detailed age-depth models, as well as the creation of an archaeological database to precisely correlate the various data sources.

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ADDITIONAL INFORMATION

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