Reconstructing climate change and ombrotrophic bog development during the last 4000 years in northern Poland using biotic proxies, stable isotopes and trait-based approach

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ABSTRACT

In this study, we present a record spanning the last 4000 years from a Baltic bog (Kusowskie Bagno) in northern Poland. Using numerous biotic and abiotic proxies, such as testate amoebae (depth to water table reconstructions), stable carbon isotopes (^{13}C), plant macrofossils (proxies for local vegetation and mire surface wetness), pollen and spores (proxies for regional vegetation and human impact), we reconstructed and identified the regional hydro-climatic signal of Kusowskie Bagno bog and compared it to other bog records around the Baltic Sea. Our aims were to: 1) combine the species traits of bryophytes and testate amoebae, and more common proxies (isotopes, plant micro-and macro-remains) to infer past peatland development, 2) compare the hydro-climatic signal of Kusowskie Bagno bog to existing records around the Baltic Sea. We found that Kusowskie Bagno bog was very wet during the last 4000 years, and even drainage and peat exploitation had not disturbed its hydrology in northern part in the last 200 years. Carbon isotopes and plant macrofossils were significantly related to specific traits of testate amoebae, which in turn reflected the water table changes over the last 4000 years. Kusowskie Bagno recorded at least the following wet shifts: AD 250, 550, 850, 1250 and 1700, while wet conditions occurred during the Migration period at ca AD 550. Furthermore, the testate amoeba-based quantitative wetness reconstruction in Kusowskie Bagno bog resembles the pattern observed in other sites around the Baltic, i.e., Estonia, Finland, Ireland, northern Britain and the 7500-year record from the Stążki bog, northern Poland. Our results provided statistically validated evidence that interactions between plant and microbe need to be more considered further to reconstruct past hydrological. This is the first study of past hydro-climatic changes in peatlands based upon a trait-based approach.

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1. Introduction

The ecological background of oceanic bogs is very different when compared to transitional and continental bogs that are covered by snow and frozen in winter and drier in the summer (Rydin and Jeglum, 2006). In addition, seasonality, temperature amplitude, and water balance are very different between continental and oceanic areas (Wieder and Vitt, 2006). Therefore, these relationships must be studied in terms of their ecology, palaeoecology, micrometeorology, and hydrology. The temperate peatlands of eastern Europe therefore have the potential to serve as a bridge between palaeorecords from peat bogs of Western Europe which developed under oceanic climatic conditions and palaeorecords from boreal peatlands of Russia. The climate and vegetation of Poland reflect its location between the oceanic West of Europe and the continental interior of Eurasia. Different pressure systems can influence the climate in this region, for example the Siberian high which strongly influences European climate. As a consequence the continental impact increases gradually with a move from west to east. Because of the contact of the oceanic and continental air masses weather is highly variable. This is principally true in winters,

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which can be more oceanic or continental. Weather and climate in Poland are mainly shaped by atmospheric circulation. Hence, this region is sensitive to climatic changes which makes the area well suited for tracking past climate states different from today (Kaspar, 2005).

Although NW Europe peatlands were intensively explored in recent decades (Charman et al., 2009; de Jong et al., 2010; Swindles et al., 2013), the spatial coverage of the palaeohydrological record from peatlands is not very dense. For example, continental eastern peatlands are not well understood or synthesised, and they cover a much larger area than other oceanic sites (Rydin and Jeglum, 2006). The temperate peatlands of eastern Europe are a bridge to the boreal peatlands of Russia, where most of the organic carbon in the N hemisphere was stored (Borren et al., 2004); research on their dynamics is therefore a priority.

Multi-proxy studies are the best approach for exploring such relationships to assess hydro-climatic changes and human impacts. However, there are problems associated with such multi-proxy syntheses (Lotter, 2003). Although macrofossils, microfossils, and palynological results are presented qualitatively or by using indirect multivariate analyses such as detrended correspondence analysis (DCA) or non-metric multidimensional scaling (NMDS) to compare the gradient of change, their synthesis is very subjective and poorly connected towards a more mechanistic and comprehensive modelling. Simultaneous changes in plant and soil (e.g. testate amoebae) components are rarely connected in palaeo-models, while the interactions between plant and soil communities can be highly affected by climate changes (V.E. Jassey et al., 2013; Kuiper et al., 2014; Nijp et al., 2014) and recorded into sediments and peat over a wide range of spatial and temporal scales (Bardgett et al., 2013). In addition, fossil records (macro- and micro-remains) present the palaeoecological patterns of rises and falls of multiple species at multiple scales of time and biological organisation, and their summaries represent an important source of information. An optimal method of synthesising such complex multivariate data is urgently required. Simplifying communities to assemblages of functional groups (e.g., mosses and vascular plants) or community-weighted means of species traits could help to develop robust predictions that would translate across time scales (Blois et al., 2013).

Testate amoebae are one of the most important quantitative proxies from peatlands. These protozoa have been intensively used in recent decades for reconstructing the hydrological and trophic status of peatlands (Mitchell et al., 2008; Lamentowicz et al., 2013b). Quantitative reconstructions are based on transfer functions that use the relative abundance of species present in the training and fossil data set (Warner, 1990; Charman, 2001) but this process shows numerous assumptions and uncertainties. In contrast, morphological traits were not widely exploited in long-term studies, although the traits of testate amoebae may reflect environmental changes (Fournier et al., 2012; Lamentowicz et al., 2013a), offering a potential new tool for investigating questions related to carbon accumulation and past climate changes.

Multi-proxy studies that reveal the Holocene peatland history of a raised bog are very rare in this part of Europe, and most of the published studies present a high-resolution palaeoecological record of the last millennium (Lamentowicz et al., 2009, 2011). In this study, we performed a high-resolution palaeoecological reconstruction from Kusowskie Bagno, a Baltic bog in northern Poland. Until now, only one complete record for the Stążki bog was analysed using many proxies (Gałka et al., 2013b). Kusowskie Bagno bog is located ca 100 km south-west from Stążki at a similar altitude and comparable distance from the Baltic Sea. Kusowskie Bagno bog is a well-preserved Baltic bog that was drained and exploited in the past. Our former investigation revealed a palaeoecological record of the last 600 years of this bog (Gałka et al., 2014), and we showed an efficient recovery of the site from human disturbance (drainage and afforestation). In this study, we decided to go deeper in time to 4000 years BP to compare the bog's palaeohydrology with other existing bog records around the Baltic Sea to identify a regional hydro-climatic signal.

We used multiple proxies and species-trait analyses to address the following two aims: i) combine, classical proxies such as isotopes, testate amoebae, plant micro- and macro-remains, and the species traits of bryophytes and testate amoebae to infer drivers of peatland development, ii) compare the reconstructed hydro-climatic signal of Kusowskie Bagno bog to similar existing bog records around the Baltic Sea. We hypothesize that synchronous hydrological changes are reflected in peat archives of the Baltic region during the last 4000 years, including traits of testate amoebae and bryophytes. This is the first study of past hydro-climatic changes in peatlands based on a trait-based approach.

2. Data and methods

2.1. Study area

Kusowskie Bagno bog is located in northern Poland (Fig. 1) in the glacial area formed by the activity of the last Scandinavian ice sheet, which retreated from this area approximately 15,000 cal. BP (Marks, 2002). The coordinates for the central part of Kusowskie Bagno bog are 53° 48′ 28″ N and 16° 35′ 14″ E. The bog is a nature reserve and is part of the Special Area of Conservation (SAC) Natura 2000 site "Lake Szczecineckie" (PLH 320009). The studied peat bog area of 318.82 ha fills up a former lake basin located on a moraine plateau. The average altitude is in the range of 150–160 m asl, and the highest elevation at Polska Góra is in the vicinity of the bog and reaches 202 m asl. The bog is surrounded by mixed forests (*Pinus sylvestris* and *Fagus sylvatica* dominated) as well as by fields and meadows. From the SE, the bog is adjacent to Lake Wielatowo (water table at 143 m asl). The analysed site has a transitional climate and is significantly influenced by oceanic air masses. The total annual precipitation reaches 650 mm. The average July temperature reaches 17 °C, whereas the average January temperature is −3 °C (Woś, 1999). Kusowskie Bagno peat bog was drained in the early 1960s for peat extraction. The peat exploitation occurred in the southern part of the bog. Currently, the peat pits are undergoing regeneration. Despite the construction of ditches, the northern part is waterlogged and most likely has retained some of its original character, with open spaces and areas where stunted pines grow. Species composition includes *Sphagnum magellanicum*, *S. cuspidatum*, *Sphagnum capillifolium*, *Baeothryon caespitosum*, *Scheuchzeria palustris*, *Drosera rotundifolia*, and *Oxycoccus palustris*. There are also small ponds. According to the drillings conducted by the authors, the maximum peat deposit in the open spaces of the northern part of the area is 795 cm, although there might be places with thicker peat layers.

2.2. Field work and subsampling

A complete 8-m core was extracted in November 2012 using a Russian sampler. The core was transported to the laboratory and stored at 4 °C in a cold room. The core was then subsampled in 1-cm intervals for the plant macrofossils analysis and in 5-cm intervals for pollen, testate amoebae, and isotope analyses.

2.3. Chronology

Plant macrofossils were carefully selected for the radiocarbon dating of eight samples. *Sphagnum* stems were selected (30–40) from the sample with a thickness of 1 cm. These samples were AMS radiocarbon dated at the Poznań Radiocarbon Laboratory and were used to create an age-depth model (the surface is assumed to be AD 2010) and an additional date in the upper disturbed layer, which further constrained the model (Table 1). The age-depth model was calculated using the software OxCal 4.2 (Bronk Ramsey, 2001). The age-depth model was calculated using OxCal (Bronk Ramsey, 2001). The IntCal13 (Reimer et al., 2013) atmospheric curve was applied to dates calibration. The most distinct changes in the peat composition and pollen concentration, which might be signal of changes in the peat accumulation rate, were

Fig. 1. Setting of Kusowskie Bagno Baltic bog.

introduced using the Boundary command. The boundary was established at depth 75 cm according to distinct changes in plant macrofossil composition marking the drainage. The calibrated dates are expressed as years AD and BC (Fig. 2).

2.4. Pollen analysis

Samples for the pollen analysis were taken every 5 cm, and the analyses were performed in the palaeoecological laboratory of Adam Mickiewicz University in Poznań. The 1-cm³ sediment samples were prepared following standard methods (Berglund and Ralska-Jasiewiczowa, 1986), which included acetolysis for 3 min. The samples were embedded in pure glycerine and stained with safranin, and a minimum of 500 terrestrial pollen grains were analysed. Pollen percentages were calculated based on the sum of trees and shrubs (AP) and herbs (NAP, except wetland and aquatic plants). The pollen diagram was plotted using the Tilia/Tilia-Graph software package (Grimm, 1987). Indicators of disturbance and human impact were considered in

Table 1
Radiocarbon dates from Kusowskie Bagno peat bog.

Depth (cm)	Material	Nr. lab.	C14 date	Age BC/AD (95.4%)
86	*Sphagnum fuscum/rubellum* stems	Poz-55361	755 ± 30 BP	1220–1285
160	*Sphagnum fuscum/rubellum* stems	Poz-55359	1055 ± 35 BP	895–1027
210	*Sphagnum fuscum/rubellum* stems	Poz-55358	1270 ± 30 BP	664–855
321	*Sphagnum fuscum/rubellum* stems	Poz-55357	1800 ± 35 BP	127–334
419	*Sphagnum fuscum/rubellum* stems	Poz-55356	2260 ± 35 BP	−397−−207
520	*Sphagnum fuscum/rubellum* stems	Poz-55355	2455 ± 35 BP	−756−−411
615	*Sphagnum fuscum/rubellum* stems	Poz-55354	3040 ± 35 BP	−1410−−1209
725	*Sphagnum magellanicum* stems	Poz-55353	3460 ± 30 BP	−1881−−1692
795	25 fruits of *Carex rostrata*	Poz-44492	3665 ± 35 BP	−2187−−1941

the analysis to identify the general patterns of forest change and human impact.

2.5. Plant macrofossils

Plant macrofossils were analysed at 1-cm intervals in contiguous samples of approximately 25 cm³. The samples were washed and sieved under warm running water over 0.20-mm mesh screens. Initially, the entire sample was analysed with the use of a stereoscopic microscope to determine the percentage of individual fossils of vascular plants and fossil carpological remains, and vegetative fragments (leaves, rootlets, epidermis) by using the available identification keys (Grosse-Brauckmann, 1972, 1974; Tobolski, 2000; Mauquoy and van Geel, 2007). The volume percentages of the different vegetative remains and *Sphagnum* sections were estimated in steps of 5%. The relative proportions of the taxonomic sections of *Sphagnum*, which is of key importance for the interpretation, were estimated under the microscope based on branch leaves on three 32 × 32-mm cover glasses. Therefore, the identification of the *Sphagnum* at the species level was performed separately based on the stem leaves using specialist keys (Lange, 1982; Laine et al., 2009; Hölzer, 2010).

The moss nomenclature followed Ochyra et al. (2003), and the vascular plants nomenclature followed (Mirek et al., 2002). *Sphagnum fuscum* and *Sphagnum rubellum* were grouped to *S. fuscum/rubellum* because of the difficulty in distinguishing the two species in the fossil state (Gałka et al. (2013b), Gałka and Lamentowicz (2014), and Hölzer (2010)). Accordingly, *S. fuscum/capillifolium* refers to *S. fuscum* and *S. capillifolium*. The volume proportion of the amorphous organic matter, which serves as a measure of peat decomposition, was estimated in classes of 25% during the sieving.

Based on moss macrofossils, we calculated a community-weighted-mean (CWM) of moisture habitat indicator values of mosses using the trait-data base BRYOATT (Hill et al., 2007). CWM is a measure of the dominant moisture habitat indicator values (hereafter CWM moss moisture) in the community (Garnier et al., 2004; Diaz et al., 2007; Garnier et al., 2007) and is calculated as: $CWM = \sum_{i=1}^{n} pi$ x $trait_i$, where CWM is the aggregated value of the trait for all species collected in the plot, p_i is the relative contribution of species *i* to the abundance of the whole testate amoeba community, and $trait_i$ is the habitat indicator values of the species *i*. Moisture indicator values of mosses were calculated for each depth layer using the Ellenberg indicator index (Ellenberg, 1991) modified by Hill and Preston (1999). This index is ranged on a scale of 1 to 12, in which 1 indicates extreme dryness and 12 indicates submerged mosses, and reflects the climatic conditions experienced by mosses. For an exact description of each species, see (Hill et al., 2007).

2.6. Testate amoebae

The testate amoebae were analysed in subsamples of 6 cm³ taken at 5-cm intervals, and the samples were prepared by sieving and back-sieving (Booth et al., 2010). The testate amoebae were analysed at a 200–400~ magnification, and a minimum of 150 tests per sample were performed whenever possible (Payne and Mitchell, 2008). The identification was performed at the highest possible taxonomical resolution based on the available literature (Grospietsch, 1958; Ogden and Hedley, 1980; Mazei and Tsyganov, 2006). The quantitative reconstruction of water-table changes (DWT) based on testate amoebae was conducted with C2 software (Juggins, 2003) using the training set (containing 123 samples) developed for northern Poland by Lamentowicz and Mitchell (2005) and Lamentowicz et al. (2008b).

A suite of five morphological traits was selected to infer past hydrologic changes: metabolic status of the species, body size, biovolume, diameter of the shell aperture, and position of the shell aperture (Supplementary Fig. 1). The metabolic status of testate amoebae (presence/absence of endosymbiotic algae) indicates whether a specimen is mixotrophic (i.e. organisms able to combine autotrophic and heterotrophic nutrition) or heterotrophic. The metabolic status of testate amoebae was showed to cope with environmental settings such as moisture, temperature and light (Jassey et al., 2011; Wilken et al., 2012). The biovolume (continuous variable: μm₃), body size (continuous variable: μm) and diameter of the shell aperture (continuous variable: μm) are important foraging traits of testate amoebae. These traits may reflect the water table depths because they can be constrained by moisture conditions; e.g. thickness of the water film of mosses may impact large species (Tsyganov et al., 2012; Lamentowicz et al., 2013a). For each taxon, the average biovolume (μm³) was calculated based on assumed geometrical shapes using dimensions measured under the microscope (length or diameter; width, and height) (Fournier et al., 2012) (Supplementary Fig. 1). Body size and diameter of shell aperture were measured under the microscope. Finally, the position of the shell aperture (semi-continuous and variably coded as 0 = axial, 1 = terminal, 2 = subterminal aperture) revealed a gradient from completely exposed to protected aperture (Supplementary Fig. 1). This trait was used as an indicator of the moisture content adaptation (Fournier et al., 2012), in which high values of shell aperture position (protected aperture) reflected a better adaptation to dry conditions. We analysed the response of individual morphological traits in the peat-core by calculating the community-weighted mean (CWM) of each standardized trait.

2.7. Stable isotopes

Stable carbon isotopes were analysed from 156 bulk peat samples between depths of 5 to 780 cm. The sampling resolution was 5 cm throughout the core, and each sample was 1-cm thick. An aliquot of the dry bulk sample was ground in a ball mill (Retsch) to homogenise the material. Approximately 250 mg of the sample powder was weighed into tin capsules to provide approximately 100 μg of carbon. The samples were combusted at 1080 °C using an elemental analyser (Thermo Scientific Flash 2000) interfaced in-line with an isotope ratio mass spectrometer (Thermo Scientific Delta V Advantage). The carbon content of the sample was determined by a peak integration of m/z 44, 45 and 46 and calibrated against elemental standards analysed in the same run. The isotope ratios were expressed as delta-values in per mil (‰), where $\delta = (R_{sample} / R_{standard} - 1) * 1000$ and R_{sample} and $R_{standard}$ are the isotope ratios ($^{13}C/^{12}C$) of the samples and standards, respectively, reported on the VPDB scale. In addition to the calibration standards, additional laboratory standard materials were inserted between samples to monitor the performance of the instrument. The overall precision of the replicate analyses was estimated as higher than $\pm 0.1‰$.

The principal applicability of bulk peat as a comparably easy and less time consuming approach for stable carbon isotope analyses in palaeoenvironmental peat studies was demonstrated by Pancost et al. (2003) and Cristea et al. (2014). Even if both authors also express the need for caution in interpreting this variable, further justification for such an approach arises from a comparison study between bulk peat and cellulose d13C which demonstrated common patterns between the two datasets (Jędrysek and Skrzypek, 2005). Due to its mixed origin, bulk peat has of course several limitations compared to organic matter or cellulose carbon isotopes of specific plant parts like *Sphagnum* stems or branches (Loader et al., 2007; Moschen et al., 2009). Broadly, these problems arise from differences in the isotopic composition of different organic macromolecules within *Sphagnum*, of different moss components, of different peat forming plants (mosses, vascular plants) as well as the admixture of rootlets of e.g. from dwarf shrubs together with differences in the isotopic offsets in time, in the mixing ratio between peat compartments and in decomposition rates (Ménot-Combes and Burns, 2001; Moschen et al., 2009; Skrzypek et al., 2010).

Irrespective of these limitations, *Sphagnum* stems and branches (Loader et al., 2007; Moschen et al., 2009), mosses and vascular plants (Ménot-Combes and Burns, 2001; Skrzypek et al., 2007) as well as

bulk peat and extracted humic acids (Zaccone et al., 2011) bear common stable carbon isotope signals (trends), respectively. Thus, the absolute carbon isotope value and the amplitude could be affected by the mixed origin of a bulk peat sample, however, it can reasonably be argued that the overall relative isotopic variations will be retained in the bulk samples (Loader et al., 2007; Skrzypek et al., 2010).

Within the Kusowo *Sphagnum* peat multiproxy approach presented here we wanted to test whether stable carbon isotopes of bulk *Sphagnum* peat can be used as qualitative indicator of mire surface wetness (Finsinger et al., 2013).

2.8. Numerical analyses

We conducted a NMDS in CANOCO 5.0 (Ter Braak and Šmilauer, 2012) to assess the compositional structure of the macrofossils, testate amoebae and pollen. For testate amoebae and plant macrofossils first axis was chosen as the most representative for the main gradient. In case of pollen analysis the third axis was selected as showing the best the change in Corylus, Fagus and Carpinus. The zonation for each proxy was determined using CONISS (Grimm, 1987) software to describe the general biostratigraphy. However, multi-proxy-based common zones were delimited visually to describe the common patterns/gradients in Kusowo profile. The criteria of common zones determination were based on palaeohydrological change and main shifts in plant macrofossil composition.

It is important to note that morphological traits of testate amoebae are used for the first time to infer past hydro-climatic changes in peatlands. In order to have a valid reconstruction of past conditions using traits, we used a modern data set (Lamentowicz et al., 2008b) including testate amoebae and observed depth to the water table (DWT) to statistically calibrate the relation between testate amoeba traits and the DWT. First, we generated generalised linear models (GLMs) to explore the ability of CWMs of testate amoeba traits to account for changes in observed DWT. Then we selected the traits accounting for the highest explained deviance of DWT using generalized additive models (GAM; family = Gaussian, link = identity). GAMs are flexible extensions of GLMs and are fully described in Hastie and Tibshirani (1990). Briefly, GAM allows the change in mean abundance over time to follow any smooth curve, not just a linear form or a sequence of unrelated estimates. The form of the predictor function is the principal difference between the GLM and GAM. Assumptions for normality and homoscedasticity of the data were previously tested. GAMs were performed using *mgcv* R package (R Core Team, 2013).

Palaeoecologists struggle to define reliable models assessing palaeoclimate reconstruction using different proxies. Here we propose to fusion 'classical' proxies such as micro- and macro-remains, isotopes, and testate amoebae with species traits of bryophytes and testate amoebae to better define past hydro-climatic changes in peatlands (Fig. 3). Using the results from GAMs and GLMs testing the relationships between proxies and DWT (data not shown), we identified six key variables we thought related to past hydro-climatic change: total moss percentage in the macro-remains, macro-remains species composition, CWM moss moisture, ^{13}C, CWM shell aperture position of testate amoebae and reconstructed DWT. We assembled our hypotheses in a causal network (see supplementary Table 1) then subjected to structural equation modelling (SEM) (Grace et al., 2014) to identify the linkages between the reconstructed DWT and proxies. We tested eight hypothetical pathways to determine whether changes in plant communities and their derivate moisture indication values (i.e. isotopes, CWM moss moisture) can explain testate amoeba variations, which by cascade effect reflect hydro-climatic changes. The adequacy of the model was determined using χ^2 tests, standardised root mean square residual index (SRMR), root mean square error of approximation index (RMSEA), and Akaike value (AIC). Adequate model fits were indicated by non-significant χ^2 tests ($P > 0.05$), low SRMR (<0.05), and low RMSEA

(<0.05) (Grace et al., 2014). SEMs were calculated with the *sem R* package (R Core Team, 2013).

For a comparison with other Baltic bogs, the irregular time series used for the DWT reconstruction from each bog (Stążki and Kusowskie Bagno in Poland, Männikjärve in Estonia, and Kontolanrahka in Finland) were regularised by assigning samples to calendar years. For calendar years lacking assignments, the time series were linearly interpolated. For calendar years with more than one assignment, the respective data were averaged. Because varying temporal resolution and interpolation cause changes in proxy variance (Kamenik et al., 2009), the time series were low-pass filtered using a 200-year triangular filter. Analyses were performed using R software, version 3.0.1 (R Core Team, 2013) with packages *vegan*, *pastecs* and *gtools*.

3. Results

3.1. Multi-proxy reconstruction of local vegetation and hydrology

Figs. 3–5 and supplementary Tables 2–4 present plant macrofossils, pollen and testate amoeba diagrams and allow a detailed reconstruction of past vegetation and peat formation at a spatial scale. The results, including the stable isotope data, are presented in Fig. 7 which is a synthesis of the multi-proxy data with common zones to identify the main stages of peatland development.

Kusowskie Bagno bog was a rapidly growing peatland that was very wet throughout its 4000 year history. The average peat accumulation rate (PAR) was 2 mm/year, and the only considerable hydrological disturbance was associated with the recent drainage that decreased the PAR. The quantitative reconstructions together with the gradients and stable isotope data are presented in Fig. 6. The water table fluctuated over time in the profile; however, it was sufficiently high (9.4 ± 3.9 cm) to sustain an almost constant and rapid peat accumulation.

BC 2150–1750 (zone KU1, depth 800–725 cm). The dominant testate amoeba species *Centropyxis aculeata* revealed the minerotrophic poor rich fen state, and *Hyalosphenia papilio* indicated extremely wet conditions. A transition into an oligotrophic state was also indicated by a change in the brown moss/Cyperaceae-*Sphagnum* dominance from *Meesia longiseta*, *Eleocharis* sp. to *Sphagnum palustre-S. palustris*. The forest vegetation consisted of *Pinus*, *Quercus*, *Betula*, *Alnus* and *Corylus*, and the pollen suggested a moderate human impact. This period was characterised by a relatively stable hydrology (10.4 ± 1.9), and stable carbon isotope values around 28.5‰.

BC 1750–1200 (zone KU2, depth 725–670 cm). The site became drier as showed by the shift that occurred from 1600 to 1400 BC. This probably resulted from the expansion of *S. magellanicum* and the increase of Ericaceae rootlets. Testate amoebae *Archerella flavum* also increased and *Hyalosphenia papilio* decreased during this period, which suggested a decreasing trophy and ground water table. There was a sharp shift around 1500 BC from *S. magellanicum* to *S. fuscum/S. rubellum*, and the new habitat persisted over the following 2800 years. *Pinus*, *Quercus*, *Betula*, *Alnus* and *Corylus* dominated the surrounding forest; however, the *Calluna* pollen increase suggested increasing dryness. Zone KU2 possessed a stable but lower average DWT (11.5 ± 2.1). The NMDS macros curve revealed a large drop ca 1300 BC that was associated with a considerable change in the peat-forming vegetation from *S. magellanicum* to *S. fuscum/rubellum*. Stable carbon isotopes show comparably strong fluctuations between −28.5‰ and −26.5‰.

BC 1200–800 (zone KU3, depth 670–610 cm). We found considerable changes in the testate amoebae composition, indicating shifts in the water table from dry (ca 1200 BC) to wet (in the middle of the zone), and then again to dry conditions (ca 800 BC). Testate amoebae record reveals intriguing, regular fluctuations of *A. flavum* in zones KU-ta-2–KU-ta-4. During that period, the openness increased through deforestation and there was a gradual expansion of *Carpinus* and *Fagus*. Zone KU3 (10.9 ± 3.1) documented a considerable but short-

term water table fluctuation. Together with the acidification and ombrotrophication, the water table fluctuations were more pronounced. The pollen gradient curve was unstable and suggested short-term changes in the surrounding vegetation. The $^{13}C_{bulk}$ of KU3 are mainly shifted to depleted values of −28.5‰ already temporarily seen in KU2.

BC 800–300 (zone KU4, depth 610–426 cm). This period showed a distinct change in the forest composition. A strong decline in *Corylus* and *Quercus* occurred at 800 BC while the pollen data showed a short event of deforestation at ca 400 BC. Pollen human indicators indicated that this deforestation was most likely caused by human activity. This environmental change was not clearly reflected by the testate amoebae and plant macrofossils. However, the beginning of the phase was associated with a decline in *S. fuscum/S. rubellum* and a change from hydrophile testate amoebae (*A. flavum*) to xerophile species (e.g., *Bullinularia indica*, *Assulina seminulum* and *Assulina muscorum*). Small peaks of *Amphitrema wrightianum* indicated an intermittent high water table. The average DWT was nearly the same as in the former zone; however, it was the most fluctuating period in the history of the peatland (10.5 ± 5.2). The NMDS curve of the macros suggested a stable composition; however, the pollen NMDS curve revealed a decreasing trend that suggested a turnover in the vegetation composition.

BC 300–AD 575 (zone KU5, depth 426–248 cm). This zone documented the dramatic changes in the peatland history. An important decline of *A. flavum* with a simultaneous increase of *Arcella discoides* during that period can be interpreted as hydrological instability. Small wet shifts revealed by *A. wrightianum* can indicate the development of pools; this species is strongly associated with an extremely wet habitat. In addition, the *Sphagnum* species *S. fuscum* and *S. rubellum* that

constituted the habitat are recognized as hydrophilous species forming wet carpet with dominance. The peaks of *A. discoides* were in line with *Eriophorum vaginatum*, which would also support an interpretation of an unstable water table (Silvan et al., 2004). Consequently, the proportion of both species was increasing towards the top of the profile. *Carpinus betulus* and *Fagus sylvatica* revealed a peak of the regeneration phase and an exploitation followed by the second regeneration. Human indicators between AD 0 and AD 450 showed a long forest transformation phase that was also reflected in the NAP increase and suggested a local deforestation. In addition, the reconstructed water table indicated that the stage has become wetter since ca 300 BC. The stability of the local vegetation composition was striking when compared to the testate amoebae variability along the profile. However, additional proxies and improved statistics are required to better understand the underlying processes because the climatic record might have been disturbed by humans that progressively changed the landscape of Central–Eastern Europe. The DWT was higher and less fluctuating (8.3 ± 3.6) with short dry shifts at the bottom and top of the zone. The pollen NMDS curve increases were a reflection of the *Carpinus* and *Fagus* expansion. The $^{13}C_{bulk}$ of KU4 and KU5 are slightly enriched compared to KU3 and, except one outlier, have a limited amplitude.

AD 570–1240 (zone KU6, depth 248–100 cm). This period showed fewer water table fluctuations as indicated by *A. flavum*. The presence of *A. wrightianum* again suggested that water appeared intermittently on the surface of the bog. The landscape was less deforested, and there was an increase of *Quercus*, *Fagus*, *Carpinus* and *Alnus*, indicating a regeneration of the forest. At approximately AD 900, three species experienced an abrupt decline that was associated with forest cutting. Between AD 550 and AD 800, the *Fagus* and *Carpinus* forest had reached
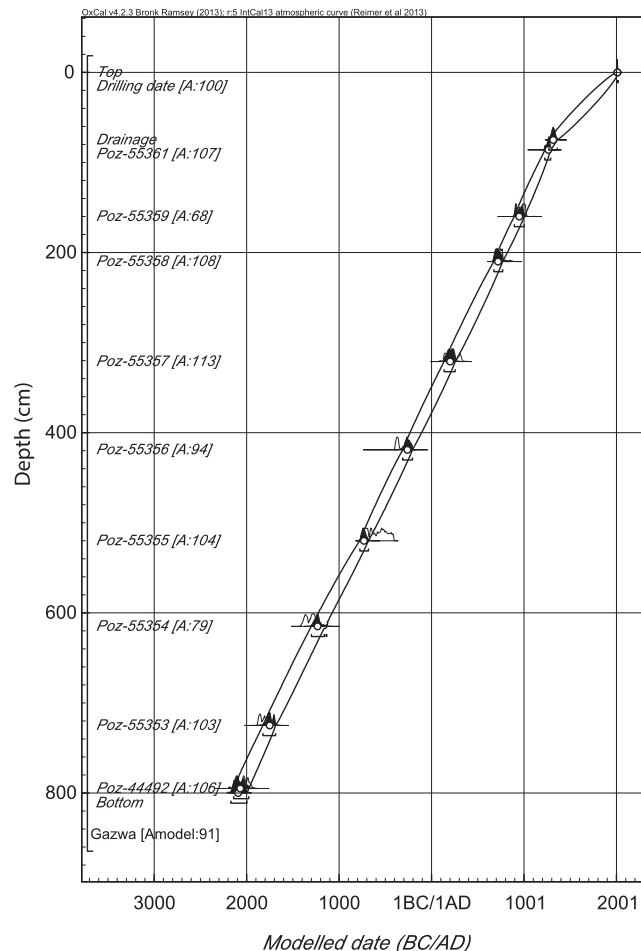

Fig. 2. Age-depth model based on Bayesian modelling using OxCal software.

its maximum for the last 4000 years. Zone KU6 documented a relatively stable water table (9.6 ± 2.3) compared to the former zones. The macro NMDS showed an abrupt shift in the local vegetation, and the tree pollen NMDS represented the anthropogenic impacts on the forest that finally led to the extensive medieval deforestations. The $^{13}C_{bulk}$ of KU6 are characterized by stronger fluctuations and probably the beginning of a decreasing trend.

AD 1240–1550 (zone KU7, depth 100–60 cm). We found that the DWT was unstable again, as indicated by *A. discoides* and *E. vaginatum*. At approximately AD 1240, the water table increased abruptly and then dropped at ca AD 1500, which was indicated by a jump of *Bullinularia indica*. The date AD 1240 also marked the beginning of new progressive deforestations, which probably had an influence on Kusowskie Bagno bog development. Furthermore, the NAP also showed a widening clear cutting. At approximately AD 1420, *Fagus* regenerated from a considerable disturbance but dropped again ca AD 1500. The *S. fuscum/S. rubellum* community disappeared at ca AD 1400 and was replaced by *Sphagnum fuscum/S. capillifolium,* which indicated that the water table was correlated with the increase in *Bullinularia indica* and the presence of Ericaceae and decomposed organic matter. This dry shift was preceded by a wet shift at ca AD 1300 as shown by *S. cuspidatum*. Zone KU7 revealed the lowest average water table, which had moderate fluctuations (5.1 ± 3.0). Pollen and testate amoebae data during this zone reflect increasing human impact through increasing openness and hydrological instability.

AD 1550–2000 (zone KU8, depth 60–0 cm). This period can be associated with a significant human impact. The landscape openness increased because of a deforestation that peaked at ca AD 1650, as shown in the NMDS pollen curve. In parallel, the decline of *A. flavum* and increase of *A. discoides* suggested less stability of the water table. The vegetation of the bog changed from the *E. vaginatum* stage to *S. capillifolium* mixed with *S. magellanicum*. During the recent stage, however, the bog remained relatively wet despite an increasing human impact on the mire and landscape. The last 200 years were significantly dramatic for Kusowskie Bagno; it was drained and exploited in the southern part. However, the northern part that was sampled was resistant enough to remain wet until the present day. In this zone, the water table was still high in the profile but the fluctuations were larger (5.7 ± 4.9). The declining trend of trees already found in KU6 became stronger during KU7 and KU8, where fossil fuel burning almost certainly influenced the lowest values observed.

3.2. Trait-based approach to infer past hydro-climatic changes

The analyses of testate amoeba traits showed distinct patterns over time, grouped into 8 zones according to clustering, and which correspond to distinct DWT conditions and CWM moss moisture in a lesser extent (Fig. 8). CWMs of the biovolume, body size and diameter of the shell aperture showed similar variations over time with 'an inverse bell-shape' response (Fig. 8). In particular, we found a highly significant relationship between CWM shell aperture size and CWM body size (adj. $R2 = 0.91$, $P < 0.001$, Suppl. Table 2), indicating that these traits are highly connected at community level and similarly affected by past bog changes. The same for CWM shell aperture position and metabolism, which were significantly correlated (adj. $R2 = 0.46$, $P < 0.001$, Suppl. Table 2). Our analyses showed that CWM biovolume, body size and shell aperture size were poorly related to changes in reconstructed DWT, while CWM shell aperture position and CWM metabolism were significantly related to reconstructed DWT variations (Fig. 8). In particular, we found that the CWM of the shell aperture position of testate amoebae was highly correlated to the DWT ($R^2 = 0.61$, $P < 0.001$, ANOVA).

The GAM based on modern testate amoeba data set and observed DWT had a good predictive power, validating our result found in the fossil data set (Fig. 9). The three successive GAM analyses based on observed DWT (Fig. 9a), modelled DWT from modern testate amoeba data set (Fig. 9b), and reconstructed DWT from testate amoeba fossil data set (Fig. 9c), respectively, were highly significant, >65% of the deviance was explained, and showed similar phases. GAM models showed that shell aperture position of testate amoebae became more protected with drier conditions until an average of 10 cm (Fig. 9).

3.3. Relationships between proxies, species traits as CWMs and past hydro-climatic changes

Multi-proxy analysis of bog development and past hydrology suggested that plant macro- and micro-remains, testate amoebae, isotopes and DWT were related. Our SEM model shows that changes in plant composition and trait over time were related to those recorded in testate amoebae, which in turn reflect the variations in hydrological changes (Fig. 10). The SEM adequately fit the data ($X^2 = 5.81$; $P = 0.33$, Fig. 10). SEM indicates that temporal changes in moss cover affected plant (macro-remain) composition and CWM moss moisture values, which then significantly explain variations in ^{13}C. This suggested that the macro-remains experienced different moisture conditions. However, these parameters were not good proxies for reconstructing DWT; their linkages with DWT were not or slightly significant (Fig. 10). The SEM showed that the CWM moss moisture and ^{13}C were directly or indirectly related to the CWM shell aperture position of the testate amoebae, which in turn was highly linked to the DWT (Fig. 10). These results suggested that variations in DWT over time directly impacted testate amoeba shell aperture trait and indirectly through changes in moisture conditions of mosses.

4. Discussion and conclusions

4.1. Trait-based approach

One of the most important goals of this study was to compare all proxies to obtain a general picture of the climatic signal. The SEMs (Fig. 10) revealed that the reconstructed water table depth was significantly reflected by the shell aperture position of the testate amoebae, which was driven by $\delta^{13}C$ and the indicator values of moss moisture. The stable carbon isotopes from bulk *Sphagnum* peat were apparently unaffected by the human impacts to the surrounding areas (in contrast to the $\delta^{13}C$ from the lakes). In oceanic areas, $\delta^{13}C$ of *Sphagnum* cellulose is used as an indicator for past-temperature changes (Moschen et al., 2011), however, in transitional climates, such as those for Kusowskie Bagno bog, the situation seems to be more complex because seasonal climates are more extreme with respect to humidity, precipitation and temperature. As previously shown by Markel et al. (2010), we found that the $\delta^{13}C$ values from macro-remains were a relatively weak indicator of water-table depth. However, our results revealed that isotopes were mainly reflected by changes in the CWM moss moisture indicator values, which is consistent with previous studies that showed that moss samples from wetter samples had less negative $\delta^{13}C$ values than moss from drier habitat (Price et al., 1997; Loisel et al., 2009). Lamentowicz et al. (2008a) suggested that the use of $\delta^{13}C$ values in palaeoecological records reflected the variability in the thickness of the water film on mosses, which is a factor linked to changes in temperature and water table depth. Furthermore, the view of stable carbon isotopes as proxy for mixed signals of temperature and moisture conditions is also supported by an alpine *Sphagnum* peatland (Mauntschas mire) high-resolution record that shows a disagreement between the reconstructed water table and carbon isotope signal (van der Knaap et al., 2011). This disagreement has not been explained sufficiently; however, a species effect caused by changes in the botanical composition of the peat might have produced noise that complicated the interpretation. In the Mauntschas mire (van der Knaap et al., 2011), high resolution records that included stable carbon isotope results were compared to the instrumental meteorological time series, and no significant correlations with temperature were revealed (who, whose data, unpublished data).
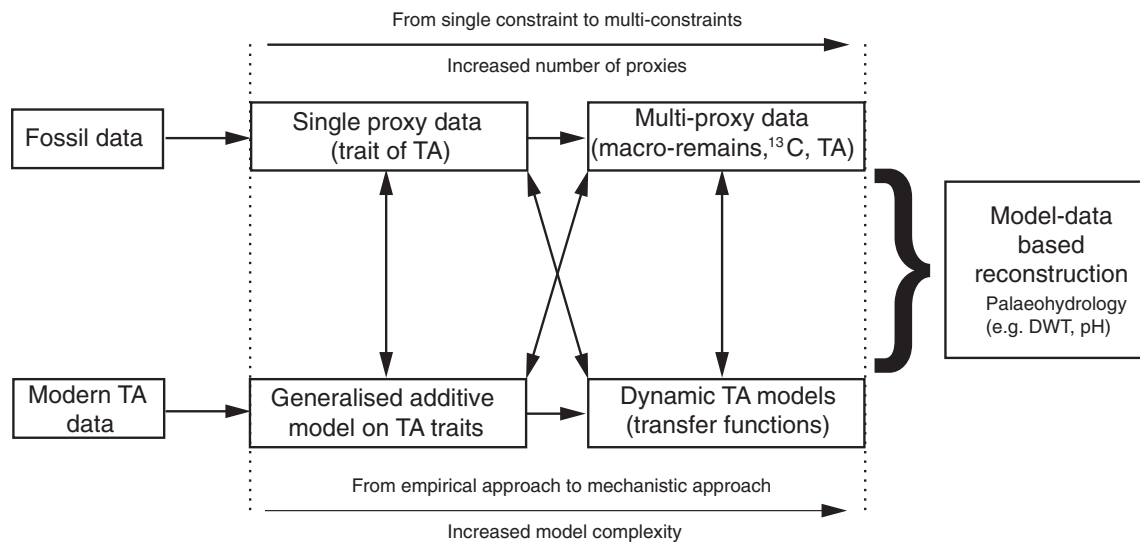
Fig. 3. Development of the causal network approach developed on Kusowo palaeodata-sets.
Adapted from Peng et al. (2011).

Such a situation shows the complexity of the interpretation of stable isotope data and calls for a better understanding of the ecological background associated with isotope fractionation, such as the photosynthetic processes of peatland bryophytes (Markel et al., 2010; Hájek, 2014).

The SEM models showed that moisture, which was reflected in the $\delta^{13}C$ values and indicator values of moss moisture conditions, is reflected in the testate amoeba community structure. Relating bulk *Sphagnum* isotopic values to testate amoebae can appear clearly to be an absolute nonsense. Recently, however, V.E.J. Jassey et al. (2013) found a significant link between *Sphagnum* $\delta^{13}C$ values and testate amoeba $\delta^{13}C$ values. These authors showed that *Sphagnum* $\delta^{13}C$ signature was related to specific testate amoebae such as *Bulinularia indica* and *A. flavum*, suggesting that a modification in *Sphagnum* $\delta^{13}C$ signature due to environmental change is likely to affect testate amoeba community composition by indirect effects of climate on *Sphagnum* species. In addition, a link was found in a palaeoecological study (Lamentowicz et al., 2009), where testate amoebae based water table reconstruction was correlated with carbon isotopes. Here, we found that changes in carbon isotope values were related to wetness changes over the last 4000 years as reconstructed in this record using specific functional traits of mosses and testate amoebae.

Our long-term approach revealed that the testate amoeba phenotypes were evolutionarily dependent on environmental conditions. Position of shell aperture is a crucial feature that evolved to allow for the survival of testate amoeba in contrasting hydrological conditions. A high correlation of shell aperture position of testate amoebae with observed DWT and the transfer function-based inferred water table in Kusowskie Bagno bog has been an important test of the reconstruction and applied transfer function, although additional points need to be included in such model to cover all possible water table changes. Despite these findings clearly deserving further investigations to better relate traits of testate amoebae and palaeohydrological reconstructions in peatlands, it underlines the potential ability of morphological traits of testate amoebae to validate reconstructed past water-table depths independently from testate amoeba species. Indeed, in the case of Kusowskie Bagno bog, this independent test strengthened and supported our quantitative approach to the water table reconstruction in this part of the world, which is not negligible considering that water-table transfer function process is made of numerous assumptions and approximations which can lead to important uncertainties.

The weak relationships between water-table depths and traits of testate amoebae such as body size and biovolume showed that these traits are poor predictors of hydro-climatic changes. However, these changes seem to be directly related to shifts in plant communities. Indeed, the shift of the testate amoeba averaged size structure (biovolume, body size and shell aperture size) corresponds to the autogenous plant succession from lake through a poor fen to bog recorded between approximately 2000–1550 BC. Several studies reported that changes in plant communities were related to changes of testate amoeba communities (Lamentowicz et al., 2010; Jassey et al., 2014), which could modify the trophic structure of testate amoeba (V.E. Jassey et al., 2013). Special relationship connected with *A. discoides* and *E. vaginatum* co-occurrence should also be mentioned. The second species expansion represents a disturbed hydrology (Silvan et al., 2004) and plays an important role in methane emission from bogs (Greenup et al., 2000). Interestingly, the average size structure of testate amoebae remained stable over ca 2800 years and abruptly increased when *S. fuscum/S. rubellum* disappeared. These changes seem also linked to an increase of wetter conditions, corresponding to the Little Ice Age climatic deterioration. Further research is needed to better define and understand the implications of such linkages between plant and testate amoebae over time, but overall may be a critical step in the understanding of the fate of peatlands under on-going climate changes and related future carbon emissions from peatlands.

4.2. Palaeohydrology, vegetation and human impact

In terms of climate change, the history of *Corylus*, *Carpinus* and *Fagus* is especially intriguing. We formerly approached this issue by analysing a profile recovered from Stążki bog, which possesses a 7500 year record (Gałka et al., 2013b). For Kusowskie Bagno bog, the changes in the surrounding vegetation can be better reconstructed because of the higher resolution, which was a consequence of peat accumulation that was twice as fast as Stążki bog. For example, the *Corylus/Carpinus* replacement was regarded as the transition from the mesocratic to oligocratic phase (Ralska-Jasiewiczowa et al., 2003). However, early forest exploitation by humans could also be responsible for this change. Kusowskie Bagno bog pollen record revealed forest clearances and recovery phases during the last 4000 years. The periodicity of the deforestation process around Kusowskie Bagno bog was visible from the occurrence of *Fagus sylvatica* and *Carpinus betulus*. These species, next to *Quercus*, were the main components of the forest from ca. 800 BC. Events connected with *Carpinus* declines were interpreted by Makohonienko (2000) as forest cutting by the different cultures in western Poland. Similar forest exploitation patterns were described by Miotk-Szpiganowicz for

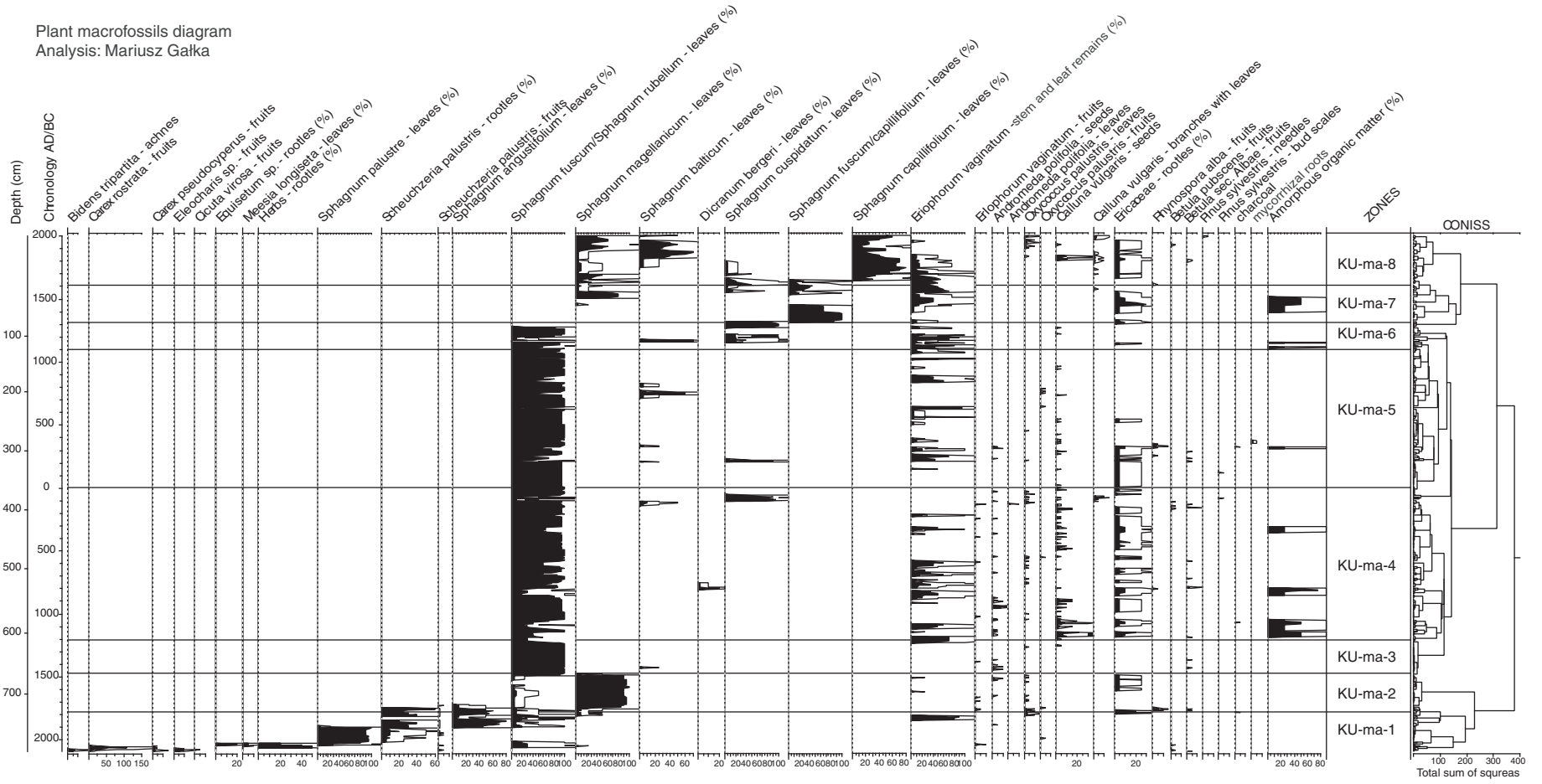Plant macrofossils diagram
Analysis: Mariusz Gałka

Fig. 4. Percentage plant macrofossil diagram.
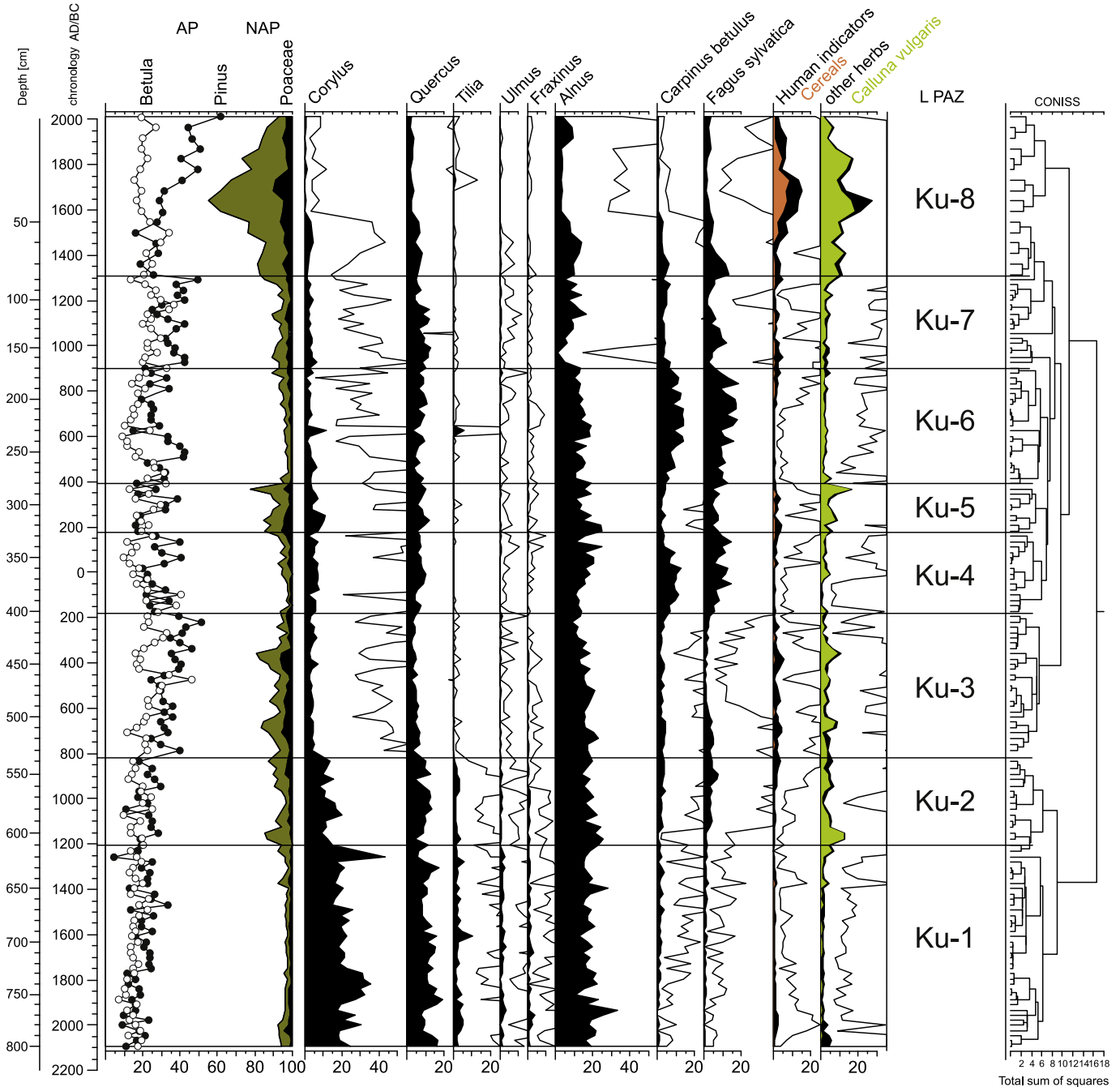
Pollen % diagram
Analysis: Milena Obremska

Fig. 5. Percentage pollen diagram.

northern Poland (Miotk-Szpiganowicz, 1992). The NMDS gradient curve and particular tree species declines appear to be correlated with several dry–wet shifts e.g. at ca 800 BC and ca 200 BC (Fig. 6). Also medieval deforestation which intensified at ca 1500 BC looks to have an importance for Kusowskie Bagno hydrology (and testate amoebae species composition reflected in NMDS curve) and *Sphagnum* that completely changed that time.

We did not found significant relationships between the regional vegetation and local hydrology over the last 4000 years (data not shown), however our data indicate that human activities were responsible for the modification of the Subboreal and Subatlantic forests. The last 300

years appear to have been critical for the development of the peatland, which was apparently still pristine at ca AD 1500; however, changes in the surrounding landscape most likely changed the catchment hydrology (Gałka et al., 2014). As a result, the base soil was a source of the mineral material that changed the chemistry of the peatlands and vegetation composition. The soil dust input over the last 500 years in Pomerania (N Poland) has been interpreted as a climatic change during the LIA (De Vleeschouwer et al., 2009); however, it is highly probable that the Słowińskie Bagno bog dust record was connected mostly with the soil openness triggered by the medieval deforestation and agriculture development (Williams, 2000). The topic of the influence of
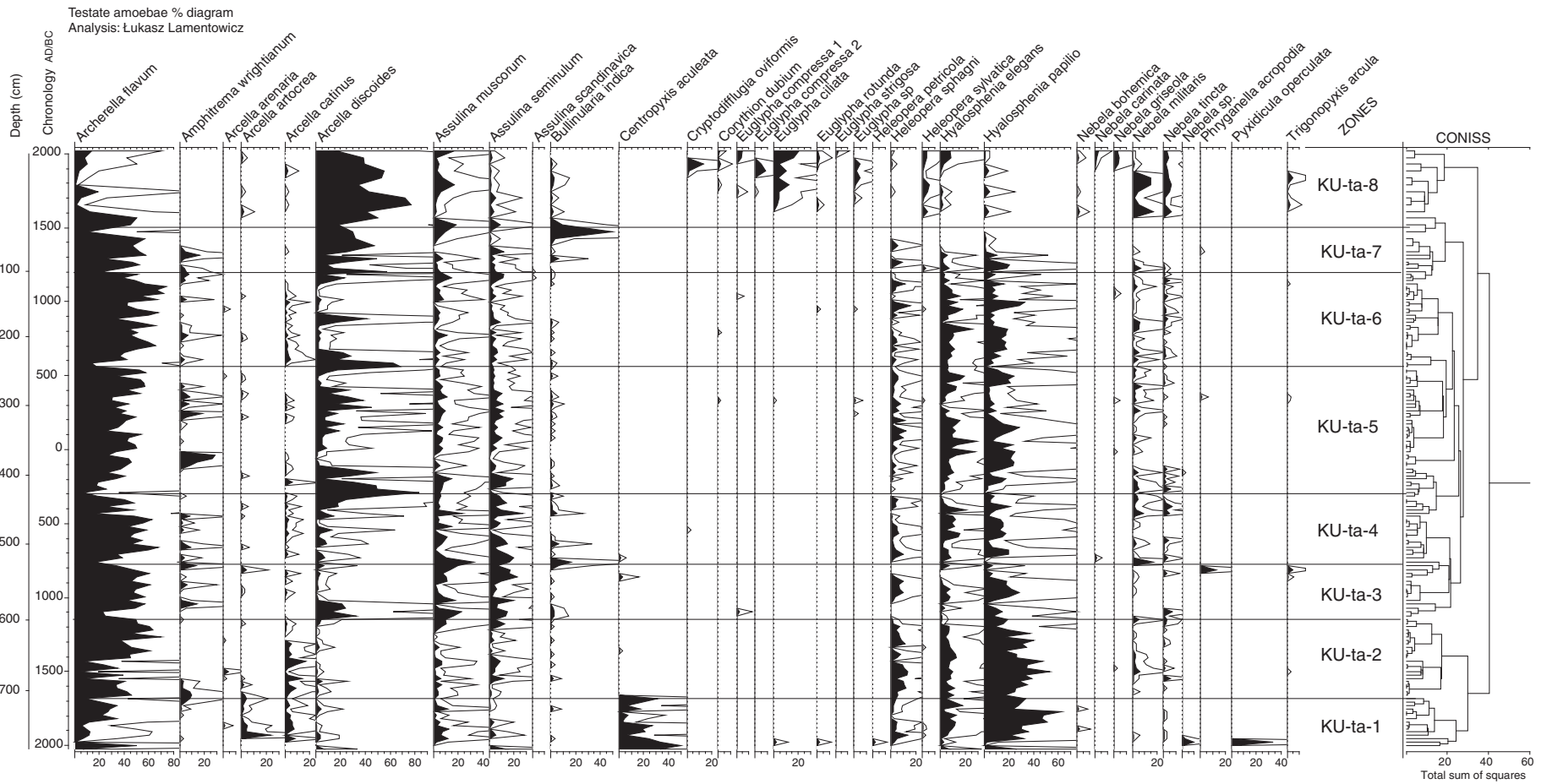
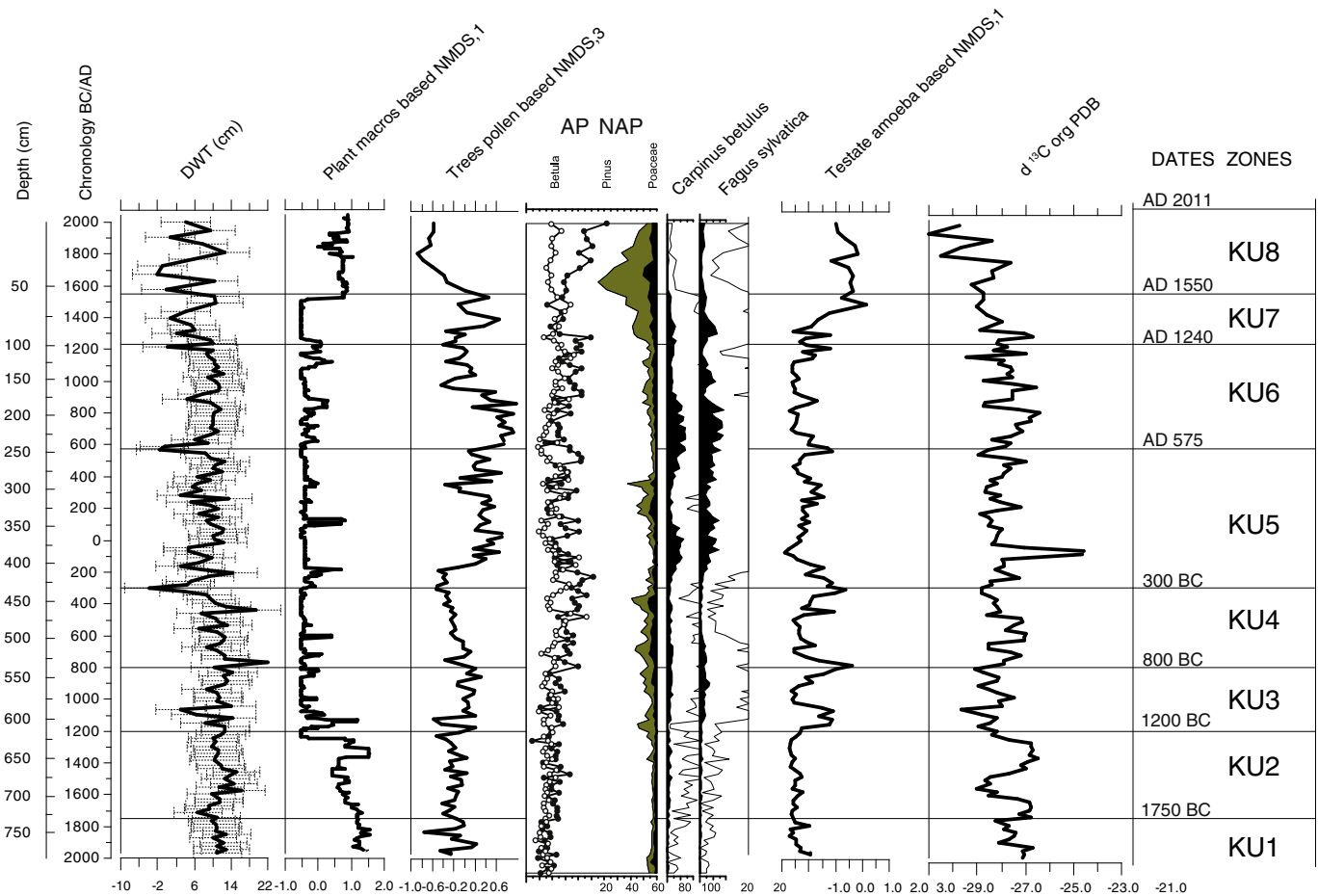**Fig. 6.** Percentage testate amoebae diagram.

Fig. 7. Summary of all of the proxies compared to the testate amoeba-based DWT reconstruction. Plant macrofossils, pollen and testate amoebae gradient curves are based on the non-metric multidimensional scaling sample scores. Curves of chosen tree taxa were added to underline woodland cutting events and particular phases of *Carpinus* and *Fagus* forest development.

deforestations on the bog chemistry, vegetation and hydrology has not been widely described. Recently, Ireland et al. (2014) presented an impact of the dust from the deforested open soil to peatlands in N America. Those authors wrote that such influence might have been more intensive on ombrotrophic peatlands than kettle-hole mires. Kusowskie Bagno bog is a large ombrotrophic peatland that is assumed to be independent from the catchment, however a considerable dry shift was identified during the medieval clear cutting (Gałka et al., 2014).

One of the effects of the environmental changes was the response of the local vegetation (van der Putten et al., 2013). Peat-forming species such as *Sphagnum* are sensitive to hydrological change (Vitt, 2000; Rydin et al., 2006). The most pronounced changes in *Sphagnum* composition were visible at the beginning of the bog's development and at ca. AD 1240. Between approximately 2000 and 1550 BC, the *Sphagnum* changes were associated with an autogenous plant succession from the lake, through a poor fen to bog. A similar pattern of plant succession in Gązwa bog (Gałka and Lamentowicz, 2014) and Mechacz Wielki bog (Gałka et al., 2013a) in northern Poland was noted. There was a *Sphagnum* change at ca. 1240 AD in which *S. fuscum/S. rubellum*, which had existing continuously for ca 2800 years, disappeared abruptly at AD 1240. This shift might have been related to the climatic change during the Little Ice Age (Gałka et al., 2014). In the case of Kontolanrahka (Väliranta et al., 2007) *S. fuscum* persided ca 1700 years. In the Gązwa bog (Gałka and Lamentowicz, 2014), the accumulation of *S. fuscum/ S. rubellum* peat was interrupted after ca. 2000 years (Gałka and Lamentowicz, 2014). The Little Ice Age climatic deterioration had

different consequences for the different ecosystems/environments (Wanner et al., 2008; Larocque-Tobler et al., 2010; Luoto and Nevalainen, 2013), and the shift in Kusowskie Bagno bog was not only associated with the alternative dry–wet events. Such a pattern supports our former data that indicated that the hydrological instability was associated with the LIA in northern Poland (Lamentowicz et al., 2009; Lamentowicz et al., 2011; Gałka et al., 2014). Such an LIA climatic effect was most likely reinforced by the land-use change, which finally led to the loss of the pristine vegetation. This pattern can be compared with the loss of *Sphagnum austinii* in NW Europe (Hughes et al., 2007, 2008).

Kusowskie Bagno bog provides an important look into the palaeoecology of the second part of the Holocene. This peatland possesses a continuous record of the last 4000 years, and Kusowo is a site that was very wet during this period. Even drainage and peat exploitation did not disturb considerably its hydrology during the last 200 years. However, the vegetation change was caused by human impacts to the peatland and its surroundings. Gałka et al. (2014) described the last 600 year history when the peatland reached a critical condition that could have led to a degraded state, which also occurred in other peatlands in Pomerania (Lamentowicz et al., 2008a, 2009). However, the history over the last four millennia shows how effectively the peat accumulated in this site, with an accumulation of 8 m of peat in 4000 years compared to the accumulation of 2 m of peat at Słowińskie Błoto during the entire Holocene (Herbichowa, 1998). The special setting of Kusowo bog (close to the Baltic coast and altitude over 200 asl) at the deep basin located on the moraine culmination of the Pomeranian
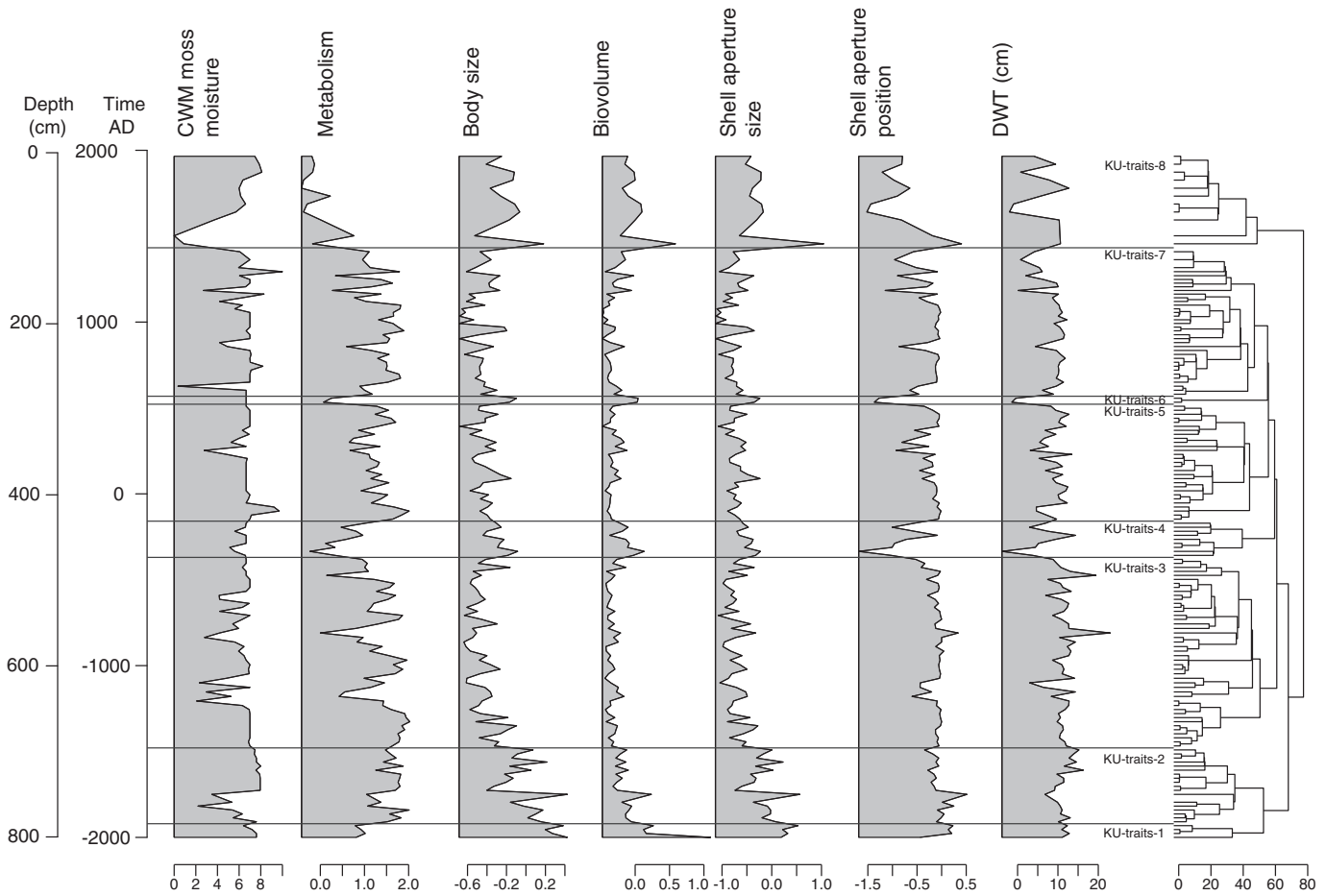
Fig. 8. Community-weighted-means (CWMs) of standardized traits of testate amoebae and mosses from Kusowo bog (Poland) and reconstructed testate amoeba-based depth to water table (DWT).

phase of the last glaciation might be responsible for such a pattern, which was influenced by autogenic and allogeneic forcing. This is the second ombrotrophic site in this part of Europe which has been analysed using a range of multi-proxy techniques and high resolution plant macrofossil analyses.

4.3. Climatic change signals in the proxies

Numerous studies have identified dry and wet shifts in European peatlands (Barber, 1981; Hughes, 2000; Charman et al., 2006). However,

most of the reconstructions are not synchronous, despite some typical climatic events (6250, 3950, 2450, 1550, 250 BC; AD 250, 550, 850, 1250 and 1700) known in north-eastern Europe (Barber and Charman, 2003). Kusowskie Bagno recorded at least five of these climatic events (AD 250, 550, 850, 1250 and 1700), while an especially pronounced wet event was identified during the Migration Period at ca AD 550 (Buntgen et al., 2011; Moschen et al., 2011; Fiałkiewicz-Kozieł, 2014). Moreover, in Kusowskie Bagno a wet shift ca 750 BC should be noticed. This event (leading to wetter conditions) can be supported by the study of Martin-Puertas et al. (2012) that revealed changes in atmospheric
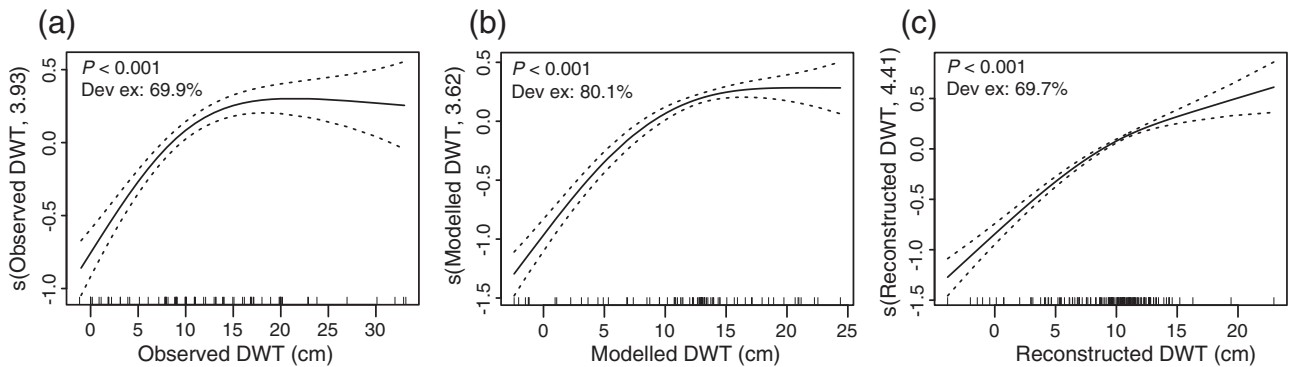

Fig. 9. Response curve of Community-Weighted-Mean shell aperture position of testate amoebae to observed DWT (a), modelled DWT from modern testate amoebae data-set (b), and reconstructed DWT from palaeo-data (c). The vertical axis indicates the relative influence of the explanatory variable on the prediction on the basis of partial residuals. Dashed lines show 95% confidence intervals, Dev ex = deviance explained in the GAM model.
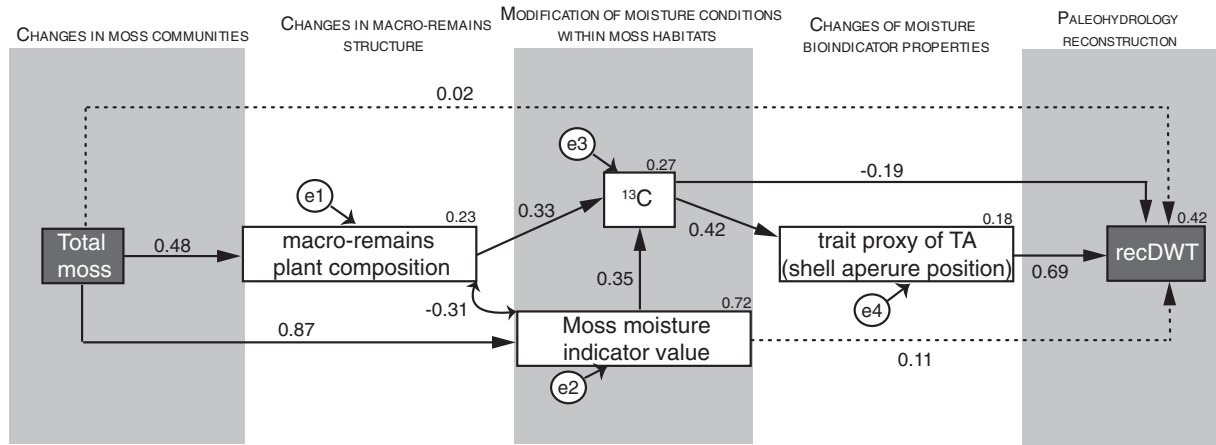
Fig. 10. Structural equation modelling of the relationships among the macro-remains, moss-trait, testate amoeba-trait and water-table depths ($X^2 = 5.81$, $P = 0.33$, CFI = 0.99, RMESA = 0.03, SRMR = 0.03). Solid arrows show significant relationships (pathways) between variables, dotted arrows indicate a non-significant relationship, and numbers next to arrows show standardised parameter estimates (i.e., standardised regression weights). Circles (e1–e4) indicate error terms, and double-headed arrows indicate significant correlations between the error terms. Squared multiple correlations (R^2) for the predicted/dependent factors are given in the box of the dependent variable. Abbreviations are: recDWT: reconstructed water-table depths; TA: testate amoebae; CWM: community-weighted mean; Total moss: total abundance of mosses in plant macrofossils.

circulation amplified the solar signal and caused abrupt climate change about 2800 years ago, coincident with a grand solar minimum. This event can be also linked to the shift in raised bog humidity proxy recorded in the Netherlands that was interpreted as evidence for the 'Homeric climate oscillation' in western Europe (van Geel et al., 1996). Compiled palaeoclimate data do not yet exist for eastern Europe, however, each year new records appear that give a novel look at the hydro-climate of the Holocene (Gałka and Lamentowicz, 2014).

We chose existing long-term quantitative palaeohydrological records from the Baltic area and compiled records from W Europe to compare past-hydrological changes. The testate amoebae-based quantitative wetness reconstruction in Kusowskie Bagno bog resembled the pattern observed in other sites around the Baltic (Fig. 11), i.e. Männikjärve in Estonia (Sillasoo et al., 2007), Kontolanrahka in southern Finland (Väliranta et al., 2007), and those from NW Europe Ireland (Swindles et al., 2013), northern Britain (Charman et al., 2006) and our former 7500-year record from northern Poland (Gałka et al.,
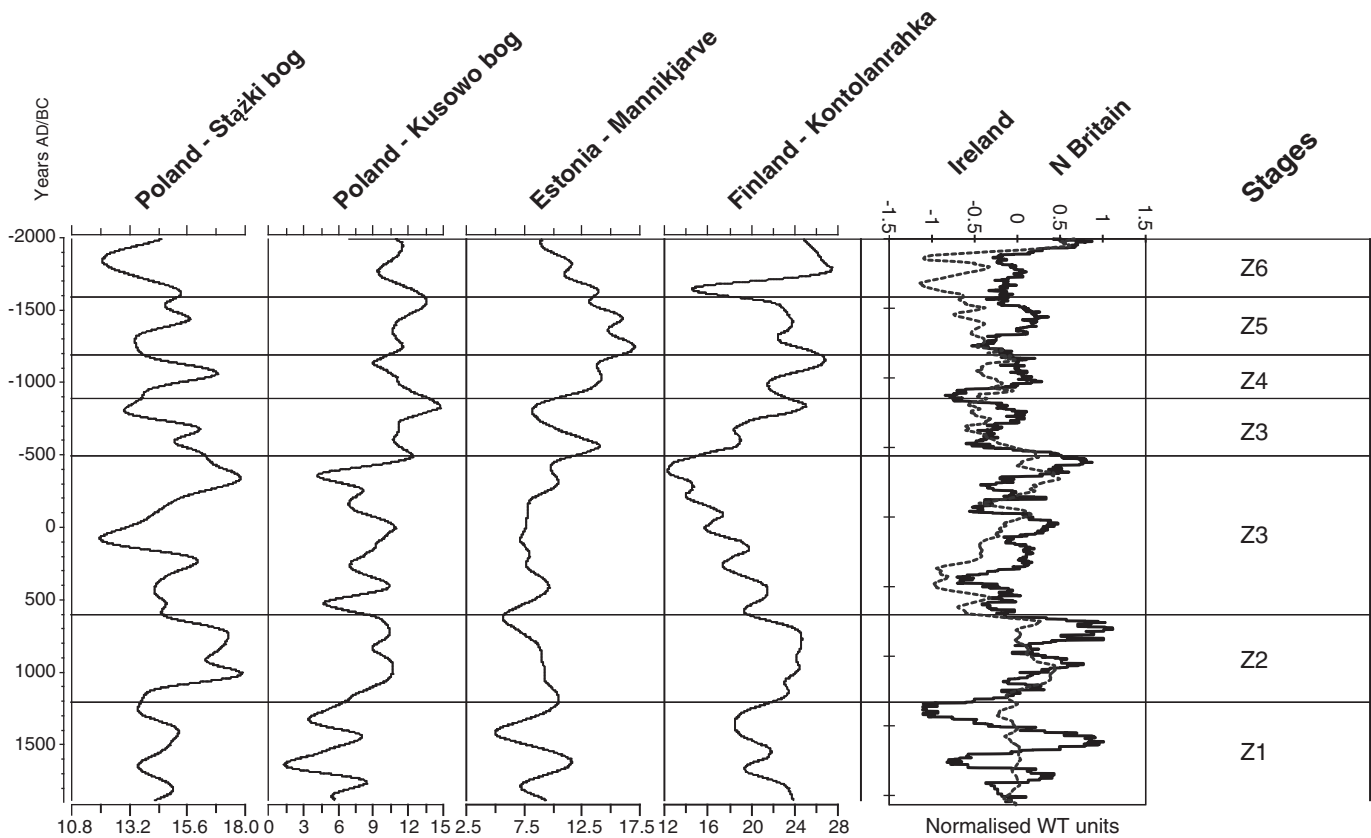

Fig. 11. Comparison of more important testate amoebae-based water table reconstructions from the Baltic area and NW Europe with the inference from Kusowskie Bagno bog. Stążki (Gałka et al., 2013b), Kusowskie Bagno bog (this study), Männikjärve, Estonia (Sillasoo et al., 2007), Kontolanrahka, Finland (Väliranta et al., 2007), UK (Charman et al., 2006) and Ireland (Swindles et al., 2013).

2013a). The time series were all similar; however, Kusowskie Bagno bog water table variability resembled sites from Estonia and Finland more than this from northern Poland. The palaeohydrology from the last 4000 years was divided into 6 phases according to trends in the DWT.

Between 2050 BC and 1250 BC, all of the sites appeared to be wet; however, the reconstructed values of the water table were dependent on the training set and habitat. The northern Britain peatlands revealed strikingly similar fluctuations to the Kusowskie Bagno bog record; however, the amplitude was much higher. It might suggest an influence of westerlies (bringing moist oceanic air masses) on the peatland during the growing season. The Irish bogs possessed a stable DWT. Despite such differences, it is interesting how clearly all four records reveal a dry shift between 1250 BC and 650 BC that suggested a regional climatic change. It is worth noting how well the record from northern Britain fits to Kusowskie Bagno bog in terms of curve fluctuations. Between 650 BC and AD 450, Stążki, Kusowskie Bagno bog, northern Britain, Ireland and Kontolanrahka revealed a wet trend and fluctuations of the water table, whereas in Stążki, the record for the DWT returned to drier conditions earlier, which might be associated with the chronology or an asynchronous response to the climatic change. From AD 450 to AD 850, the water table was decreasing in Kusowskie Bagno bog, Kontolanrahka and northern Britain and increasing in Männikjärve, Stążki and Ireland. Furthermore, there was a general decreasing trend in Stążki, Kontolanrahka and Mannikjarve between AD 850 and AD 1150, whereas in Kusowo bog, the water table increased simultaneously. Between AD 1150 and AD 1550, all of the sites experienced water table fluctuations and the similar pattern disappeared. In the period from AD 1550 to the present times, there was a wet shift which was then modified by human impacts, at least in the case of the Stążki and Kusowskie Bagno bogs. This might have been associated with peat exploitation and drainage leading to a considerable water table drop (Gałka et al., 2014). However, the differences might also have resulted from the different resolutions of the reconstructions and different approaches to the age-depth modelling. In addition, we should consider that internal feedback (Swindles et al., 2012) and autogenic vegetation change (Zobel, 1988) might hide a climatic signal and only compilation of records might give information about regional hydrological signal. Finally our hypothesis about similarities can be partly supported, however, changes are not synchronous and differ in the amplitude of changes as well as reconstructed values that result from the different calibration data sets used for the reconstruction.

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Acknowledgements

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