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ORIGINAL PAPER

Characeae-dominated vegetation succession as a key to understanding the late glacial environmental changes (ca. 14,600–13,500 cal yrs BP): a multi-proxy record of palaeo-waterbody developed within the Klaklowo landslide, the Outer Western Carpathians, S Poland

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Abstract Aquatic ecosystems developed within landslide depressions are common in the region of the Outer Western Carpathi, and they frequently record detailed pond-to-fen vegetation successions initiated by the warming climate of the Bølling-Allerød period. In the Klaklowo landslide fen (the Beskid Makowski Mountains, S Poland) the late glacial deposits are represented by a long (approximately 2.5 m) minerogenic-organic sequence with a distinct section corresponding to the Older Dryas cooling. Here, we applied a high-resolution multi-proxy study (grain size, geochemical, pollen and macrofossil analyses, radiocarbon dating), and we reconstructed vegetation, hydrological and climate changes recorded in the bottom part of the Klaklowo fen sequence (depth range of 250–367 cm). A special emphasis was put on investigating the conditions affecting development of Characeae-dominated vegetation succession and possible reasons behind the discontinuous pollen record. Multi-proxy results revealed that the late glacial sequence (ca. 14,600–13,500 mod. cal yrs BP) of the Klaklowo fen consisted of five palaeoecological stages of development which correspond to the Greenland ice core and Gerzensee chronologies. During the first stage, presumably dry and cold conditions of steppe-tundra prevailed in the surroundings of a poor-in-vegetation Klaklowo waterbody I, matching the Oldest Dryas and Bølling climatic phases. Deterioration of the pollen record observed within this stage

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most probably resulted from the post-depositional oxidation due to periodical water-level changes of the waterbody I. During the second stage, palaeo-pond was transformed into a short-lasting fen likely with a more wide-spread steppe-tundra vegetation in the catchment area reflecting the dry and cold climate of the Older Dryas. Further two sub-stages of the Klaklowo waterbody II were characterized by aquatic vegetation and boreal forest succession signalizing the Allerød warming. The co-occurrence of macrophytes dominated by wide-spread Characeae meadows and intense precipitation of calcium carbonate indicate that alkaline conditions prevailed in the Klaklowo waterbody II at that time. Carbonate formation probably resulted from leaching of carbonate-bearing bedrock in the catchment area and calcium-rich groundwater supply to the pond intensified by increased precipitation. The last stage is characterized by the disappearance of Characeae meadows which may be attributed to multiple factors including the transition of the palaeo-pond into a fen and related acidification.

Keywords Landslide fen · Macrofossil analysis · Discontinuous pollen record · Bølling · Older Dryas · Allerød

Introduction

For the late glacial period, Bølling and Allerød climate warmings were separated by a short (ca. 100–200 years) climate cooling called Older Dryas that is observed within the climate-biostratigraphic division for Scandinavia (Iversen 1954). Among deposits of peatlands and lakes from various hypsometrical settings, the Bølling-Older Dryas-Allerød sequence is often distinctively expressed in palaeo-records of mountainous sites due to the possible proximity of vegetation ecotones and favourable local environmental features, e.g. altitude, exposure, topography and hydrology (Feurdean et al. 2007; Ammann et al. 2013; Margielewski et al. 2022a). Previous research conducted in the Outer Western Carpathians has proven that landslide fens, small peatlands developed within landslide depressions, are sensitive indicators of palaeoenvironmental and palaeoclimatic changes (Margielewski 2018). In the Klaklowo landslide fen, as well as in the neighbouring Kotoń landslide fen (Beskid Makowski Mountains, Outer Western Carpathians, S Poland), multi-proxy analysis of the fen deposits revealed a long (ca. 2.5 m and 3.5 m, respectively) minerogenic-organic sequence of the late glacial (Margielewski 2001; Margielewski et al. 2003). Based on the plant-macrofossil analysis previously conducted for the Kotoń site, lacustrine clastic deposits of the Bølling Interstadial showed some evidence of a warmer climate only within a thin organic horizon with seeds of *Viola palustris* (Margielewski et al. 2003). During the Older Dryas cooling the Kotoń waterbody was shallow and eutrophic, surrounded by reeds and inhabited by *Chara* sp. and other macrophytes (Margielewski et al. 2003). With the onset of Allerød warming, the share of sedges increased and became dominant, in this way causing overgrowing of the palaeo-waterbody by vegetation (Margielewski et al. 2003). As a result, the Bølling-Older Dryas-Allerød climatic oscillations were well-documented by the local aquatic and boggy plant succession of the Kotoń landslide fen.

In modern freshwater ecosystems, which constitute analogues to ancient lakes and peatlands, the dynamics of Characeae macroalgae and other macrophytes have been thoroughly studied from the perspective of the ongoing climate change (Hargeby et al. 2004; Rip et al. 2007; Sleith et al. 2018). Growth and stability of Characeae phytocenosis depends on many environmental factors: low turbidity of water, favourable depth of waterbody, oligo- to mesotrophic conditions, basic pH and buffering capacity of water, temperature (including interannual changes influencing the length of a spring clear-water phase), salinity and others (Kufel and Kufel 2002; Hargeby et al. 2004; Pełechaty et al. 2013; Choudhury et al. 2019). These in-situ factors are, in turn, modified by different external drivers, mostly related to characteristics of the lake catchment (e.g. nutrient and solid material delivery) and climate (Hargeby et al. 2004).

Water-level fluctuations in palaeo-lakes and mires were frequently triggered by climate changes, thus, they may be effectively correlated with changes in the pollen sequences (Słowiński et al. 2016; Margielewski et al. 2022b, 2024). Water-table lowering may also, however, result in aerobic conditions, which in turn can cause the decomposition of pollen grains. Deteriorated pollen records, either in a form of entirely sterile or partially depleted sequences (sterile horizons), frequently hamper a detailed reconstruction of past vegetation (Carrión et al. 2007, 2009). Among 221 study sites in the Iberian Peninsula investigated in terms of discontinuous pollen records, 36 localities concerned lakes/palaeolakes and peat bogs (Carrión et al. 2009). On the other hand, discontinuous pollen records and other proxies may indicate prolonged exposure to subaerial conditions. For instance, as iron oxidizes faster than manganese, low Fe/Mn ratios determined by geochemical analysis indicate good oxygenation of bottom water and can be used for palaeo-reconstructions of redox conditions (Naeher et al. 2013). Furthermore, geochemical indicators usually used in soil research can be applied: high levels of oxygenation cause mineralization of ammonium nitrogen to nitrate nitrogen, resulting in NO_3/NH_4 ratios higher than 1 (Gotkiewicz 1973, 1996). Additionally, water-table fluctuations can be indirectly interpreted from changing contents of soil organic carbon (SOC) and total nitrogen (TN), as well as SOC/TN ratios. These parameters allow for determining increased biomass input and terrestrial vs aquatic sources of organic matter in lacustrine/peatland sediments (Zeng et al. 2017).

Here, we present results of a new multi-proxy study of recently collected sediment cores from the Klaklowo landslide fen, including grain size, geochemical (SOC, TN, N–NH_4, N–NO_3, P–PO_4, $CaCO_3$, and selected results of ICP–MS analysis: Mn and Fe), palynological and non-pollen palynomorphs, and—particularly—plant macrofossil analyses with the addition of determinable taxa of animal remains (e.g. Ostracoda, Porifera, Chironomidae), and radiocarbon dating. The main research objective was to reconstruct past vegetation, climate and hydrological changes recorded in the bottom part of the late glacial sedimentary sequence (depth section of 250–367 cm; Bølling, Older Dryas and the beginning of Allerød). A special attention was paid to the development of a well-pronounced Characeae-dominated aquatic plant succession revealed—similarly to the neighbouring Kotoń site—by plant-macrofossil analysis in the supposed Older Dryas deposits. Furthermore, the possible reasons behind the discontinuous pollen record were investigated for the Klaklowo fen deposits.

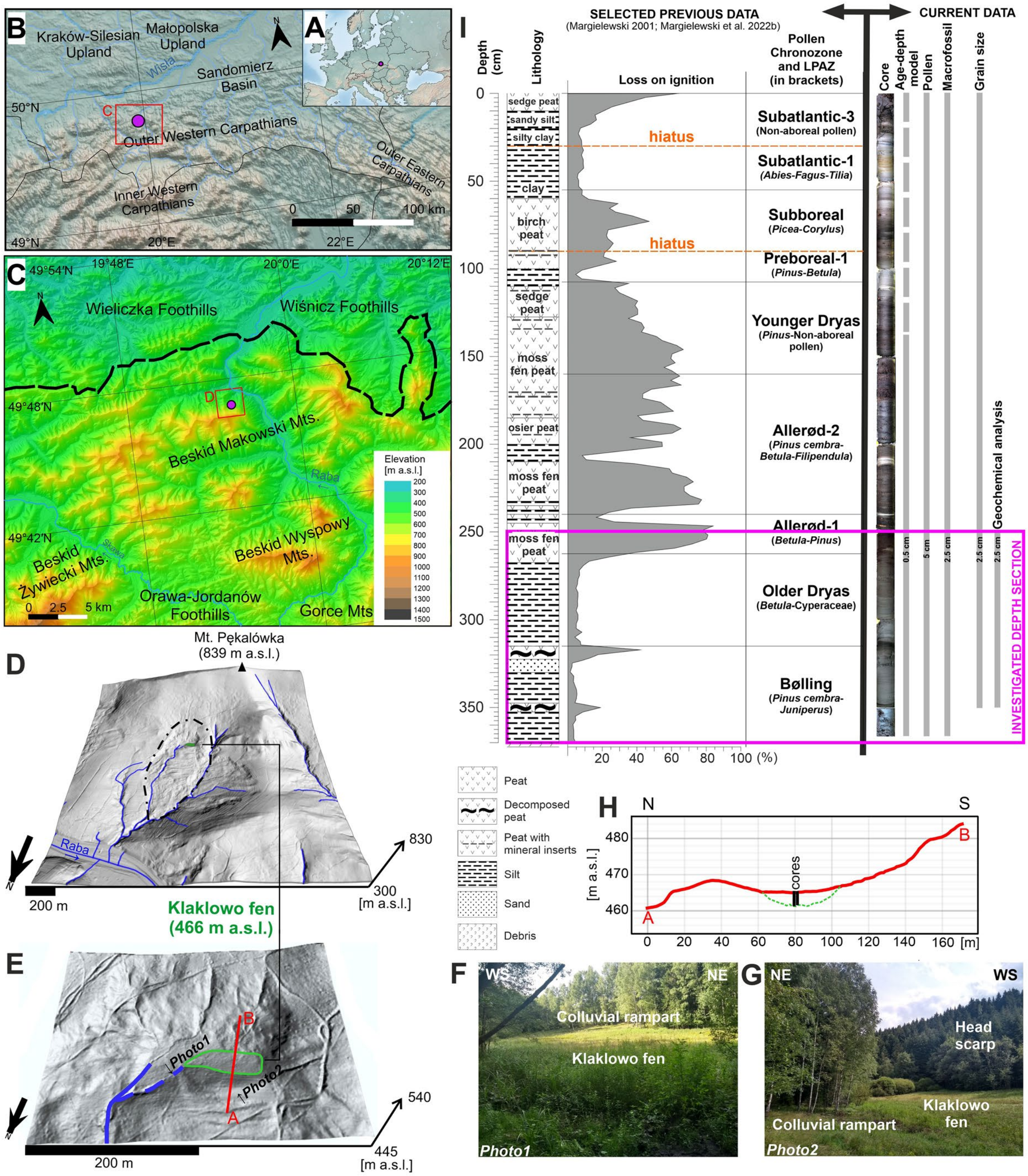
Site description

Geological and geomorphological setting

The study site is located in the Beskid Makowski Mountains, which is part of the Outer Western Carpathians in the south of Poland (Fig. 1 A and B). Geologically, it is situated within the Siary Subunit of the Magura Unit (Książkiewicz et al. 2016), which is one of the overthrust tectonic units (nappes) that form the Outer Western Carpathians. The Carpathian orogen is built of flysch rocks comprising siliciclastic-clayey turbidites (occasionally also of carbonate and siliceous rocks) of the age ranging from Late Jurassic to Early Miocene (Książkiewicz 1972). The investigated Klaklowo landslide (centre at 450 m a.s.l.) and the subsequently formed peatland is embedded in the northern slope of Mt. Pękalówka (839 m a.s.l.), opening toward the valley of one of the Raba River tributaries (Fig. 1 D). Details on the landslide geometry and geological description are given in the Electronic Supplementary Material (ESM). The depression of the Klaklowo fen is elongated latitudinally (about 100 m long), shorter longitudinally (40 m wide) with a shape that is slightly bent southward due to the semicircular head scarp of the landslide (70 m high) encompassing it from the south (Fig. 1 E–H). From the north the depression is dammed with colluvial rampart, on the right of which a stream is flowing out from the fen into the valley (Fig. 1 E–H). At present, the Klaklowo landslide's sub-scarp depression is a mire of minerogenic type (a fen) (Fig. 1 F and G).

Climate, hydrology and vegetation

The mean annual precipitation for the Beskid Makowski Mountains is 800–1000 mm and mean annual temperature ranges from 8.0 to 8.5 °C (Tomczyk and Bednorz 2022). With respect to surface waters, there are small watercourses (some of them periodical) flowing down from the head scarp, mixing within the basin of the fen and flowing out as one stream along the eastern boundary of the landslide (Fig. 1 E). Regional and local topography, climate and hydrology influence the vegetation patterns



A
B
Kraków-Silesian Upland
Małopolska Upland
Wisła
Sandomierz Basin
50°N
C
Outer Western Carpathians
Outer Eastern Carpathians
Inner Western Carpathians
0 50 100 km
49°N
20°E
22°E
C
49°54′N
19°48′E
20°0′E
20°12′E
Wieliczka Foothills
Wiśnicz Foothills
49°48′N
D
Beskid Makowski Mts.
Raba
Elevation [m a.s.l.]
200 300 400 500 600 700 800 900 1000 1100 1200 1300 1400 1500
49°42′N
Beskid Żywiecki Mts.
Beskid Wyspowy Mts.
Orawa-Jordanów Foothills
Gorce Mts
0 2.5 5 km
D
Mt. Pękalówka (839 m a.s.l.)
Raba
830
300 [m a.s.l.]
200 m
Klaklowo fen (466 m a.s.l.)
E
Photo1
Photo2
A
B
540
445 [m a.s.l.]
200 m
I
SELECTED PREVIOUS DATA
(Margielewski 2001; Margielewski et al. 2022b)
CURRENT DATA
Depth (cm)
Lithology
Loss on ignition
Pollen Chronozone and LPAZ (in brackets)
Core
Age-depth model
Pollen
Macrofossil
Grain size
Geochemical analysis
sedge peat
sandy silt
silty clay
clay
birch peat
sedge peat
moss fen peat
osier peat
moss fen peat
moss fen peat
hiatus
hiatus
Subatlantic-3 (Non-aboreal pollen)
Subatlantic-1 (Abies-Fagus-Tilia)
Subboreal (Picea-Corylus)
Preboreal-1 (Pinus-Betula)
Younger Dryas (Pinus-Non-aboreal pollen)
Allerød-2 (Pinus cembra-Betula-Filipendula)
Allerød-1 (Betula-Pinus)
Older Dryas (Betula-Cyperaceae)
Bølling (Pinus cembra-Juniperus)
0.5 cm
5 cm
2.5 cm
2.5 cm
2.5 cm
INVESTIGATED DEPTH SECTION
0 50 100 150 200 250 300 350
20 40 60 80 100 (%)
Peat
Decomposed peat
Peat with mineral inserts
Silt
Sand
Debris
H
N
S
480
470
460
[m a.s.l.]
cores
A
B
0 20 40 60 80 100 120 140 160 [m]
F
WS
NE
Colluvial rampart
Klaklowo fen
Photo1
G
NE
WS
Head scarp
Klaklowo fen
Colluvial rampart
Photo2

◂**Fig. 1** Location of the Klaklowo landslide fen (purple circle) in Europe (**A**), the region of the Outer Western Carpathian (**B**) and the Beskid Makowski Mountains (**C**), dashed line in part C—boundary between foothills and Beskids' relief zones; **D** Klaklowo landslide zone (outlined with the dashed line) with the position of the Klaklowo landslide fen (area in green), **E** present-day area (green solid line) of the fen with A-B cross-section (see H); **F** and **G** present-day Klaklowo fen (photo by Jolanta Pilch); **H** A, B cross-section through fen (see E) with the position of the cores collected for the purpose of the current study; **I** on the left—selected results from the previous study of the Klaklowo landslide fen (Margielewski 2001; Margielewski et al. 2022b): lithology/peat type description, loss on ignition curve, chronozones and local pollen assemblages zones (LPAZ) (by V. Zernitskaya); on the right—new analyses carried out in the present study—length of a grey bar shows the extent of the analysis along the core, dashed bar—sections with analysis in progress; investigated depth section—section of the deposits presented in this paper. Sources of basemaps used in Fig. 1 are given in ESM

(Fig. 1 F and G): nowadays the slopes of the Beskid Makowski Mountains are located within submontane (< 550 m a.s.l.) and the lower montane vegetation belt (550–870 m a.s.l.) and are overgrown mainly with mixed forest with predominance of beech (*Fagus sylvatica*) and fir (*Abies alba*) and some occurrence of spruce (*Picea* sp.). Birch (*Betula* sp.) appears locally on the landslide surfaces and it is also present in the Klaklowo fen vicinity. Willow (*Salix* sp.) shrubs are present at the swampy sites, whereas wet margins of streams are covered by alder (*Alnus* sp.) (Mirek 2013).

Materials and methods

Coring and sampling

Sediment cores were collected from the central (deepest) part of the Klaklowo fen depression (N 49^0 46.772'; E 19^0 55.383'; 466 m a.s.l.; Fig. 1 H) using INSTORF Russian peat sampler (diameter: 8 cm). The drilling site was repeated at the same location which was probed during an earlier study (Margielewski 2001) to enable comparison between the profiles. Bedrock of the fen was reached at the maximum depth of 367 cm (Fig. 1 H and I). Subsequently, cores were sampled for multi-proxy analyses: pollen and NPPs, plant macrofossils, radiocarbon dating, grain size and geochemistry (Fig. 1 I). To investigate the targeted late glacial climatic oscillations, the depth section of 250–367 cm was selected as the primary area of subsampling. Sampling interval was 2.5 cm except for the pollen analysis in which it was 5 cm (Fig. 1). However, the sampling interval was modified at some depth points of the profile according to requirements of a given analysis (e.g. excluding samples made of pure organics in granulometric analysis), what resulted in a slightly changing number of samples per proxy. All maps, 3D views and cross-sections presenting localization of the study area and drilling site (Fig. 1) were compiled in QGIS 3.10.8.

Radiocarbon dating and age-depth model

In total, ten radiocarbon dates were obtained from a depth section of 140–367 cm of the sediment core at sampling spots corresponding to stratigraphic boundaries or significant changes in lithology (Table 1). Organic material (mostly plant fruits and aerial parts of moss stems) was selected during macrofossil analysis for Acceleration Mass Spectrometry (AMS) dating. Obtained ^{14}C age data were further calibrated using the OxCal v. 4.4 software (Bronk Ramsey 2009) and the IntCal20 calibration curve (Reimer et al. 2020) (Table 1). The chronology of the Klaklowo sediment sequence was derived by constructing the Bayesian age-depth model based on eight ^{14}C AMS dates. Two dates, MKL–A5610 and MKL–A5462, which constituted the two first attempts of dating the beginning of the accumulation of the peat sequence at a depth of approx. 260–270 cm, were excluded from the calculations due to their distinctively overestimated ages. The modelling of the age-depth curve was performed in the OxCal software using the P_sequence function, interpolation = 2 (0.5 cm), parameters k0 = 1 and log10(k/k0) = U(− 1,1), and by applying the IntCal 20 calibration curve. The modelled age (μ values rounded to tens) expressed as mod. cal yrs BP and sedimentation rate expressed in mm year^{-1} were determined for the sediment sequence.

Grain-size analysis

The grain-size analysis was carried out using laser diffraction with the Mastersizer 3000 granulometer (Malvern Panalytical, United Kingdom). Content

Table 1 Results of radiocarbon dating of the Klaklowo landslide fen deposits

No	Depth (cm)	Material	Macrofossil type	Lab code*	Age ^{14}C (yrs BP)	Calibrated age 2σ 95.4% (cal yrs BP)	Mean μ (cal yrs BP)	Sigma σ (cal yrs)	Context of dating
1	140.0–142.5	Moss-fen peat	Needles of *Larix decidua*	MKL-A6288	9860 ± 33	11,390–11,379 (1.9%), 11,326–11,202 (93.6%)	11,261	38	Within the Younger Dryas chronozone
2	160.0–162.5	Moss-fen peat	Needles of *Pinus sylvestris*	MKL-A6289	10,395 ± 30	12,479–12,096 (92.9%), 12,086–12,058 (2.6%)	12,279	119	Allerød and Younger Dryas boundary
3	200.0–202.5	Peat intercalated with silt	Needles of *Pinus sylvestris*	MKL-A6290	11,080 ± 29	13,092–12,918 (95.4%)	13,009	52	Gerzensee oscillation
4	239.5–241.5	Peat intercalated with silt	Needles of *Pinus sylvestris*	MKL-A6291	11,678 ± 30	13,596–13,475 (95.4%)	13,539	37	Allerød-1 and Allerød-2 boundary
5	260.0–262.5	Organic-clastic sediment	Needles of *Pinus sylvestris*	MKL-A6130	11,700 ± 31	13,604–13,481 (95.4%)	13,549	39	Beginning of accumulation of peat sequence
6	262.5–265.0	Organic-clastic sediment	Stems of mosses	MKL-A5610	12,253 ± 37	14,761–14,746 (0.8%) 14,324–14,061 (94.6%)	14,190	127	Beginning of accumulation of peat sequence
7	270.0–272.5	Clastic-organic sediment	Needles of *Pinus sylvestris*, stems of mosses	MKL-A5462	13,353 ± 37	16,228–15,906 (95.4%)	16,068	79	Beginning of accumulation of peat sequence
8	319.0–322.5	Decomposed peat	Fruits of *Eleocharis palustris*, stems of mosses	MKL-A5463	11,981 ± 35	14,024–13,906 (48.2%), 13,894–13,785 (47.2%)	13,898	75	Centre of the second organic horizon
9	347.5–350.0	Decomposed peat	Stems of mosses	MKL-A5464	12,238 ± 34	14,309–14,059 (95.4%)	14,160	100	Top of the first organic horizon
10	355.0–357.5	Decomposed peat	Stems of mosses	MKL-A5465	12,422 ± 42	14,896–14,277 (95.4%)	14,568	176	Bottom of the first organic horizon

*Laboratory of Absolute Dating in Kraków, Poland, in collaboration with the Center For Applied Isotope Studies, University of Georgia, U.S.A of sediment fractions, sediment type and statistical parameters of the grain-size distribution according to Folk and Ward's (1957) graphical method were calculated in GRADISTAT software (Blott and Pye 2001). Transport and deposition mechanisms of sediments were determined based on C–M diagram (Passega and Byramjee 1969). The peat-type description was adopted from a previous study (Margielewski 2001), in which it was determined based on plant-tissue analysis and the classification of Tołpa et al. (1967) (Fig. 1 I).

Geochemical analyses

The carbonate content (equivalent of $CaCO_3$ obtained from CO_2 concentration released in the reaction with 10% HCl) was determined using Scheibler's volumetric method (Loeppert and Suarez 1996). Further, a set of geochemical proxies usually applied in soil research (Wang et al. 2022) was employed. Total carbon and total nitrogen content (TN) were determined by dry combustion using a Vario Micro Cube CHN elemental analyser with TCD detection (Elementar Analysensysteme GmbH, Langenselbold, Germany) (Nelson and Sommers 1996). For most samples (due to the absence of carbonates), the total carbon content was assumed to correspond to the SOC content. However, if carbonates were present, the SOC content was calculated by subtracting the inorganic carbon content ($eqCaCO_3 \times 0.12$) from the total carbon content. The content of labile forms of mineral phosphorus ($P–PO_4$), soluble in deionized water, was measured using a spectrophotometric method at a wavelength of 550 nm (Levy and Schlesinger 1999). The content of nitrate nitrogen ($N–NO_3$) in 1% K_2SO_4 solutions was determined using phenyldisulfonic acid and measuring the absorbance at a wavelength of 410 nm (Gotkiewicz 1983). The content of ammonium nitrogen ($N–NH_4$) in 1% K_2SO_4 solutions was determined using direct Nesslerization and measuring the absorbance at a wavelength of 436 nm (Gotkiewicz 1983). The contents of $P–PO_4$, $N–NO_3$ and $N–NH_4$ were determined for the solid material of the sample (pore water was not investigated). Although the content of P and N fractions in peatland deposits is subjected to various syn– and post-depositional processes (Salmon et al. 2021), the potential relationship with other palaeoecological data was qualitatively investigated. $N–NO_3/N–NH_4$ ratios were calculated to reconstruct level of oxygenation (Gotkiewicz 1973). Additionally, a set of elements were measured (Ca, Mg, K, Na, Fe, Mn, Ni, Cu, Zn, Pb) using an Agilent 8900 Triple Quadrupole ICP–MS (Agilent Technologies, USA) instrument (details in ESM; results of the whole analysis will be presented in separate paper), and Fe/Mn ratios were determined to reconstruct redox conditions (Naeher et al. 2013).

Pollen and non-pollen palynomorphs (NPPs) analysis

A standard chemical preparation for palynological analysis (Erdtman 1960; Fægri and Iversen 1989) was applied to each sample (approx. 1 cm^3 of sediment volume). Quantitative analysis of pollen and NPPs included counting pollen grains of trees and shrubs up to at least 600 per sample under a light microscope. Pollen and NPP identification was based on available keys and the reference collection of modern pollen slides (full list in ESM). Percentage pollen data for each given taxon was determined from the sum of arboreal (AP—trees, shrubs and dwarf shrubs) and non-arboreal (NAP—terrestrial herbs) plant pollen given as $\Sigma AP + \Sigma NAP = \Sigma P$. Taxa of spore-producing plants, non-pollen palynomorphs and corroded pollen were excluded from this sum. Percentage data for taxa of these groups were calculated from the $\Sigma P +$ sum of grains from a corresponding group = 100%. All calculations and data plotting were done using Tilia software (Grimm 1991).

Macrofossil analysis

The sediment samples, after disaggregration and elimination of humic substances by boiling in water with detergent and KOH, were mildly washed through a 200 µm mesh sieve. Macrofossil examination was performed with a ZEISS Stemi 508 stereomicroscope at 10–16 × magnifications. Fruits, seeds, plant vegetative fragments and other macrofossil types were identified according to various keys and publications (full list in ESM). The collection of modern diaspores and specimens of fossil flora from the National Biodiversity

Collection of Recent and Fossil Organisms stored at W. Szafer Institute of Botany PAS in Kraków (herbarium KRAM) were also used for comparison. A full list of references for the macrofossil identification (including animal remains of e.g. Ostracoda, Porifera, Chironomidae), botanical nomenclature, phytosociological nomenclature and palaeoecological indicators is given in ESM. Identified plant and animal taxa were grouped according to specific habitats and plotted on the macrofossil diagram using Tilia software (Grimm 1991) as absolute macrofossil counts per sample volume.

Statistical methods and zonation

Cluster analysis was conducted separately for macrofossil and geochemical data to derive two sets of zonation. Pollen data were not possible to analyse due to the depth interval with lack or scarcity of pollen. Plant macrofossil counts were converted to concentrations (per 20 cm^3), and subsequently, both macrofossil and geochemical data (SOC, TN, $N–NH_4$, $N–NO_3$, $P–PO_4$, $CaCO_3$) were transformed by $\log10(x+1)$ function, in which x is a data value (Birks 2014). Constrained incremental sum of squares cluster analysis (CONISS, Grimm 1987) was applied and the number of statistically significant zones was determined using the broken stick model (Bennett 1996). Moreover, in case of plant macrofossil data CONISS zonation was also established separately for each habitat group of taxa to capture changes within different parts of the basin, and then compiled together into local macrofossil assemblage zones (LMAZ). All calculations were carried out in R version 4.2.2 (R Core Team 2022) and using package Rioja (Juggins 2022). Eventually, the established geochemical and macrofossil zonations were compiled together by qualitative interpretation into five units which reflect the main palaeoecological stages of the Klaklowo landslide-fen development.

Results

Absolute chronology and sedimentation rate

The calculated age-depth model (Fig. 2—here presented only the 250–370 cm depth section of the entire model) is reliable due to the agreement index A_{model} equal to 66%, which exceeds the recommended minimum of 60% for the model robustness (Bronk Ramsey

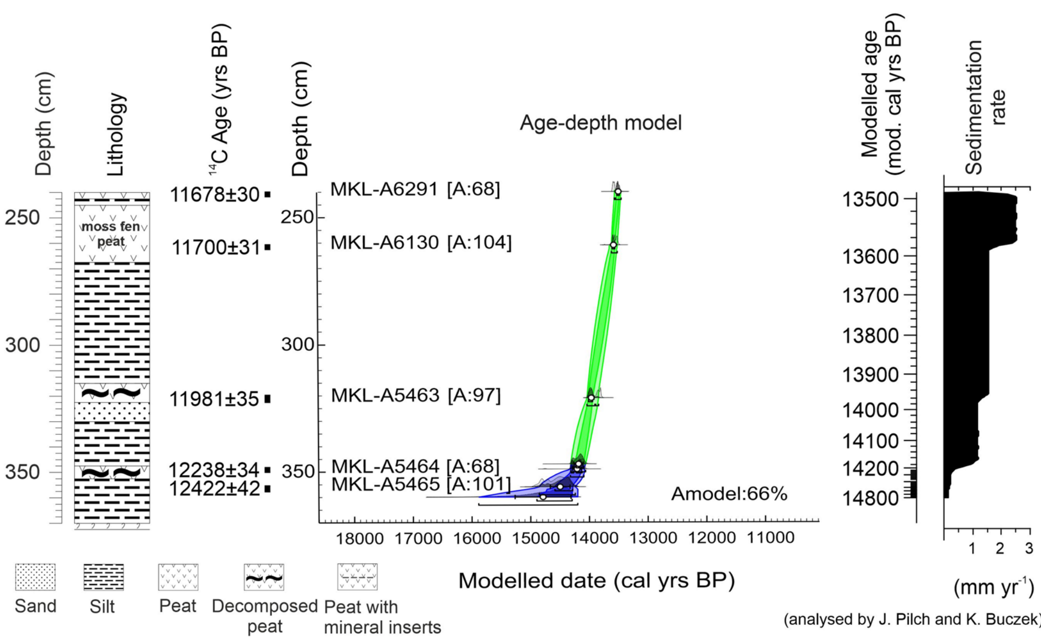


Fig. 2 From the left: lithological column of the Klaklowo fen deposits, uncalibrated ^{14}C ages of sediment samples, section of the age-depth model presented in this paper (250–370 cm), modelled ^{14}C age and sedimentation rate

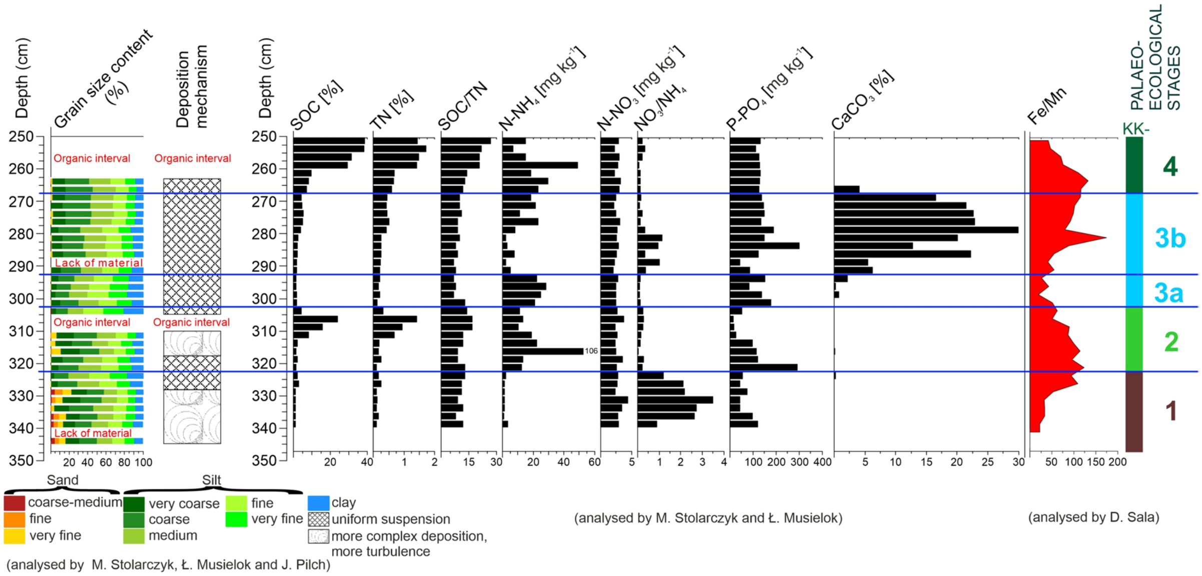


Fig. 3 Sediment-grain size, deposition mechanism and geochemical data of the depth section of 250–350 cm of the Klaklowo landslide-fen deposits

2009). According to the model and AMS dates, the accumulation of organic-minerogenic deposits of the Klaklowo landslide fen began some time before 14,896–14,277 cal yrs BP (the lowermost AMS date). Taking the timeframes between 14,600 mod. cal yrs BP (approximated μ value of the lowermost AMS date) and 13,500 mod. cal yrs BP (approximated μ value from the age-depth model for the depth 250 cm), the accumulation lasted around 1100 mod. years. The sedimentation rate varied throughout the profile, from low: 0.2 mm yr^{-1} (347–360 cm), through medium: 1.2–1.5 mm yr^{-1} (261–347 cm), to the highest: 2.5 mm yr^{-1} above a depth of 261 cm, at which moss fen peat accumulation begun.

Grain-size data

Grain-size results show that the minerogenic sediment of the Klaklowo fen sequence can be classified as silt varying from fine to coarse, with noticeable admixture of very fine to medium and coarse sand occurring at a depth of 327.5–345.0 cm and of very fine sand at a depth of 310.0–317.5 cm (Fig. 3). Due to the small variability, a detailed description of sediment types along the profile according to Folk and Ward's (1957) (ESM–Fig. 2) parameters and interpretation of deposition mechanisms based on C–M diagram (Passega and Byramjee 1969) (ESM–Fig. 3) are given in the ESM.

Geochemical data

CONISS analysis of the geochemical data allowed to distinguish five geochemical zones corresponding to five palaeoecological stages (Fig. 3; CONISS dendrogram in ESM–Fig. 4). Stage KK-1 (322.5–340.0 cm) was characterized by a relative increase in the content of organic matter and a trace amount of carbonates and a clear dominance of nitrate N over ammonium N, expressed by NO_3/NH_4 values higher than 1, with an average of 2.17. P concentrations in the lowermost zone were characterized by the lowest average value among all analysed zones, amounting to 67.7 mg kg^{-1}. Fe/Mn ratios were also among the lowest (22.4–109.5) of all stages, however, from around 330.0–332.5 cm they started to increase noticeably. Stage KK-2 (302.5–322.5 cm) was characterized by an organic-rich insert (up to 23.9% SOC, 1.1% TN) occurring in the uppermost part, while in the lower part of this zone both SOC and TN showed a gradual decrease with values ranging from 1.3 to 2.2% and from 0.1 to 0.3%, respectively. The upper boundary of the stage KK-2 displayed a clear decrease in P concentration compared to the stage KK-3, along with a relative increase in P–PO_4 with depth, ranging from 15.5 to 291.2 mg kg^{-1}. Moreover, at a depth of 315.0–317.5 cm, the highest concentration of ammonium N (105.93 mg kg^{-1}) in the entire profile was recorded. Fe/Mn values, with some fluctuations, kept on a high level (average value 95.0) and decreased gradually in the upper part of the zone to 50.7. Stage KK-3a (292.5–302.5 cm) was characterized by trace amounts of carbonates (up to 2.1% eq$CaCO_3$) occurring in the uppermost part, while the content of other analysed elements was aligned through the whole depth. Similarly to KK-1, Fe/Mn values were low (43.8 on average). Stage KK-3b (267.5–292.5 cm) contained carbonate-rich material (5.4–29.9% eq$CaCO_3$) which in its upper part showed relatively high content of organic matter (3.8–5.2% SOC and 0.4–0.5% TN). The interval 280.0–285.5 cm showed a relative decrease in N–NH_4 to N–NO_3 concentrations (with an average NO_3/NH_4 ratio of 1.03), coinciding with notably higher concentrations of P–PO_4. Fe/Mn ratio was increasing with decreasing depth (from 26.7 to 102.1), with a sudden rise to the highest value (174.9) in the entire investigated section at a sample depth of 280.0–282.5 cm and a subsequent drop to lower values. Stage KK-4 (250.0–267.5 cm) was characterized by the highest contents of SOC (7.0–38.5%) and TN (0.6–1.7%). Both elements increased gradually with the decreasing depth. The ratio of N–NO_3 to N–NH_4 was low (0.16 on average), indicating a predominance of ammonium N over nitrate N. The P–PO_4 content was in a range from 110.7 to 133.4 mg kg^{-1}. Fe/Mn ratios continued to increase in the lower part up to the ratio of 132.3, but then started to decrease (to 42.2 in the uppermost sample).

Pollen and NPP data

The conducted pollen analysis showed the absence or strong scarcity of pollen grains along with up to 55% share of corroded pollen in the lowermost part (287.5−367.0 cm) of the investigated Klaklowo sediment sequence. Therefore, distinguishing local pollen assemblage zones (LPAZ) and chronozones was not possible for this depth interval (Fig. 4). Instead, based only on a number of pollen grains found in sediment, three pollen zones were established for the depth section of 250–367 cm (Fig. 4): zone P1 (332.5–367.0 cm)—lack of pollen, zone P2 (287.5–332.5 cm)—poor in pollen, and zone P3 (250.0–287.5 cm)—abundant amount of pollen.

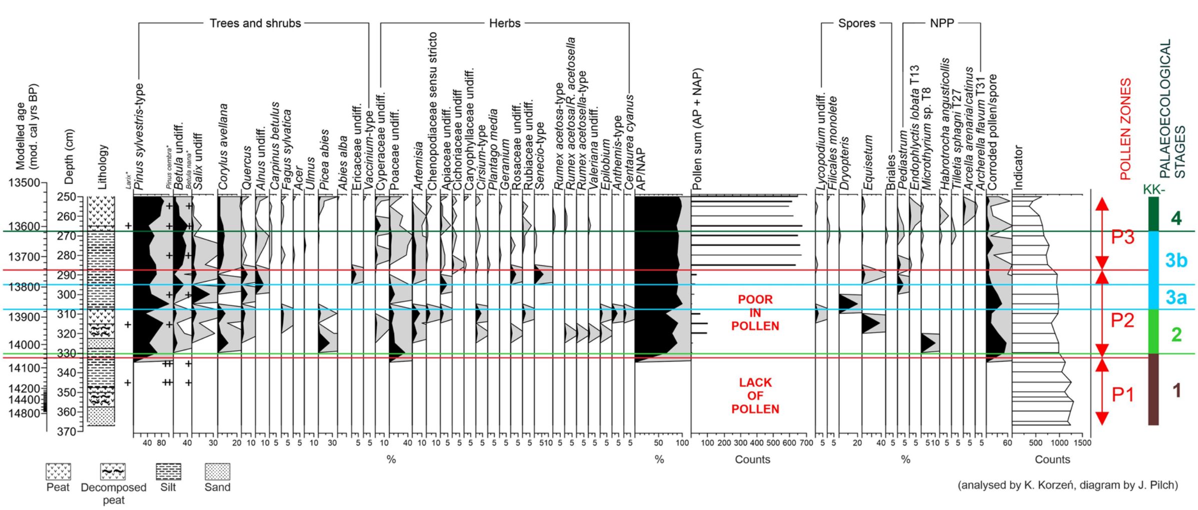


Fig. 4 Pollen-percentage diagram of the depth section 250–367 cm of the Klaklowo landslide-fen deposits. Zonation is represented by three pollen zones and five palaeoecological stages of development. See ESM-Table 1 for detailed description of the zones. Notice that for convenience pollen data from zone P2 are expressed as percentage data, but it is not interpretable due to pollen scarcity. *occurrence of pollen of *Larix*, *Pinus cembra* and *Betula nana* distinguished in the previous study (Margielewski 2001): +– 1–8 pollen grains; + +– 9–36 pollen grains

Table 2 Palaeoenvironmental reconstruction of stages of the Klaklowo fen development (see also Fig. 6 for summary interpretation)

Palaeoecological stage of the Klaklowo fen development	Description
Stage KK-1 (ca. 14,040–> 14,790 mod. cal yrs BP, ca. > 750 mod. years): Development of the waterbody I after formation of the Klaklowo landslide and sub-scarp depression	Existence of a waterbody during the stage KK-1 is mainly confirmed by the nature of sedimentation of detrital particles from a complex uniform suspension in water and possibly also with some elements of graded suspension (sorting by bottom current) (Fig. 3)—both mechanisms are characteristic for low turbulence conditions. Clastic sedimentation and reduction in biomass input is also reflected in the very low contents of SOC and TN (Fig. 3) (Zeng et al. 2017). Low redox conditions in this zone are indicated by low Fe/Mn ratios and $N–NO_3/N–NH_4$ ratios higher than 1 (Fig. 3) (Gotkiewicz 1973; Naeher et al. 2013). Sand and debris material from the bottom part of the fen deposits reflect the dynamic slope processes around the Klaklowo sub-scarp depression possibly intensified by the lack of vegetation cover within the freshly formed landslide colluvium (Fig. 3) The Klaklowo waterbody I was oligo- to mesotrophic, only sparsely inhabited by aquatic plants, and it underwent a process of shallowing with development of a fen (decomposed peat containing *Bryales* sp. — according to Margielewski 2001; macrofossils were dominated by *Juncus* sp.) and some drainage and desiccation event at a depth of ca. 350 cm (Figs. 5 and 6). This zone is devoid of pollen (zone P1) (Figs. 4 and 6) Arctic/alpine plant species (*Dianthus glacialis*, *Arabis alpina*) redeposited to the Klaklowo basin during the stage KK-1 are characteristic for dry and cold conditions of steppe-tundra, within which some tree-shrub stands (*Larix decidua, Pinus sylvestris, Betula humilis*) probably occurred (Fig. 5). Based on abundant charcoal fragments found, events of palaeo-fires were also common
Stage KK-2 (ca. 13,870–14,040 mod. cal yrs BP, ca. 170 mod. years): Basin drainage and formation of a short-lasting fen	In the lowest part of KK-2 a layer of noticeably coarser sediment (Fig. 3) and a high abundance of sclerotia of *Cenococcum geophilum* (Fig. 5), again suggest the intensification of slope processes. Within this depth interval of elevated turbulence, an insert of exceptionally high concentrations of $N–NH_4$ occurs (Fig. 3, 315.0–317.5 cm), suggesting that this N fraction may have allochthonous origin and might be re-reposited to the palaeo-pond from catchment area, e.g. with enhanced surficial flow Plant macrofossils redeposited to the basin during stage KK-2 (*Dryas octopetala*, *Poa* cf. *alpina*, *Androsace* cf. *chamaejasme,* to lesser degree: *Parnassia palustris* and *Melandrium rubrum*) are again representative for cold and dry habitat of steppe-tundra (Fig. 5). The peat horizon occurring in the zone KK-2 is expressed as an increase in SOC and TN values (Fig. 3) suggesting the enhanced biological production and biomass input (Zeng et al. 2017). Peat-forming plant taxa (*Bryales* sp. and *Carex* sp.—according to Margielewski 2001) entered the shallowing Klaklowo waterbody I creating a short-lasting fen. A high decomposition degree of plant macro-remains is evidence for further basin drainage and peat rotting (Fig. 5). Enhanced input from boggy and terrestrial plants is also reflected in slightly higher SOC/TN ratios (Fig. 3). Decomposed peat layer is also characterized by the lowered values of $N–NH_4$ and $P–PO_4$, suggesting a decrease rather than intensification of mineralization processes, which would be expected in conditions of a lowered water table (Zeng et al. 2017). According to Gotkiewicz (1996), moisture content above 75–80% significantly inhibits mineralization and reduces especially the release of nitrates The dominating occurrence of the boggy taxa *Valeriana simplicifolia*, *Carex rostrata*, *Carex diandra, Eleocharis palustris* and *Phragmites australis* suggests water depth less than 1 m with the interannual fluctuations of 1 m (Gaillard and Birks 2007) and perhaps some pools with standing water (Characeae) (Fig. 5). plant-taxa composition suggests that conditions in the fen were mostly eutrophic (with trend to mesotrophic) and neutral to alkaline (for *Carex* sp. with trend to acidic). As indicated by Fe/Mn ratios, during stage KK-2, low redox conditions prevailed, decreasing toward the upper boundary. This zone is poor in pollen (zone P2) (Figs. 4 and 6)

Table 2 (continued)

Palaeoecological stage of the Klaklowo fen development	Description
Stage KK-3a (ca. 13,790–13,870 mod. cal yrs BP, ca. 80 mod. years): Colonization of waterbody II	Abundant presence of aquatic plants (Fig. 5) and sedimentation of coarse silt from uniform suspension (no sorting by bottom current) (Fig. 3) indicate that during this stage, a waterbody developed once again and was subsequently colonized mostly by Characeae and other macrophytes. Palaeo-pond probably possessed a (eulittoral) zone with boggy plant taxa (*Carex* sp. and *Scirpus sylvaticus* but with Bryopsida mosses withdrawal) and was surrounded by some tree patches of *Larix decidua*, *Pinus sylvestris* and *Betula* sp. The expansion of Characeae implies alkaline and oligo- to mesotrophic conditions. In this zone, elevated contents of P–PO_4 and N–NH_4 correspond to elevated oxygenation of the environment (Fig. 3). This stage is also poor in pollen (zone P2) (Figs. 4 and 6)
Stage KK-3b (ca. 13,620–13,790 mod. cal yrs BP, ca. 170 mod. years): Waterbody II overgrowing	Accumulation of coarse silt continued in the Klaklowo waterbody II throughout the stage KK-3b. The prominent feature of this zone is precipitation of carbonates: $CaCO_3$ content increases gradually from the lower boundary of KK-3b to a maximum carbonate concentration at a depth of 277.5–280.0 cm, and then it decreases at slower pace upward to the upper boundary of KK-3b at which it sharply ends (Figs. 3, 5 and 6). Parallel, the oxygenation level is decreasing. In the same depth interval, vast submerged Characeae meadows spread at the bottom of the waterbody (Figs. 5 and 6). Carbonate precipitation was also expressed in the form of calcified oospores (gyrogonites) (Apolinarska et al. 2011) abundantly found in this sediment interval. Characeae presence and precipitation of carbonates indicate that the local aquatic environment was alkaline. Moreover,presumably water was also well-transparent and oligo- to mesotrophic. Other macrophyte representatives (*Potamogeton pusillus*, *Myriophyllum verticillatum* and *Hippuris vulgaris*) confirm the alkaline conditions, however, they can thrive also in more eutrophic waterbodies Clastic sedimentation in the palaeo-pond II is also expressed in low values of SOC and TN, however, they slightly increase with the decreasing depth. This increase may signalize the beginning of organic matter accumulation in situ by vegetation overgrowing the pond as well as possibly from external delivery of terrestrial organic material to the pond (Zeng et al. 2017). A growing number of macrofossils of *Betula nana*, *Betula pubescens*, *Carex rostrata, Carex diandra* and Bryopsida mosses during this stage also reflects the terrestrial plants succession (*Betula*-dominated boreal forest). These plant taxa point at oligotrophic-mesotrophic conditions and moderately acidic soils around palaeo-pond (in case of *Betula nana* even highly acidic) Moreover, during this stage the abundant amount of pollen is finally recorded (Fig. 4), probably coupled with vegetation development. It is characterized by predominance of AP vs NAP vegetation, with highest percentage of *Pinus sylvestris* (ca. 40−80%) and *Betula* undiff. (ca. 25−40%). The pollen curves of these taxa stay in agreement with macrofossil results: in the 267.5–287.5 cm interval the progression of *Betula* undiff. can be observed, whereas *Pinus sylvestris* slightly declines. Among pollen curves of herbs, Cyperaceae also show an increase. Among NPP *Pediastrum* is present, confirming the aquatic conditions Apart from the occurrence of *Dryas octopetala*, Asteraceae and some minor amounts of Poaceae, non-arboreal indicators of dry and cold conditions are absent in this zone, but some areas of dry open-land habitat probably still occurred in the vicinity of the Klaklowo waterbody (Fig. 5)

Table 2 (continued)

Palaeoecological stage of the Klaklowo fen development	Description
Stage KK-4 (< 13,530–13,620 mod. cal yrs BP, ca. > 90 mod. years): Waterbody II transition to a long-lasting fen	This stage documents a transition from Klaklowo palaeo-pond II into a long-lasting Klaklowo fen, which is also confirmed by results of previous plant-tissue analysis of the Klaklowo sediment core, indicating the formation of moss-fen peat (*Bryalo-Parvocariconi bryalet* consisting of *Phragmites australis* and *Bryales* mosses—according to Margielewski 2001). Organic material accumulation is also expressed as gradually increasing SOC and TN values and other geochemical data (Fig. 3). Increasing SOC/TN ratios indicate the increased input from boggy and terrestrial plants (Meyers and Ishiwatari 1993) In the catchment of the Klaklowo fen a boreal forest dominated by *Pinus sylvestris* started prevailing at that time (probably outcompeting *Betula nana* and *Betula pubescens*) (Figs. 5 and 6). The fen was water-logged (decreasing oxygenation indicated by increasing Fe/Mn ratios, Fig. 3) and probably mesotrophic, however, in the upper part of the zone sedges (*Carex* sp.) and Bryopsida mosses were also gradually diminishing (Figs. 5 and 6). Instead, plant taxa of slightly different conditions started to occur sporadically (*Taraxacum officinale*, *Caltha palustris*, *Glyceria maxima*) perhaps suggesting another change to more alkaline and eutrophic conditions in the Klaklowo fen

Detailed description of these zones can be found in ESM-Table 1. Results essential for interpretation are summarized in Table 2 and Fig. 6.

Macrofossil data

CONISS analysis performed separately for each plant ecological group allowed to eventually compile eleven LMAZ units (CONISS dendrograms in ESM-Fig. 5a–e). A detailed description of LMAZ and local palaeoecological interpretation, divided into five palaeoecological stages is given in ESM-Table 2. A macrofossil diagram divided into stages from KK-1 to KK-4 is presented in Fig. 5. Data essential for interpretation are summarized in Table 2 and Fig. 6.

Discussion

Palaeoecological development stages of the Klaklowo fen in the light of palaeoclimatic interpretation and correlation with extraregional chronologies

Based on the result of multi-proxy analysis and zonation of geochemical and macrofossil data derived from cluster analysis, five palaeoecological stages of the Klaklowo landslide-fen development were ultimately distinguished for the investigated late glacial deposits of the fen (a depth interval of 250−367 cm, time span: ca. 14,600 and 13,500 mod. cal yrs BP). Detailed palaeoenvironmental reconstruction of these stages is given in Table 2, whereas an interpretation summary and the most essential proxies are shown in Fig. 6.

Palaeoclimatic conditions inferred from established palaeoecological stages revealed a general change from colder to warmer climate. As indicated by macrofossils of Arctic/alpine plant species (*Dianthus glacialis*, *Arabis alpina*; Fig. 5) during stage KK-1, dry and cold conditions of steppe-tundra prevailed in the surroundings of the presumably periodical and oligotrophic Klaklowo waterbody I (Fig. 6). Occurrence of *Parnassia palustris* suggests minimum mean July temperatures around 7 °C (Aalbersberg and Litt 1998).

Stage KK-2 is also characterized by cold and dry climate (macrofossils of: *Dryas octopetala*, *Poa* cf. *alpina*, *Androsace* cf. *chamaejasme*), and moreover—as a number of determined taxa specific to these conditions is higher than for the stage KK-1—steppe-tundra was probably even more wide-spread around the Klaklowo basin (Figs. 5 and 6). Plant taxa associated with formation of a short-lasting fen (*Parnassia palustris*, *Eriophorum vaginatum*, *Eleocharis palustris*) point at minimum mean July temperatures around 7−10 °C (Aalbersberg and Litt 1998).

Characeae and other macrophytes colonised the Klaklowo waterbody II during the stages of KK-3a and KK-3b prior to the terrestrial plant succession recorded during stages KK-3b and KK-4 (Figs. 5 and 6). Taxa of aquatic plants found in this zone include *Batrachium* sp., *Potamogeton pusillus*, *Myriophyllum verticillatum* and *Hippuris vulgaris* suggesting minimum mean July temperatures > 10 °C (optimum: > 13 °C) (Aalbersberg and Litt 1998; Gaillard and Birks 2007). Soon after, the birch-dominated boreal forest developed in the Klaklowo waterbody catchment, with *Betula nana* indicating the minimum mean July temperatures 7 °C and *Carex rostrata*—around 8 °C (Aalbersberg and Litt 1998). Pioneering aquatic and subsequent terrestrial plant succession (boreal forest) signalizes warming and moistening of the climate (Iversen 1954).

During stage KK-4, the Klaklowo palaeo-pond was transformed into a minerogenic fen dominated by Bryidae mosses (moss fen peat *Bryalo-Parvocariconi bryalet* consisting of *Phragmites australis* and *Bryales* pl. sp. — according to Margielewski 2001), whereas the boreal forest became predominated by *Pinus sylvestris*. The abundant presence of pioneering species *Pinus* and *Betula* reflects their expansion and rising production of pollen and fruits due to elevated temperatures (Feurdean et al. 2007), confirming the ongoing climatic warming (Figs. 4, 5 and 6).

Vegetation changes of the stages KK-3 and KK-4 observed consistently both in macrofossil (Figs. 5 and 6) and pollen data (Figs. 4 and 6) seem to correspond to the climate warming of Allerød—then this climatic amelioration took place earlier than established by previous pollen-based chronozones (Margielewski 2001) (Figs. 1 I and 6). Based on the obtained Klaklowo radiocarbon absolute chronology (Fig. 2) in reference to different extraregional chronologies, the late glacial sequence of the Klaklowo fen in a greater can be correlated in a greater extent with the Greenland ice core record (Rasmussen et al. 2014) and the Gerzensee Lake deposits, Switzerland (Ammann et al. 2013), than with the Meerfelder Maar deposits, Eifel region, Germany (Litt et al. 2001) (Fig. 6). According to NGRIP and Gerzensee chronologies, stage KK-1 corresponds to the Oldest Dryas climate cooling and Bølling climate warming, stage KK-2 to the Older Dryas cooling, whereas stages KK-3a, KK-3b and KK-4 correspond to the Allerød warming. In the light of data collected in the current research, previous stratigraphic position of the supposed Older Dryas deposits (Margielewski 2001) cannot be confirmed, however, attribution of the stage KK-2 to the Older Dryas climate cooling should be done with caution (Rasmussen et al. 2014).

Characeae-dominated aquatic organisms' response to alkalinity changes, boreal forest development and pond overgrowing

Characeae meadows development

A high content of calcium carbonate (5.4–29.9% $eqCaCO_3$) in the Klaklowo deposits during the stage KK-3b (267.5–295.0 cm) correlates with the abundant macrofossils of Characeae meadows (around 2000 estimated oospores per sample) as well as with the presence of other macrophytes (*Potamogeton pusillus*; *Myriophyllum verticillatum* and *Hippuris vulgaris,* Figs. 5 and 6). This co-occurrence indicates that alkaline conditions and intense autochthonous precipitation of carbonates prevailed in the water of the Klaklowo palaeo-pond II at that time (Kufel and Kufel 2002; Pełechaty et al. 2013). In lakes, autochthonous production of $CaCO_3$ by phytoplankton and macrophytes results from their photosynthetic activity, i.e. the assimilation of CO_2 from inorganic carbon source—the bicarbonates dissolved in water. Moreover, calcium concentration was found as one of the most essential variable affecting the distribution of Characeae habitats in the area of present-day Europe and USA (Sleith et al. 2018). Carbonate ions are also utilized by Ostracoda (aquatic crustaceans) to build their shells and their presence in the Klaklowo sedimentary record also corresponds to the depth range of $CaCO_3$ and Characeae occurrence (Fig. 6). It is, however, important to notice that although most freshwater species of ostracods thrive in alkaline or slightly acidic waters, some of them show a wide range of pH tolerance (Ruiz et al. 2013).

Research on lakes of various age formed in recently deglaciated areas showed that with a lake development, a decline of pH, alkalinity and rise in dissolved organic carbon can be observed, as a result of hydrologic change, vegetational succession and soil formation in the catchment area (Engstrom et al. 2000). Calcium and bicarbonate ions can be available for carbonate precipitation from leaching of bedrock in the catchment area. Within geologic formations occurring in the Klaklowo fen basin, sandstones, mudstones and shales with calcareous

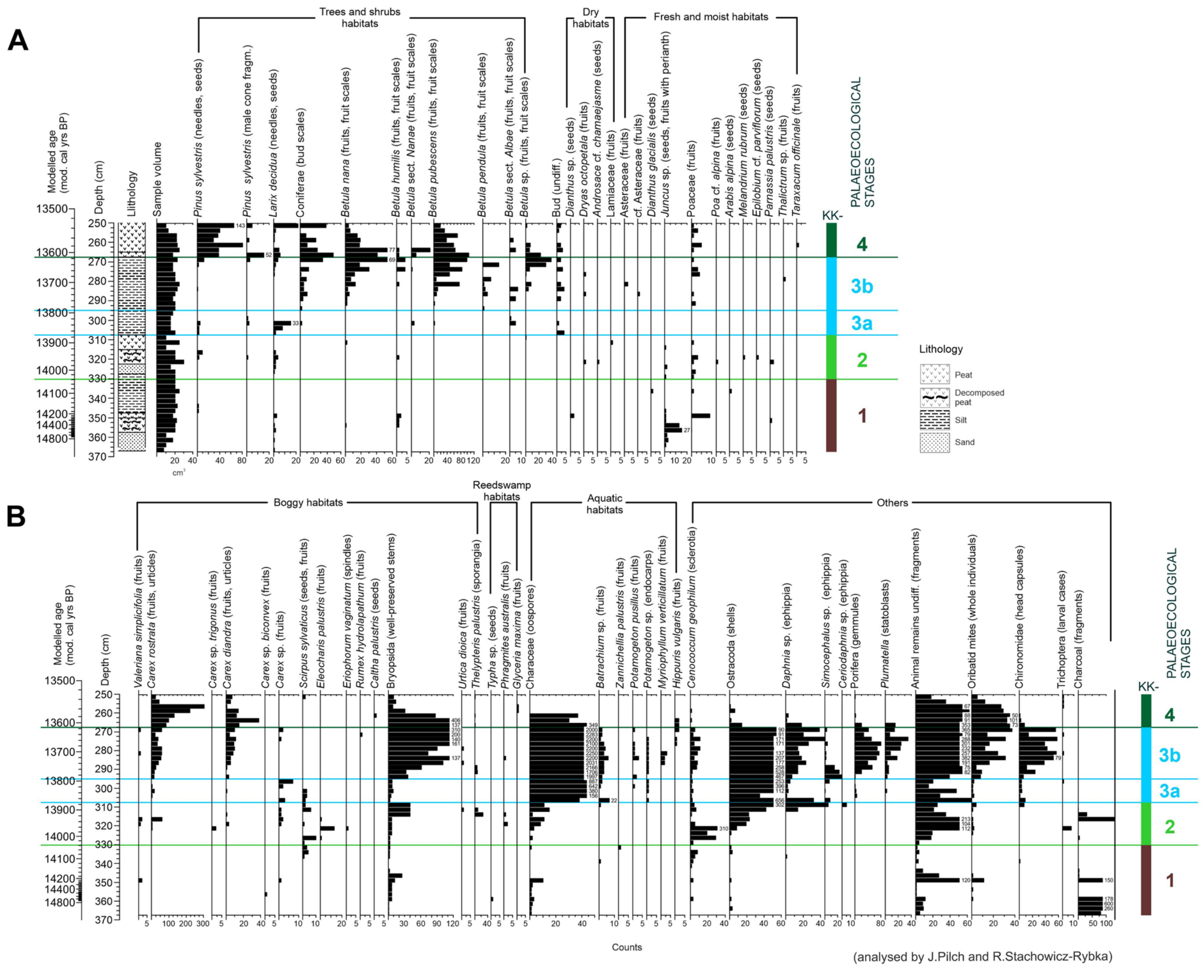


Fig. 5 **A** and **B** Macrofossil diagram of the depth section 250–367 cm of the Klaklowo landslide-fen deposits divided into parts according to ecological groups (habitats). Values are absolute counts per sample (sample volumes presented on the left)

cements as well as marls (Książkiewicz et al. 2016) may constitute a possible source of these ions (ESM Fig. 1). Moreover, rising temperatures and precipitation of the Allerød climatic phase possibly triggered changes in water circulation and chemistry (Margielewski et al. 2022b), and intensified leaching processes. The access to carbonate ions likely resulted from the groundwater supply, because the Klaklowo palaeo-pond was probably (similarly to the subsequently formed Klaklowo fen) characterized by complex recharge system including surface flow, subsurface storm flow and direct influx to landslide depression from shallow aquifer (Margielewski 2001). Additional factors that influenced the water chemistry of tundra lakes possibly included permafrost degradation in the catchment area, which led to elevated ion concentrations and improved water transparency, and subsequently allowed for colonization by characean algae and other aquatic plants (Mesquita et al. 2010).

Decline of Characeae meadows and other aquatic organisms

In the middle of the stage KK-3b (at a depth of 277.5–280.0 cm) a peak of calcium carbonate content was observed, with concentrations gradually diminishing further upward in the sediment profile. At a depth of ca. 267.5 cm carbonate precipitation ended, whereas Characeae oospores abruptly drop in number

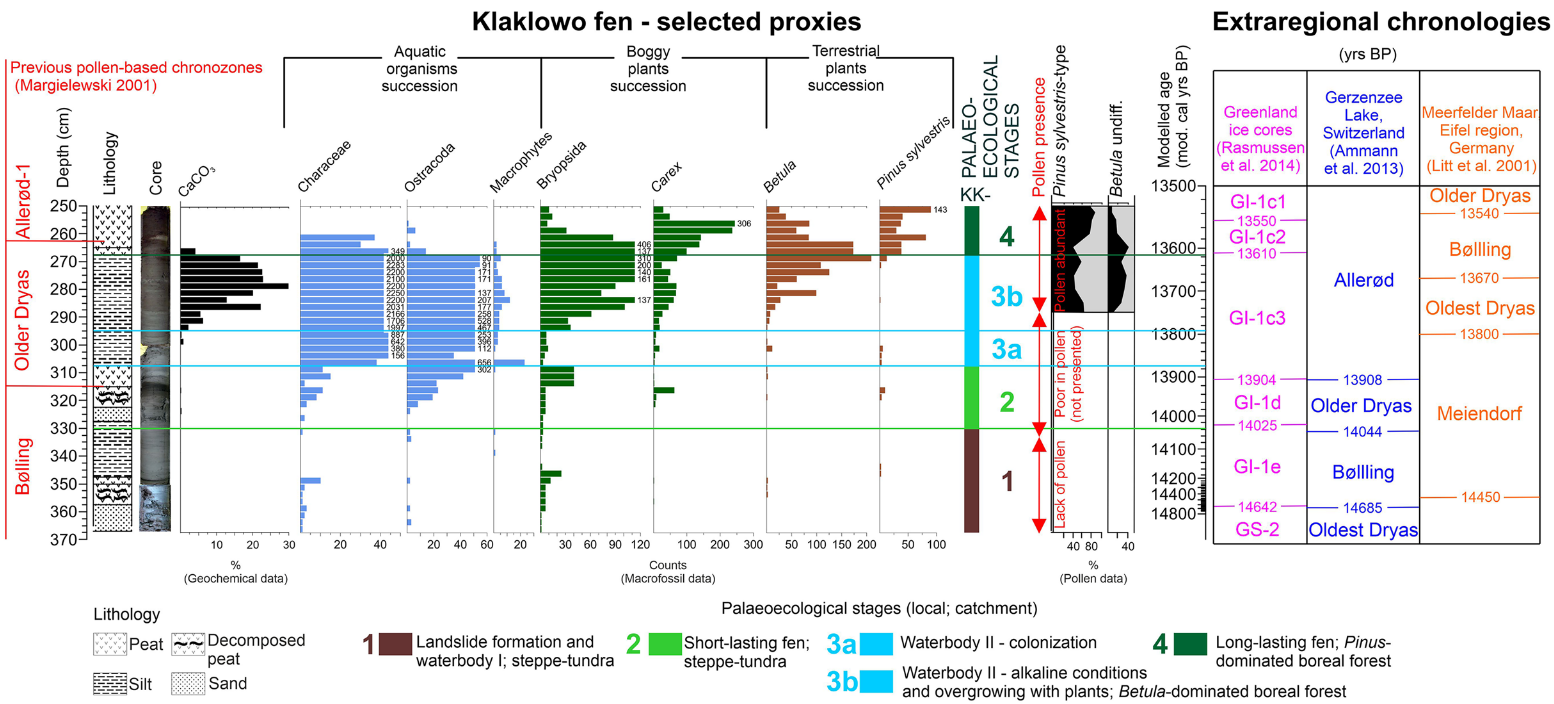


Fig. 6 Selected proxies and summary interpretation of the palaeoecological stages of the Klaklowo landslide-fen development compiled with previous pollen-based stratigraphy and other extraregional chronologies spanning 14,600–13,500 cal yrs BP. Columns with macrofossil data of macrophytes, *Carex* and *Betula* show a sum of macrofossil counts determined for the species belonging to these groups

and soon after this macroalgae group, along with other macrophytes, disappeared from the Klaklowo palaeo-pond II (Fig. 6). Furthermore, withdrawal of aquatic plants coincided with the spreading of boggy and terrestrial plants (development of boreal forest dominated by birch) and the overgrowing of palaeo-pond II revealed by macrofossil and pollen data (Figs. 4, 5 and 6). Presence of plant taxa including *Betula nana*, *Betula pubescens*, *Carex rostrata* and *Carex diandra* points at an occurrence of moderately acidic soils (in case of *Betula nana* even highly acidic). The immigration of trees to the Klaklowo catchment, especially conifers during the stage KK-4, probably resulted in enhanced delivery of (acidic) organic substances to the palaeo-pond II which, in turn, affected water chemistry and led to the decline of Characeae meadows and other aquatic organisms (Fallu et al. 2005). Beside acidification caused by vegetation and soil development, another driver which affected the change in carbonate-ion availability and water pH in the Klaklowo palaeo-pond was probably related to a shift in water supply from calcium-rich (high-alkalinity) groundwater inflows to dominance of calcium-depleted (low-alkalinity) overland flow and precipitation (Engstrom et al. 2000). Engstrom et al. (2000) stated that even with a moderate but constant groundwater flow to the lake, water chemistry and buffering capacity remained resistant to the influence of the terrestrial plant succession.

Additional stressors which executed the disappearance of Characeae meadows possibly included some other phenomena: (1) change from oligo-mesotrophic to eutrophic conditions as indicated by some sporadic plant taxa in the zone KK-4 (Fig. 5, Table 2); development of low-oxygenated conditions confirmed by increasing Fe/Mn ratios throughout the stage KK-3b (Fig. 3); increasing shade from terrestrial plants caused by plant primary succession (Figs. 5 and 6); and shallowing of the waterbody due to mineral material/peat accumulation and/or water-level fluctuations (Fig. 6). Characeae retreat was probably also associated with increasing water turbidity due to climatically-driven eutrophication and brownification (Rip et al. 2007; Choudhury et al. 2019).

Discontinuity of the pollen record—possible causes and significance for palaeoenvironmental reconstruction of the Klaklowo waterbody I

Pollen analysis of the Klaklowo fen deposits revealed partial absence and depletion in pollen grains hindering from development of reliable LPAZ and climate-vegetation zonation for the lowest part of the sediment sequence (pollen zones: lack of pollen, poor in pollen and abundant pollen in Figs. 4 and 6). According to a previous study of the Klaklowo landslide fen (Margielewski 2001) in which LPAZ/chronozones were distinguished, the new pollen spectrum has only a slightly greater depth range (ca. 8 cm, to a depth 340 cm), whereas pollen grains are also scarce (ca. 100–200 grains in bottom parts).

Generally, factors controlling pollen content and distribution in aquatic environments include primary productivity of the terrestrial plants, transport to and spreading over the basin, and subsequent degradation. The primary factor influencing pollen decay might be oxidation occurring in different forms at pre-, syn- and post-depositional stages (Carrión et al. 2009). Lacustrine and peatland deposits are usually pollen-bearing, however, pollen-sterile horizons may intercalate the sedimentary sequence as a result of inwash of soil and sandy material already depleted in pollen due to oxidation at pre-depositional stage. This process relates to intensified erosion in the lake/fen surroundings and may be especially valid for the Klaklowo fen deposits during stage KK-1 and the beginning of KK-2 (Fig. 3). For the Tarnowiec site in the Central Western Carpathians, the deposits of the Older Dryas climatic cooling were characterized by low pollen concentration due to high content of minerogenic materials (Harmata 1987). Pollen depletion in such clastic layers may be additionally coupled with decreased primary pollen productivity by plants and sparse vegetation cover during climate deterioration (Fallu et al. 2005). Moreover, in the Pleistocene and Holocene sediment sequences in Europe and North America, decay of pollen grains was commonly observed to be also caused by mechanical damage and oxidizing conditions during fluvial transport (Delcourt and Delcourt 1980; Carrión et al. 2009). Therefore, the pollen-depleted sandy horizon accumulated at the beginning of stage KK-2 (Figs. 3 and 6) could be also attributed to the delivery of high-energy fluvial sediments at the syn-depositional stage.

At post-depositional stage, pollen decomposition may be connected with fluctuations of lake/fen-water level, including the number of wet-dry cycles (oxidation–reduction cycles) and timespan of exposure to sub-aerial conditions (Campbell 1994; Carrión et al. 2009). For the first stage of the Klaklowo landslide-fen development (KK-1), low Fe/Mn ratios and $N–NO_3/N–NH_4$ ratios above 1 (Fig. 3) point to occurrence of aerobic conditions (Gotkiewicz 1973; Naeher et al. 2013), suggesting that Klaklowo waterbody I was characterized by strong fluctuations of water level. Two horizons of decomposed peat (within stage KK-1 and KK-2) resulted from drainage and desiccation events, and are also evidence of a decreasing water table of the Klaklowo palaeo-pond I. Interseasonal and/or interannual periodicity in the palaeo-pond occurrence cannot be excluded as a factor conditioning repetitive oxidation–reduction and subsequent pollen decomposition. Periodical water-level fluctuations were observed, for instance, in the case of a thermokarst lake in the Swiss Alps, which experienced water drainage due to the unfreezing of the lake bottom every year during late spring (Kääb and Haeberli 2001). Therefore, hydrological changes in Klaklowo waterbody were probable also influenced by permafrost. Moreover, interpreting depletion in pollen as a result of water-level fluctuations may become an asset to the palaeoenvironmental reconstruction of the stage KK-1, giving the possible explanation to poor aquatic life determined by macrofossil analysis for the Klaklowo waterbody I.

Conclusions

Presented high-resolution multi-proxy analysis of the Klaklowo fen-sediment sequence allowed us to reconstruct past vegetation, climate and hydrological changes during the late glacial (ca. 14,600–13,500 mod. cal yrs BP). We inferred that:

1. The development of the Klaklowo palaeo-pond was multi-staged (five palaeoecological stages) and included: waterbody I (KK-1), short-lasting fen (KK-2), waterbody II (divided into two sub-stages KK-3a and KK-3b) and a long-lasting fen (KK-4). These stages corresponded to phases of climate-vegetation changes in the palaeo-pond catchment: from steppe-tundra (KK-1 and KK-2) to *Betula*-dominated (KK-3a and KK-3b) and later *Pinus*-dominated boreal forest (KK-4). Based on the Klaklowo radiocarbon absolute chronology correlated with the records of Greenland ice cores and Gerzensee Lake deposits, stage of waterbody I corresponds to the Oldest Dryas climate cooling and Bølling climate warming, the short-lasting fen stage documents the Older Dryas cooling, whereas the aquatic and terrestrial vegetation succession observed for the stages of waterbody II and a long-lasting fen reflect the climate warming of the Allerød.
2. The co-occurrence of macrophytes dominated by wide-spread Characeae meadows and intense precipitation of $CaCO_3$ indicate that alkaline conditions prevailed in the Klaklowo waterbody II at the beginning of the Allerød climate warming. Bicarbonate ions may have derived from (climatically intensified) leaching of carbonate-bearing bedrock in the catchment area which also provided calcium-rich groundwater to the pond. With time, similarly to present-day lakes of tundra and boreal regions, Klaklowo palaeo-pond II probably experienced a reduction of water alkalinity and increased input of (acidic) organic substances as a result of the boggy and terrestrial vegetation succession (especially conifers), soil formation and change of hydrological regime. In addition to acidification, some other phenomena related to the palaeo-pond transition into a fen possibly affected the basin too. Therefore, the disappearance of the Characeae meadows should be attributed to multiple factors.
3. Frequent fluctuations of the water level, characteristic for waterbodies and fens developed within landslide depressions, and resulting oxidation conditions (as inferred from geochemical proxies) were probably one of the most prominent causes of the pollen deterioration during the development of the Klaklowo palaeo-pond I. Other pre-, syn- and post-depositional processes should be also considered. However, the issue of the discontinuous pollen record requires further studies.

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Author contribution Field works were done by WM, KB and JP. Sample collection was done by JP. Conceptualization was done by WM, RSR, KB and JP. Supervision was done by WM and RSR. Macrofossil analysis was done by JP and RSR. Age-depth model was prepared by JP and KB. Grain-size analysis was done by ŁM, MS and JP. Geochemical analysis was done by ŁM, MS and DS. Pollen and NPPs analysis was done by KK. Macrofossil, grain size, pollen and geochemical data processing and visualization was done by JP. Statistical analysis was done by JP. Palaeoenvironmental interpretation was done by JP, WM, RSR and KB. Writing—original draft was prepared by JP. Writing—editing was done by JP, WM, RSR, KB, MS and ŁM. All authors reviewed the manuscript.

Data availability The data will be made available on request.

Declarations

Competing interests The authors declare no competing interests.

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