Unveiling exceptional Baltic bog hydrology, autogenic succession and climate change in
the last 2000 years in CE Europe using replicate cores, multi-proxy data and functional
traits of testate amoebae

Mariusz Galka¹*, Kazimierz Tobolski¹, Łukasz Lamentowicz², Vasile Ersek³, Vincent E.J.
Jassey⁴,⁵, Willem O. van der Knaap⁶, Mariusz Lamentowicz¹,⁷

¹Department of Biogeography and Palaeoecology, Faculty of Geographical and Geological
Sciences, Adam Mickiewicz University in Poznań, B. Krygowskiego 10, 61-680 Poznań,
Poland

²Faculty of Biology, Adam Mickiewicz University, Umultowska 89, 61-614 Poznań, Poland

³Department of Geography, Northumbria University, Newcastle upon Tyne, NE1 8ST, UK

⁴Swiss Federal Research Institute-WSL, Community Ecology Research Unit, Station 2, CH-
1015 Lausanne, Switzerland

⁵École Polytechnique Fédérale de Lausanne (EPFL), School of Architecture, Civil and
Environmental, Engineering (ENAC), Laboratory of Ecological Systems (ECOS), Station 2,
CH-1015 Lausanne, Switzerland

⁶Institute of Plant Sciences and Oeschger Centre for Climate Change Research, University of
Bern, Altenbergrain 21, CH-3013 Bern, Switzerland

⁷Laboratory of Wetland Ecology and Monitoring, Faculty of Geographical and Geological
Sciences, Adam Mickiewicz University, B. Krygowskiego 10, PL–61 680 Poznań, Poland

*Corresponding author
Abstract

In this paper we present results of high-resolution multi-proxy palaeoecological studies of two parallel peat cores from the Baltic raised bog Mechacz Wielki in NE Poland. We aim to disentangle the effect of the regional climate from the autogenic processes of the raised bog itself in driving the vegetation and hydrology dynamics. Based on partly synchronous changes in Sphagnum communities in the two study cores we suggest that extrinsic factors (climate) played an important role as a driver in mire development during the bog stage (AD 500–2012). Using testate amoebae transfer function, we found that the bog revealed exceptionally stable hydrological conditions during the last 2k with a relatively high water table and lack of local fire events that allowed for rapid peat accumulation (2.75 mm/year) in the bog. Further, the strong correlation between pH and community-weighted mean of testate amoeba traits suggests that other variables than water-table depth play a role in driving microbial properties under stable hydrological conditions. There is a difference in hydrological dynamics in bogs between NW and NE Poland until ca CE 1500, after which the water table reconstructions possess more similarities. The most different case is Linje mire, which most probably driven by land-use changes partly coinciding with the Little Ice Age. Our results show how various functional traits relate to different environmental variables in a range of trophic and hydrological scenarios on long time scales. Moreover, our data suggest a common regional climatic forcing in Mechacz Wielki, Gązwa and Kontolanrahka. Though it may still be too early to attempt a regional summary of wetness change in the southern Baltic region, this study is a next step to the long-term perspective of peatland palaeohydrology in Europe.
Keywords: climate change, pollen, plant macrofossils, testate amoebae, palaeohydrology, Holocene, *Sphagnum* succession

1. Introduction

Understanding the impact of the past climate change on ecosystems is critical for predicting the response of ecological communities to on-going climate change (Blois et al., 2013, Lyons et al., 2016). Although climatic forcing is not obvious in many records, peatlands records show both extrinsic (allogenic) and intrinsic (autogenic) processes. Drivers of development of peatlands are often difficult to identify but they are very important to infer past climate and human impacts (Hughes et al., 2002). As suggested by Swindles et al. (2012), autogenic processes might be underestimated as drivers of peatland development. Morris et al. (2015) tried to explore complex behaviours connected with oceanic raised bog development in the United Kingdom using the DigiBog model, especially water table and peat decomposition. However, it should be stressed that not much is known about the development mechanisms of the continental peatlands that cover large surfaces of the northern Hemisphere. Therefore, attention should be paid to continental bogs as key areas to the world carbon accumulation.

Until now two theories were put forward to explain the ombrotrophic development of peatlands. In the first, presented by Osvald (1923) and Kulczyński (1949), the development of local vegetation, mainly of *Sphagnum*, was regarded as a cyclic regeneration of bog microforms by regular alternation of hummocks and hollows. The second theory holds that the development of ombrotrophic mires is closely associated with climate change (Barber, 1981; Mauquoy and Barber, 1999; Schoning et al., 2005; Charman et al., 2006). During wet phases the dominant plant species usually occur in wet habitat (wet lawn or hollows), like *Sphagnum cuspidatum, S. balticum* or *Scheuchzeria palustris*. Consequently, these taxa can be used in palaeoecological reconstructions as indicators for wet climatic stages (Sillasoo et
Dry climatic stages lead to the development of plant communities dominated by *Sphagnum fuscum*, *S. rubellum* or *Calluna vulgaris*, that usually occur in dry microforms such as hummocks (Hölzer, 2010; Laine et al., 2011), so the fossils of these plants can be used as indicators for a dry climatic stage (Sillasoo et al., 2007; Väliranta et al., 2012). Actually, cyclical development of raised bog vegetation has not been proven so far, despite the fact that various authors studied the potential signal of solar activity in peat records (Mauquoy et al., 2004, 2008). However, Turner et al. (2016) warned that one should be very careful in interpreting such data, because solar-type signals might be the product of random variations. Consequently, recent palaeoecological research and palaeohydrological reconstructions from ombrotrophic peatlands in southern Finland (Tuittila et al., 2007), northern–eastern Europe (Swindles et al., 2012), and in Patagonia (Loisel and Yu 2013) showed that the mechanisms of peatland development can be very complex. Human pressure on peatland ecosystems, like drainage, fires, deforestation in their catchment or deposition of minerals and nitrogen on peatland surfaces can indeed lead to disturbances in peatland development (Hughes et al., 2008; McClymont et al., 2008; Galka et al., 2015; Swindles et al., 2015). Such disturbances bring additional difficulties to disentangle climatic impact and autogenic succession.

In this context, Baltic raised bogs are a good model ecosystem to study local vegetation development and its relationship to climate changes, because they had an undisturbed history of vegetation development and peat and carbon accumulation. But even though many of these valuable ecosystems are protected by law, their development and response to climate change are still poorly understood. These bogs are of particular importance for research because in many areas of the world the natural peat dynamics in bogs have been profoundly modified by anthropogenic influences (Chambers et al., 2013). In the
last 200 years, almost all bogs in Europe have been modified by human action (Joosten and Clarke, 2002; Minayeva and Sirin, 2009).

Multi-proxy studies of Baltic raised bogs (including macrofossils, testate amoebae, pollen, micro- and macro-charcoal, isotopes and peat characteristics) covering a range of time spans and concerning on various palaeoecological aspects were conducted in Sweden (van der Linden and van Geel 2006; Andersson and Schoning, 2010), Finland (Tuittila et al., 2007; Välimäki et al., 2007), Estonia (Sillasoo et al., 2007), and Poland (Gałka et al., 2013, 2014, 2015; Lamentowicz et al., 2008, 2009, 2015), Germany and Denmark (Barber et al., 2004).

Testate amoebae are widely used for estimating past water tables and trophic state in peatlands (Charman, 2001; Mitchell et al., 2008). Actually, these fossil protist assemblages are up to today the only source of quantitative data from raised bogs that have been used for regional palaeohydrological syntheses (Charman et al., 2006; Swindles et al., 2013). Recently, functional traits of testate amoebae became important in palaeoecological reconstructions from peatlands (Kajukało et al., 2016; Lamentowicz et al., 2015; Fournier et al., 2015b). This novel and promising approach enables to study peatland ecosystem functioning on long time scales based on a more generalised interpretation of testate amoeba morphology and functional diversity.

However, despite previous multi-proxy studies, the knowledge of continental ombrotrophic peatlands development is still unsatisfactory. High-resolution long-term studies with replicate coring are lacking in central-east Europe and very scarce in the rest of the world (but see Lamentowicz et al., 2011 and Gałka et al., 2016). Here, we aim i) to reconstruct local and regional vegetation changes in Mechacz Wielki bog; ii) to reconstruct long-term peatland ecosystem dynamics using testate-amoebra functional traits and diversity; iii) to compare the palaeohydrological signal in this bog with that in other Baltic raised bogs; iv) to evaluate the relative importance of climatic influence and autogenic succession in the development of the
bog; and v) to reconstruct former the *Sphagnum* communities in the bog and assess their resilience to disturbance, as an aid in further protection and management of the area.

Specially, we tested whether local vegetation and hydrology (including testate-amoebe communities and functional traits) during the last 2000 years were driven either by regional climate change – i.e. extrinsic control- or by autogenic development (succession) of peatland microforms – i.e. intrinsic control.

### 2. Study site

We selected Mechacz Wielki (northeastern Poland, Fig. 1) bog for two reasons. First, the site, despite some drainage in the 1960s, preserved its natural character, which is very rare in this part of Europe. Remains of the pristine ombrotrophic plant communities with the very rare *Sphagnum fuscum*, *S. cuspidatum* or *Rubus chamaemorus* (typical for the Baltic bog vegetation) still occur within the bog, which is the reason for its protection. Human activity in this region was very low due to low industry and settlement development and increased only ca. 1700 CE, so we can exclude human impact on the bog ecosystem before that time (Gałka et al., 2014). Second, Mechacz Wielki bog is located at the southern distribution limit of Baltic raised bogs, which are shaped by the climatic influences of both western oceanic and eastern continental air masses.

Furthermore, Mechacz Wielki mire is a nature reserve with an area of peatland of approximately 146,72 ha. The peatland is located within the large Romincka Forest complex, a major portion of which is located in the territory of Russia. The peatland was drained in the 1960s, but was later restored by a system of dams on ditches. This area was subjected to the last (Vistulian) glaciation (Krzywicki 2002). The land relief is determined by numerous morainic and kame hills, with a height of approximately 200 m a.s.l. The hills are composed
of silty clays, glacial sands and erratic boulders (Krzywicki 2002). The highest point in the vicinity of the peatland is 295.4 m a.s.l. and the lowest 150 m a.s.l.

The influence of the continental climate is very clear in the study area. Mean temperature is approximately -5°C in January and 16–17°C in July (Woś 1999), mean annual temperature is +6.4°C, and the precipitation reaches 700 mm annually. The vegetation of the peatland has a highly mosaic character. Only the central part of the peatland has raised bog vegetation and is overgrown with dwarf pine. Part of the peatland has hummock–hollow structures. The hummocks are dominated by *Sphagnum magellanicum*, *S. rubellum*, *S. fuscum*, in addition to *Eriophorum vaginatum*, *Andromeda polifolia*, and *Oxycoccus palustris*. *Empetrum nigrum* and *Rubus chamaemorus* are less numerous on the hummocks. The hollows are occupied by *S. cuspidatum* and *S. balticum*. The edge of the peatland is covered with coniferous forest of *Pinus sylvestris* and *Picea abies*. The *Sphagnum* mosses in forested areas are represented by such species as *S. girgensohnii* and *S. squarrosum.*

3. Material and methods

3.1. Field and laboratory works

Coring and sampling were performed using a Russian peat corer, which is 7 cm in diameter and 100 cm in length. Coordinates of Site MWI are 54°19'51.80 N, 21°26'31.30 E, of Site MWII they are 54°19'51.80 N, 22°26'17.40 E (Fig. 1). The two peat cores were taken ca. 50 m apart in similar plant communities formed by *Sphagnum magellanicum*, *S. rubellum* and *S. fuscum* occurring in lawn. The sediments were placed in PVC tubes and wrapped. In the laboratory the sediment was unpacked, cleaned and sliced into 1-cm slices using surgical tools.

3.2. Chronology
Nine AMS (Accelerator Mass Spectrometry) radiocarbon dates measured on hand-picked plant macrofossils during plant macrofossils analysis were used to provide chronology for the core MWI, and six AMS dates for core MWII (Table 1). Radiocarbon dates were performed at the Poznań Radiocarbon Laboratory. The calibration of the radiocarbon dates and the construction of the age–depth curve were performed with OxCal 4.1 software (Bronk-Ramsey 2009) and the IntCal13 curve (Reimer et al. 2013) applying a P_Sequence function with a k parameter of 1 cm⁻¹ and 1-cm resolution. The most distinct changes in the peat composition, which might indicate a change in the peat accumulation rate, were introduced using the “boundary” command (Fig. 2). The modelled ages are expressed as calendar years AD/BC.

3.3. Palaeoecological analysis

Plant macrofossils were analysed at 1 cm intervals in contiguous samples of approximately 15 cm³ in the two cores. The samples were washed and sieved under a warm water current over 0.25 mesh screens. The vascular plant composition was determined on the basis of carpological remains and vegetative fragments (leaves, rootlets, epiderm) using the available identification keys (Grosse-Brauckmann, 1974; Tobolski, 2000; Velichkevich and Zastawniak, 2006; 2008). Volume percentage of the different vegetative remains and of Sphagnum sections were estimated in steps of 5%. Relative proportions of taxonomic sections within Sphagnum, which is of key importance for the interpretation, were estimated under the microscope on the basis of branch leaves on two 32 x 32 mm cover glasses. Therefore, identification of Sphagnum to species level was carried out separately on the basis stem leaves using specialist keys (Hölzer, 2010; Laine et al., 2012) and recent reference materials, collected in Department of Biogeography and Palaeoecology in Poznań. Sphagnum nomenclature follows Ochyra et al. (2003). The results are presented in the form of diagrams of plant macroremains (Fig. 3 and 4), which were prepared with the computer program C2.
Sphagnum fuscum and S. rubellum have been reported together due to the difficulty of differentiating them in fossil state, particularly when stem leaves are lacking (Hölzer, 2010; Gałka et al., 2013). However, these two species occur in a similar habitat. Both are typical ombrotrophic species which occur together in e.g. relatively dry hummocks or lawn (Rydin and McDonald, 1985; Laine et al., 2011), so in palaeoecological reconstructions they record similar environmental information.

Testate amoebae were analysed in sub-samples of 5 cm³ taken at 5 cm intervals with a vertical thickness of 1 cm. The samples were prepared by means of sieving and back-sieving (Booth et al., 2010b). The testate amoebae were analysed at 200–400x magnification, aiming at a minimum of 150 tests per sample whenever possible. Identification was carried out at the highest possible taxonomical resolution based on the available literature (e.g. Grospietsch, 1958; Ogden and Hedley, 1980; Mazei and Tsyganov, 2006).

Pollen and spores were identified and counted in sediment samples of 1 cm³ volume and 1 cm vertical thickness, taken every 5 cm depth. The samples were boiled in 10% KOH and acetolysed (Berglund and Ralska-Jasiewiczowa, 1986; Faegri and Iversen, 1989). Samples that contained mineral matter were treated with cold HF for 48 h. On average 507 pollen grains of trees, shrubs and herbs were counted in each sample. In samples with low concentrations, up to two slides were counted with a surface area of 22 x 22 mm each. The basis for calculating percentages is the sum of the pollen of trees and shrubs (AP) and terrestrial herbaceous plants (NAP). Summary curves were made for human activity indicators distinguished according to Behre (1981) and van der Linden and van Geel (2006).

3.4. Numerical analyses and data visualization

Quantitative reconstruction of the water table changes based on testate amoebae was carried out in C2 software (Juggins, 2003), using the transfer function developed for northern Poland.
by Lamentowicz and Mitchell (2005) and Lamentowicz et al. (2008b). The testate amoeba

diagram was constructed in C2. Zonation was determined using CONISS (Grimm, 1987)
software to describe the general biostratigraphy. Pollen results were visualized using Tilia 2
and Tilia-Graph software (Grimm, 1992).

3.5 Wavelet analysis

Continuous wavelet transforms are useful for analysing data that contain non-stationary
power at several different frequencies and can therefore identify cycles both in time and
frequency domains. We used squared wavelet coherence to evaluate the coherence of the
wavelet transforms and the phasing between the timeseries analysed. The data were
interpolated to equal time steps of 4 years with a Gaussian window of 12 years and we used a
Morlet wavelet in order to evaluate the presence of non-stationary cycles in our time series
(Torrence and Compo, 1998).

3.5. Functional traits of testate amoebae

For testate amoebae, the following eight basic traits were selected to complement the species–
environment relations provided by the transfer function: metabolic status of the species
(mixotrophic or heterotrophic), body length, body width, biovolume, body range,
pseudostome size, and position of the pseudostome (Marcisz et al., 2016). The metabolic
status is expected to respond to changes in pH, since mixotrophic species are reported to cope
better with rare food sources in acidic conditions (Fournier et al., 2015). However,
mixotrophy is also related to light availability through the presence of the symbiotic algae
(Marcisz et al., 2014). Body size, pseudostome size and pseudostome position were shown to
be related to water-table depth (Lamentowicz et al., 2013), since low moisture conditions
could impact larger species, as well as those with open aperture (Lamentowicz et al., 2015).
Functional alpha diversity (FD) of communities was calculated using the Rao quadratic entropy (Q) index (Ricotta, 2005): Rao’s Q value (RaoQ) is unitless and is a measure for the functional diversity within a community (Rao, 1982). The response of individual species traits was further analyzed by calculating the community-weighted mean (CWM) of each morphological traits, which is a measure of the dominant trait values in a community (Díaz et al., 2007; Garnier et al., 2007, 2004). Morphological traits and FD were calculated using the FD R package (Villéger et al., 2008, R Core Team, 2013). All data are presented as diagrams and plotted using C2 software (Juggins, 2003) and the R package ‘rioja’ (Juggins 2012).

4. Results

4.1. Chronology and lithology

Nearly straight lines in age–depth models (Fig. 2) suggest constant and rapid accumulation rates and absence of hiatuses. The peat accumulation rates in both cores were very rapid, with an average of 2.75 mm/year in core MWI and ca. 2.3 mm/year in core MWII. The lithology of both cores is similar. In the bottom part of both cores, in core MWI between AD 1 and 120 and in core MWII between 200 and 20 BC, detritus gyttja is present with aquatic macrofossils of e.g. Potamogeton natans, Nymphaea alba, and Stratiotes aloides (Fig. 3 and 4). A thin brown-moss–herbaceous peat layer overlies lake sediments dated AD 120–250 in core MWI and 20 BC–AD 1 in core MWII, which is mainly composed by Hamatocaulis vernicosus and Cyperaceae remains. Then between ca. AD 250 and 520 in core MWI and between AD 1 and 300 in core MWII a peat layer with Sphagnum obtusum, S. angustifolium, and Scheuchzeria palustris is present. Above this layer in both cores is a peat layer composed of S. fuscum/rubellum, S. cuspidatum as well as S. magellanicum with Eriophorum vaginatum and Ericaceae macrofossils.
4.2. Plant macrofossils

Seven zones in local vegetation development were visually delimited in the macrofossils of core MWI (Fig. 3). Zone MWI-ma-1 (AD -1-120), represents a shallow lake with aquatic plants such as *Potamogeton natans*, *Stratiotes aloides*, and *Nymphaea alba*. In zone MWI-ma-2 (AD 120-250), a poor-fen developed. The following plants appeared: *Sphagnum* sect. Acutifolia and S. sect. *Hamatocaulis vernicosus* and *Carex rostrata*, and *Comarum palustre* and *Scheuchzeria palustris* were also recorded. In zone MWI-ma-3 (AD 250–520), *Sphagnum obtusum* followed by *S. angustifolium*, and *Eriophorum vaginatum* were dominant species. In zone MWI-ma-4 (AD 520–790), a raised bog developed, with the main role played by *S. magellanicum* and *Sphagnum cuspidatum*, and *Oxycoccus palustris* appeared. In zone MWI-ma-5 (AD 790–1250) *Sphagnum fuscum/rubellum* dominated. Numerous *Calluna vulgaris* remains were also noted. In zone MWI-ma-6 (AD 1250–1640) *S. fuscum/rubellum* again dominated and there were two peaks of *S. cuspidatum* and *E. vaginatum*. In bottom part of zone MWI-ma-7 (AD 1640–2012) *S. cuspidatum* dominated, in the upper part reappeared *S. fuscum/rubellum* and *S. magellanicum*, and *Sphagnum balticum* appeared for the first time.

Six zones in local vegetation development were visually delimited in core MWII (Fig. 4). Zone MWII-ma-1 (160–50 BC) represents a shallow lake with aquatic plants, such as *Potamogeton natans*, *Stratiotes aloides*, *Nymphaea candida*, and *Nuphar* sp. In zone MWII-ma-2 (50 BC–AD 100) a poor-fen developed with *Calliergon cordifolium*, *Sphagnum palustre*, *S. obtusum*, and *S. teres*. Numerous *Carex rostrata* and *Comarum palustre* remains were also recorded. In zone MWII-ma-3 (AD 100–800), *S. angustifolium* followed by *S. magellanicum* and *S. fuscum/rubellum* were dominant species. In the upper part of this zone increased the role of *Eriophorum vaginatum*. During zone MWII-ma-4 (AD 800–1380) a raised bog developed, with the main role played by *S. fuscum/rubellum* and *S. cuspidatum*,
which dominated alternatively. *Eriophorum vaginatum* increased in upper part or the zone. In zone MWII-ma-5 (AD 1380–1830) *S. fuscum/rubellum, S. balticum*, and *S. cuspidatum* played a main role. In zone MWII-ma-6 (AD 1830–2012) *S. fuscum/rubellum* and *S. magellanicum* were the dominants. In the uppermost part of this zone numerous *Calluna vulgaris* and *Oxycoccus palustris* macrofossils appeared.

4.3. Testate amoebae analysis, water table and pH

Five testate amoebae zones were delimited in core MWI (Fig. 5A). Zone MWI-ta-1 (AD 10–250) is characterised by dominant *Arcella discoides* and *Centropyxis aculeata*. In the upper part of the zone *Archerella flavum* and *Hyalosphenia papilio* increased. The water table oscillated between 1.5 and 5 cm below the peat surface and pH between 5 and 7.3. In zone MWI-ta-2 (AD 250–500) *Archerella flavum* and *Hyalosphenia papilio* dominated, and *Cyclopyxis arcelloides* was also recorded. The water table was rather stable at ca. 5 cm and pH between 4.4 and 6.0. In zone MWI-ta-3 (AD 500–780) three species were dominant: *Archerella flavum*, *Hyalosphenia papilio* and *Amphitrema wrightianum*. *Hyalosphenia elegans* increased. *Assulina muscorum* and *A. seminulum* were important in the lower part of the zone. At ca. AD 680 the water table increased to 3.9 cm and pH had a decreasing trend down to 3.9. In zone MWI-ta-4 (AD 780–1680) *Archerella flavum*, *Hyalosphenia papilio* and *H. elegans* played dominant role, and there was an increasing role of *Assulina muscorum*, *A. seminulum* and *Nebela militaris*. The water table was about 12 cm and had a wetter trend. pH was unstable lower in the zone, then ranged between 4.0 and 4.5. In the bottom part of zone MWI-ta-5 (AD 1680–2012) *Archerella flavum* and *Amphitrema wrightianum* were dominant. In most of the upper part of this zone *Arcella discoides*, *Hyalosphenia elegans*, *Nebela militaris*, and *Nebela tincta* increased. The water table had a decreasing trend down to ca. 25
cm and pH was the lowest of the entire analysed period, reaching ca. 3.6 at the top of the profile.

4.4. Testate amoebae traits and environmental change

Functional diversity (FD), CWM metabolism, pseudostome position and body range were increasing in zone MWI-ta-1 (AD 10–250) together with a decreasing water table and pH (Fig. 5B). The CWM of the other functional traits had a decreasing trend. Then in MWI-ta-2 (AD 250–500), when the water table was stable (contrasting with the still decreasing pH), FD reached its highest value. However, CWM metabolism and body range sustained an increasing trend whereas other traits decreased. Zone MWI-ta-3 (AD 500–780) delimits a wet shift and pH lowering connected with an increase of CWM metabolism and CWM body range. FD was relatively stable with a peak ca. AD 650. Then, around AD 520 the peatland reached the state of oligotrophy according to testate-amoeba-based pH and traits data. Zone MWI-ta-4 (AD 780–1680) was relatively stable in terms of water table and pH, and also FD and CWMs had no significant fluctuations. Zone MWI-ta-5 (AD 1680–2012) includes a considerable increase of the water table and then a drying trend. Most of the traits responded to this trend, but FD remained stable. Especially relevant is the decrease of mixotrophic species since AD 1680, that continued after AD 1800 – this date is really important for decreasing in FD. Such decrease suggests a functional diversity response to probable human impact connected with deforestation and then drainage. Also CWM body length, body width and biovolume increase until ca AD 1850 followed by a decrease, which is probably also connected with the recent hydrological disturbances. CWM body range gradually decreased together with the water table.

We observed a strong correlation between pH and body length (r=0.8, p<0.001) as well as between pH and pseudostome size (r=0.8, p<0.001) (Figure 6). pH was also
significantly correlated with biovolume (r=0.7, p<0.001). The water table was only correlated negatively (r=-0.5, p<0.001) with pseudostome size. Furthermore, we found that changes in vegetation in response to pH were strongly related to changes in TA functionality in response to pH (Figure 7) while a slight correlation was found between the response of vegetation composition and TA functionality to water table.

4.5. Pollen

Six pollen zones in regional and local vegetation development at core MWI were statically delimited (Fig. 8). In terms of deciduous trees, zone MWI-po-1 (AD 1–540) was dominated by Quercus, Corylus, and Ulmus and Tilia. Pinus and Betula had similar values of approximately 20%, whereas Alnus ranged between 10 and 25%. In the lower part were large quantities of Equisetum spores and Cyperaceae, and Potamogeton and Pediastrum were also noted. In zone MWI-po-2 (AD 540–730) the Carpinus increase (from 10 to 17%) was the most pronounced. Zone MWI-po-3 (AD 730–1060) shows increases of Picea, with two peaks up to 40%. Betula increased and Alnus decreased significantly in the upper part of the zone, and Ericaceae increased. Zone MWI-po-4 (AD 1060–1660) is characterized by a Picea increase with two peaks (up to 36%) in upper part. Pinus (approximately 30%) and Carpinus (approximately 10%) remained rather constant. In the upper part increased the indicators for human activity, and Fagopyrum appeared for the first time. Zone MWI-po-5 (AD 1660–2012) shows a sharp decline of deciduous trees, including Quercus, Carpinus, Tilia and Alnus as well as increasing herbaceous plants (NAP), which is largely due to human activities (Artemisia, Rumex, Cerealia, Secale, and Triticum). The human indicator curve between AD 1940 and 1950 decreased.

4.6. Wavelet analysis (Fig. 9)
The squared wavelet coherence shows how coherent the cross wavelet transforms are in time frequency space and is similar to a localised correlation coefficient in time frequency space which also shows the phasing between two time series (Grinsted et al., 2004). In MWII, *Sphagnum fuscum/rubellum* and *Sphagnum cuspidatum* have a clear anti-phase relationship through most of the core, at periods ranging from multi-centennial to decadal. This anti-phase relationship is also present in MWI, but both weaker and less persistent at all periods.

5. Discussion

5.1. Autogenic plant succession vs climate impact in peatland development

The role of autogenic plant succession and possible climate impact on Mechacz Wielki (MW) bog development are described in two parts, because of the clear lithological boundary in both cores that divides the MW bog development into two stages.

5.1.1. Lake–poor-fen transition (AD 1–500)

It is likely that terrestrialisation (filling up of the lake) was during the first stage of MW bog development the main driver of plant succession from aquatic to ombrotrophic vegetation, which implies that the plant succession was autogenic. The successive plant communities during terrestrialization from lake to bog were described in detail in several studies (e.g. Weber, 1902; Zobel, 1988; Rydin and Jeglum, 2001), and this type of terrestrialisation occurs commonly across the northern hemisphere in previously glaciated areas. The presence of *Hamatocaulis vernicosus*, *Calliergon cordifolium*, *Sphagnum* sect. Cuspidata and vascular plants like *Comarum palustre*, *Cicuta virosa* and numerous *Carex* species suggests that a floating mat developed. Gradual isolation from the groundwater favoured the expansion of *Sphagnum* species like *S. obtusum* and *S. angustifolium*, typical for poor-fen ecosystems (Hölzer, 2010; Laine et al., 2011).
An alternative possibility is that a warm climate such as that of the Roman period triggered a lowering of the water table in the former lake, resulting in a faster development of poor fen on the organic lake sediments (Büntgen et al., 2011). However, an argument against this idea is that we did so far not observe any synchronous lake–fen transitions in the Baltic bogs of Pomerania; these transitions range from 2000 years ago in this study, 4000 years ago in Bagno Kusowo (Lamentowicz et al., 2015), 6200 years ago in Gązwa (Galka et al., 2015), and 7500 years ago in Stążki (Galka et al., 2013). Furthermore, at the time of lake–fen transition in Mechacz Wielki we have no indications for any abrupt changes in plant succession on a regional scale that might suggest a lowering of the ground-water table in the surrounding peatlands. Further, the lack of pollen indicators for increased human activity in the region between AD 1 and 200 allows us to exclude increased human pressure on bog development. Together, this suggests that terrestrialisation in Baltic Bog development was mainly determined by geomorphological characteristics and that the rate of change was mostly related to the depth of the basin.

5.1.2. Bog stage (AD 500–2012)

After approximately AD 500 both cores of Mechacz Wielki show that the development of the vegetation and the peatland was independent of mineral-rich groundwater. In both cores the local plant communities started to depend on water derived from precipitation (Fig. 10). This ombrotrophication resulted in a rapid lowering of the pH (Gorham and Janssens 1992; Kuhry et al. 1993; Hughes, 2000) and led at both sampling sites to the development of plant communities in which *S. cuspidatum* and *S. fuscum/rubellum*, species typical for ombrotrophic peatland (Hölzer, 2010; Laine et al., 2011), played a main role. Oligotrophic conditions since this time are also indicated by the pH shift from ca. 5.0 to 4.0 reconstructed with testate amoebae during the *S. cuspidatum* phase in core WMI. However, according to the
pH reconstruction full independence from groundwater was most probably reached later, ca. AD 650. This would suggest that testate amoebae have a higher sensitivity to water chemistry than vegetation. A similar phenomenon was found in Mauntschas bog in SE Switzerland (Engadine Valley), where the peat core was mostly composed of *Sphagnum fuscum* and yielded a large diversity and turnover of testate amoebae during the last millennium when peatland became independent of mineral-rich ground water (van der Knaap et al., 2011).

On the basis of the partly synchronous changes in *Sphagnum* communities in the two cores of Mechacz Wielki (Fig. 10), we suggest that extrinsic factors (e.g. climate) played an important role in the vegetation development during the bog stage. In core MWI the oligotrophic taxon *S. fuscum/rubellum* appeared around AD 480, followed by mainly *S. cuspidatum* and *S. magellanicum*. *Sphagnum balticum*, a common species in oligotrophic habitats, occurred in this core only between AD 1750 and 1920. Core MWII was characterised by almost constant presence of *S. fuscum/rubellum*, followed by *S. cuspidatum* and *S. balticum*, whereas *S. magellanicum* played a larger role only after AD 1850 (Fig. 8). Of particular interest is the repeated appearance of *S. cuspidatum* in both cores. *S. cuspidatum* occupies the wettest places in the bogs (Hölzer, 2010). *S. cuspidatum* was recorded in core MWI ca. AD 500–800, 1250–1340, 1450, 1500, 1640–1770, and 1800–1860, and in core MWII ca. AD 800, 1150, 1250, 1420, 1500, 1550, 1710, and 1770–1840. However, it should be noted that the short duration of events with *S. cuspidatum* presence, chronological uncertainties, and the matching of wiggles in climate based on different cores complicate the picture of globally synchronous rapid climate changes (Baillie, 1991; Blaauw, 2012) and of the response of local plant communities in MW bog. Several appearances of *S. cuspidatum* in MW bog coincide with well-known climatic cooling events such as the Oort, Wolf, Spörer, Maunder, and Dalton Minimum during Medieval Warm Period and Little Ice Age period (Fig. 8). The periodic occurrence of *S. cuspidatum* in both cores at the same time must have been
caused by increasing water tables, which coincides with increased humidity during cooler periods. The climate shifts and development of *Sphagnum* sect. Cuspidata (including *S. cuspidatum* and *S. balticum* and others) populations took place during solar minima that are in NW Europe interpreted as wet climatic stages (Mauquoy et al., 2008; De Vleeschouwer et al., 2012). However, Gałka et al. (2014, 2016) reconstructed for NW Poland hydrological disturbances toward drier conditions during these periods.

Alternatively, the alternate appearance of *S. fuscum/rubellum* and *S. cuspidatum*, accompanied by *S. balticum*, could suggest a re-appearance of hummock–hollow structures during the bog stage. This type of oceanic and continental peatland development was presented by Osvald (1923) and Kulczyński (1949). If we apply this theory to our case, *S. fuscum/rubellum* would build hummocks because it usually occurs on the dry side of the hydrological gradient in bogs or poor-fen (Hölzer 2010; Laine et al. 2011; Hajkova et al., 2012), whereas *S. cuspidatum* would occupy the hollows between the hummocks. However, if such hummocks existed, they can not have been tall, because according to TA-based reconstructions the water table decreased to a mere 18 cm below peatland surface during two very short periods only. The reconstructed wet hydrological conditions for *S. fuscum/rubellum* communities in MW bog agree well with findings in Gązwa bog (Gałka et al., 2015) and Bagno Kusowo (Lamentowicz et al., 2015), where *Sphagnum fuscum/rubellum* grew with a water table fluctuating around 14 cm resp. 10 cm below the peatland surface. This strongly indicates that during periods with *S. fuscum/rubellum* dominance in MW bog, extensive *Sphagnum* lawns developed under stable moisture conditions, without hummocks. The absence of drier hummocks is supported by the absence during the MW bog stage of *Polytrichum* ssp., *Dicranum* spp. and *Aulacomnium palustre* macrofossils, which are taxa that usually occupy the driest places in bogs such as hummocks (Smith 2004; Manukjanová et al., 2014).
We tested the temporal coherence between *S. fuscum/rubellum* and *S. cuspidatum* in both cores using wavelet coherence analysis. They are in clear anti-phase in core MWII through most of the core, periods ranging from multi-centennial to decadal. An anti-phase relationship was also found in MWI, most clearly pronounced at periods of ~200 years, but in generally both weaker and less persistent at all periods than in MWII. This suggests that while there seems to be a common forcing factor, local influences on bog development are also important.

It was shown elsewhere that hydrological disturbance in the catchment can influence the peatland ecosystem even when the mire itself was not drained (Tahvanainen, 2011). Pollen, however, indicates absence of significant human activity in the surroundings of MW bog up to the eighteenth century, from which we conclude that changes in local plant communities found in both cores up to ca. AD 1700 are not associated with hydrological disturbance outside the bog. We therefore suggest that climate played the main role in the MW bog development. The differences between the two cores MWI and MWII were the result of autogenous plant succession causing small-scale patterns in the bog vegetation under generally stable hydrological conditions.

5.2. Palaeohydrology, climate and autogenic processes

The Mechacz Wielki (MW) bog archive includes a continuous palaeohydrological record. Five meters of peat accumulated during the last two millennia. The peatland is exceptional in that so much peat accumulated with a strikingly stable water table of on average ca 10 cm below the surface for the entire period. A first decrease of the water table was associated with lake–fen–bog transition (Fig. 11). Such a pathway of development was found in many sites in the Northern Hemisphere (Hughes and Barber, 2003; Lamentowicz et al., 2008b; Succow and Joosten, 2001; Charman, 2002; Rydin and Jeglum, 2006). Our studies indicate that the lake–
fen–bog transition in MW 2000 years ago was autogenous, not forced externally, since this
transition took place in other Baltic bogs in N Poland not synchronously but at different times
between 7500 and 2000 years ago (Gałka et al., 2013; Lamentowicz et al., 2015). The
different timings might be related to differences in geomorphology such as size, depth and
form of the basin and permeability of the underlying moranic plateau. However, once the bog
stage has stabilised we might expect that the peatland ecosystem is sensitive to climatic
changes. We indeed found two major and several minor fluctuations in the water table. While
minor fluctuations might be connected with local microsite changes, the larger fluctuations
might well be related to climatic shifts. We therefore compared the water table curves of all
studied peatlands around the Baltic (Fig. 11). Stążki, Bagno Kusowo (Lamentowicz et al.,
2015) and Linje (Marcisz et al., 2015) reveal widely different fluctuations, whereas similar
trends were observed in Gązwa (Gałka et al., 2015) and our present site (Mechacz Wielki) in
NE Poland, Männikjärve in Estonia (Sillasoo et al., 2007) and Kontolanrahka in Finland
(Väliranta et al., 2007). Bagno Kusowo bog yields a wet trend during the Little Ice Age
similar to that in most other sites except Linje that was dry until 1650 and then became wetter
until AD 1800. Such similarities might suggest a common regional climatic forcing in
Mechacz Wielki, Gązwa and Kontolanrahka. Though it may still be too early to attempt a
regional summary of wetness change in the southern Baltic region, this study is a next step to
the long-term perspective of peatland palaeohydrology in Europe.

The number of sites studied in the Baltic region is steadily increasing, and what we
can assess already now is that there were two pronounced wet shifts during the last 2000 years
in NE Poland. One can be dated to ca. AD 550–850, the other to AD 1450–1800. In NW
Poland on the other hand, the latter wet shift looks quite unstable in the Baltic Bogs Bagno
Kusowo and Stążki (Gałka et al., 2016; Lamentowicz et al., 2009; Lamentowicz et al.,
2008a). It may be that peatland change in NW Poland was driven differently by climate,
resulting in less hydrological instability leading to dry conditions from ca AD 1600 to AD 1800. In general, the water table was more variable in NW Polish bogs, whereas water table trends are strikingly similar between the two sites in NE Poland lying closest together Gązwa and Mechacz Wielki (distance ca. 100 km).

At this stage of the research we focus on the Baltic region. Many studies are in preparation now, and more general conclusions for the Baltic region will follow in the future. A main challenge is to separate intrinsic and extrinsic drivers of bog development in Baltic raised bogs. This can be done by comparing multiple sites of different sizes using various proxies for validation. One future aim is tracking dry climatic shifts by combining information on past fires and past hydrology. Summarising, there is a difference in hydrological dynamics in bogs between NW and NE Poland until ca AD 1500, after which the water table reconstructions possess more similarities. The most different case is Linje mire, which most probably driven by land-use changes partly coinciding with the Little Ice Age.

5.3. Testate-amoebae functional traits over long time scales

We analysed functional traits of testate amoebae and their functional diversity to study how these responded to the past environmental disturbances. Modern studies revealed a clear pattern of change in functional diversity/traits along the altitudinal gradient (Lamentowicz et al., 2013), fen–bog gradient (Jassey et al., 2014) and continental gradient with increasing frost intensity (Jassey et al., 2016). Not many studies have been done so far to explore long-term changes in testate-amoeba traits (Fournier et al., 2015b; Lamentowicz et al., 2015; Kajukało et al., 2016, Marcisz et al., 2016). Only one study found a close relationship between hydrology and aperture position/type, namely in a quantitative reconstruction and calibration data set (Lamentowicz et al., 2015). Kajukało et al. (2016) found a moderately significant correlation of the water table with pseudostome position in the montane peatland Jagnięcy
Potok in SW Poland. Based on these earlier findings, we expected a clear relationship in Mechacz Wielki (MW) between functional traits and hydrological disturbance. However, functional diversity and traits in MW were surprisingly stable in time. The only changes that were recorded were during the lake–bog transition and the recent (last 500 years) change connected with deforestation and drainage.

We found a correlation between the water-table depth and pseudostome position in Bagno Kusowo studied earlier (Lamentowicz et al., 2015), but no correlation in Mechacz Wielki. However, in MW a strong correlation was found between pH and CWM (community-weighted mean) of the traits pseudostome position, body length and biovolume. This suggests that under stable hydrological conditions, other variables than water-table depth play a role in driving microbial functional properties. The change in pH was connected with the fen–bog transition, whereas the entire pH decrease took about 800 years. Such a long time window of relative stability was apparently long enough to drive functional traits, resulting in a simultaneous shift to species with smaller pseudostome size, smaller biovolume and smaller body length. As a result the testate-amoeoba community became dominated by the small *Archerella flavum*. This species was after AD 1700 gradually replaced by *Arcella discoides*, which may be related to the land-use change around the bog shown by the increase of human pollen indicators and NAP (non-arboreal pollen). In Bagno Kusowo bog with its more unstable hydrology, on the other hand, many more shifts like this occurred in its 4000-years’ history (Lamentowicz et al., 2015). Lamentowicz et al. (2009) already noticed that *Arcella discoides* indicates hydrological instability or at least a shift to a different hydrological state, which is also connected with the decrease of mixotrophic species such as *Archerella flavum* or *Hyalosphenia papilio*. Mixotrophic species are also sensitive to pollution and hydrological change, so their loss should be regarded as an important warning signal for a change in peatland functioning in terms of carbon accumulation (Jassey et al., 2015).
The strong correlation of biovolume and body length with pH can be explained by the dominance of small species as a result of oligotrophication. It is however intriguing that large-bodied species, and also indicators of wetness and oligotrophy like *Hyalosphenia papilio*, had no more than low abundances during the oligotrophic phase. We hypothesise that the dominance of *Archerella flavum* reflects the openness and high light availability resulting from the scarcity of trees on the mire due to the high ground-water table. This is supported by the study of Payne et al. (2015), who showed how strongly testate amoebae communities are affected by forest encroachment. They also suggested that increased tree recruitment on open peatlands has important consequences for both microbial diversity and microbially-mediated ecosystem processes, and also that it reduces the contribution of mixotrophic testate amoebae to primary production.

The correlation between reconstructed pH and biovolume, body length and pseudostome size indicate that testate amoeba species show morphological adaptations to the different niches in which they are living. The change in morphological traits during the fen–bog transition is particularly clear. It suggests that larger species were existing in the fen and poor-fen phase, whereas smaller, mixotrophic species dominated in the purely oligotrophic and stable wet phase. The answer why the dominance of *Hyalosphenia papilio* (large mixotrope) shifted to that of *Archerella flavum* (small mixotrope) in relatively stable conditions still remains to be answered. It may be that *Archerella flavum* needs a special food source in stable hydrological conditions as well as more light for photosynthesis than *Hyalosphenia papilio*.

Connected to these findings, we found that pH-induced changes in vegetation were related to pH-induced changes in testate amoeba functionality (Fig. 7). These results indicate a determining role of vegetation composition on soil microbial function over time, driven by intrinsic changes within the mire (i.e. decreasing pH). The control of vegetation on testate
amoeba functionality might ultimately have exerted an effect on ecosystem processes like C
and nutrient cycling (Jassey et al. 2014). Smaller community size structure of testate amoebae
and lower mixotrophic abundance under acidic pH were recently related to higher microbial
activity in peatlands (Lamentowicz et al. 2013; Jassey et al. 2016). This suggests that during
stable water level but decreasing pH, the shifts in testate amoeba functionality might have
resulted in higher microbial activity in the bog, promoting nutrient cycling. Summarizing, our
study shows how various functional traits relate to different environmental variables in a
range of trophic and hydrological scenarios on long time scales.

5.5. The dynamics of peat-bog growth around Baltic Sea

Peat accumulation rates and their feedbacks were reconstructed for many bogs in various
parts of Europe (e.g. Aaby and Tauber, 1974; Belyea and Clymo, 2001; Kalnina et al., 2014).
The average peat accumulation rate in Mechacz Wielki bog was high: 2.75 mm/yr in core
MWI and 2.3 mm/yr in core MWII (Tab. 2). Such high rates were not found before in bogs of
the Baltic region (Aaby and Tauber, 1974; Table 2). This fast rate are connected with the
stable hydrological conditions. We reconstructed only two very short periods with water
levels deeper than 15 cm below the peatland surface, around AD 1100 and around 1970.
During nearly the entire 1800 years of bog development the water depth ranged between 5
and 12 cm the below the peatland surface. We did not find any macroscopic charcoal in the
two analyzed cores, which means that there were no peatland fires of any importance. Wet
ombrotrophic bogs with relatively high water tables are generally resilient to surface fire
(Magnan et al., 2012; Gałka et al., 2015). In Mechacz Wielki bog, the stable hydrological
conditions together with a relatively high water table and absence of local fire events allowed
continuous and rapid Sphagnum growth with undisturbed peat accumulation.
Conclusions

The simultaneous study of various biotic proxies (plant macrofossils, pollen, testate amoebae) followed by radiocarbon dating and statistics analysis in the southern Baltic bog Mechacz Wielki in NE Poland allowed us to reconstruct palaeoenvironmental changes during the last 2000 yr in the southern Baltic region. The results of the study suggest the following:

1. Despite drainage, which was carried out on Mechacz Wielki bog in the twentieth century, local plant succession continued without changes. This bog still is occupied by rare, valuable, and protected ombrotrophic *Sphagnum* species and vascular plants typical for Baltic raised bog ecosystems. This site is very important for the conservation of biodiversity and the determination of reference conditions during restoration processes of degraded Baltic raised bogs.

2. On the basis of partly synchronous changes in *Sphagnum* communities in two cores, we suggest that extrinsic factors (e.g. climate) played an important role as a driver in Mechacz Wielki bog development during the bog stage.

3. The stable hydrological conditions with a relatively high water table and lack of local fire events allowed for a rapid peat accumulation in Mechacz Wielki bog.

4. There is a difference in hydrological dynamics of Baltic bogs between the NW and NE Baltic region until ca. AD 1500, after which the water-table reconstructions possess more similarities. The most different case is Linje mire, which was most probably caused by land-use changes overlapping with Little Ice Age.

5. The link between reconstructed pH and biovolume, body length and pseudostome size show that different species of testate amoebae have morphological adaptations according to the niches in which they live.

6. Our study shows how various functional traits relate to different environmental variables in a range of trophic and hydrological scenarios in long time scales.
7. Palaeoecological studies are the key to understanding the development of Baltic raised bogs and are very helpful in creating the plan of protection of raised bogs.

Acknowledgements

The study was financed through a grant from the Polish Science Centre awarded for the following project: Multi-proxy study of the Baltic bogs in N Poland with the aim to provide reference conditions for active nature protection (No. NN305 062 240) and grant no 2015/17/B/ST10/01656. We thank Adam Hölzer (Karlsruhe, Germany) and Dale Vitt (Carbondale, USA) for help in the identification of Sphagnum and brown-moss species. This research was supported by grant PSPB-013/2010 from Switzerland through the Swiss Contribution to the enlarged European Union.

References


Barber, K.E., 1981. Peat stratigraphy and climatic change. A palaeoecological test of the theory of cyclic bog regeneration. A. A. Balkema, Rotterdam, NL.


Hughes, P.D.M., Barber, K.E., 2003. Mire development across the fen-bog transition on the Teifi floodplain at Tregaron Bog, Ceredigion, Wales, and a comparison with 13 other raised bogs. J. Ecol. 91, 253-264.


Juggins, S., 2012. rioja: Analysis of Quaternary Science Data, R package version (0.8-4).


associated with solar variability during the mid-late Holocene. J. Quaternary Sci. 23, 745-763.


Bryologist 100, 302–7.


889 Becker, K., Armit, I., 2013. Centennial-scale climate change in Ireland during the
891 Tobolski, K., 2000. Przewodnik do oznaczania torfów i osadów jeziornych, Warszawa. PWN.
893 Soc. 79, 61–78.
895 controls of mire vegetation succession in a southern boreal bog in Finland using
896 partial ordinations. J. Veg. Sci. 18, 891-902.
897 Turner, T.E., Swindles, G.T., Charman, D.J., Langdon, P.G., Morris, P.J., Booth, R.K., Parry,
900 Väliranta, M., Korhola, A., Seppä, H., Tuittila, E.-S., Sarmaja-Korjonen, K., Laine, J. and
901 Alm, J., 2007. High-resolution reconstruction of wetness dynamics in a southern
902 boreal raised bog, Finland, during the late Holocene: a quantitative approach.
903 Holocene 17, 1093-1107.
905 Ireland) during the last 850 years and a test of the temperature indicator value of
906 2H/1H measurements of peat samples in relation to historical sources and
908 van der Linden, M. and van Geel, B., 2006. Late Holocene climate change and human impact
909 recorded in a south Swedish ombrotrophic peat bog. Palaeogeogr. Palaeoclimatol.
910 Palaeoecol. 240, 649-667.
912 of Central and Eastern Europe. Part 1: Pteridophytes and monocotyledons. Instytut
913 Botaniki im. W. Szafera, Polska Akademia Nauk, Kraków.
Figure captions

Figure 1. Setting of the study site. (source: http://pl.wikipedia.org/w/index.php?title=Plik:Europe_topography_map.png&filetimestamp=20080612084157, Author: San Jose; modified) together with the location of the sites (black dots) cited in the text.

Figure 2. Age–depth model of the peat profile in Mechacz Wielki: A - core I, B - core II.

Figure 3. Plant macrofossils. Taxa with (%) are estimated volume percentages, others are counts (note differences in X-axis scale labels) or presence/absence (no labels on X-axis).

Figure 4. Plant macrofossils. Taxa with (%) are estimated volume percentages, others are counts (note differences in X-axis scale labels) or presence/absence (no labels on X-axis).

Figure 5. Testate amoebae % diagram.

Figure 6. A - functional diversity and traits of testate amoebae, B - correlation matrix with histograms and scatter plots.

Figure 7. Biplots showing the relationships between the response of vegetation and testate amoeba functionality to extrinsic (DWT) and intrinsic (pH) changes in the Mechacz Wielki mire over time. The response of vegetation and testate amoeba functionality to DWT and pH
was tested using a redundancy analysis. Testate amoeba functionality is characterized by the CWMs of each trait.

Figure 8. Pollen, spores and palynomorphs. Percentages are shown in black, 5 times exaggeration in grey.

Figure 9. Wavelength analysis. Squared wavelet coherence between *Sphagnum fuscum/rubellum* and *Sphagnum cuspidatum* in (A) core WMI and (B) core WMII. The phase between the two time series in each core is shown by arrows (with in-phase relationship represented by arrows pointing to the right, anti-phase pointing to the left and *S. fuscum* leading *S. cuspidatum* by 90 degrees pointing down). The statistical significance of wavelet coherence was estimated using Monte Carlo methods and the thick black contour line in each panel indicates the 5% significance level against red noise. The lighter shade represents the cone of influence below which analysis could be distorted due to edge effects.

Figure 10. Comparison of chosen taxa from three data sets: plant macrofossils and pollen with reconstruction of depth-to-water table (WTD).

Figure 11. Water table changes in bogs of S and SE Baltic: Bagno Kusowo (Lamentowicz et al., 2015), Stążki (Gałka et al., 2013b), Linje (Marcisz et al., 2015), Gązwa (Gałka et al., 2015), Männikjärve, Estonia (Sillasoo et al., 2007), and Kontolanrahka, Finland (Väkiranta et al., 2007).

**Table captions**

Table 1. Radiocarbon dates from Mechacz Wielki bog, core I and core II.

Table 2. Peat accumulation rates for selected raised bogs around Baltic Sea.
Tab.1. Radiocarbon dates from Mechacz Wielki bog, core I and core II.

<table>
<thead>
<tr>
<th>Depth (cm)</th>
<th>Material</th>
<th>Nr. Lab.</th>
<th>14C date (AMS)</th>
<th>Age BC/AD (95.4%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>WMII 79</td>
<td><em>Sphagnum stems</em></td>
<td>Poz-52923</td>
<td>205 ± 30 BP</td>
<td>AD 1646-1955</td>
</tr>
<tr>
<td>WMII 160</td>
<td><em>Sphagnum stems</em></td>
<td>Poz-52924</td>
<td>870 ± 30 BP</td>
<td>AD 1045-1252</td>
</tr>
<tr>
<td>WMII 270</td>
<td><em>Sphagnum stems</em></td>
<td>Poz-52925</td>
<td>1330 ± 30 BP</td>
<td>AD 647-770</td>
</tr>
<tr>
<td>WMII 385</td>
<td><em>Sphagnum stems</em></td>
<td>Poz-52365</td>
<td>1560 ± 30 BP</td>
<td>AD 424-565</td>
</tr>
<tr>
<td>WMII 475</td>
<td>5 fruits of <em>Carex rostrata</em>, 1 fruit of <em>Carex pseudocyperus</em>, 2 fruits of <em>Betula pubescens</em>, 1 fruits of <em>Sparganium</em></td>
<td>Poz-44491</td>
<td>2005 ± 30 BP</td>
<td>BC 90-AD 70</td>
</tr>
<tr>
<td>WMII 571</td>
<td><em>Picea abies</em> seed and periderm</td>
<td>Poz-52364</td>
<td>3125 ± 30 BP</td>
<td>BC 1493-1311</td>
</tr>
</tbody>
</table>
Table 2. Peat accumulation rates for selected raised bogs around Baltic Sea.

<table>
<thead>
<tr>
<th>Site</th>
<th>Length of peat core (mm)</th>
<th>Period (years)</th>
<th>PAR mm/yr</th>
<th>References</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mechacz Wielki (NE Poland)</td>
<td>5150</td>
<td>1880/2060</td>
<td>2.75/2.3</td>
<td>This study</td>
</tr>
<tr>
<td>Bagno Kusowo (N Poland)</td>
<td>7940</td>
<td>4000</td>
<td>1.99</td>
<td>Lamentowicz et al. 2015</td>
</tr>
<tr>
<td>Gąźwa (NE Poland)</td>
<td>8350</td>
<td>5700</td>
<td>1.52</td>
<td>Galka et al. 2015</td>
</tr>
<tr>
<td>Stążki (N Poland)</td>
<td>7420</td>
<td>7500</td>
<td>1.01</td>
<td>Galka et al. 2013</td>
</tr>
<tr>
<td>Kontolanrahka (S Finland)</td>
<td>5000</td>
<td>4950</td>
<td>1.01</td>
<td>Valiranta et al. 2009</td>
</tr>
<tr>
<td>Männikjärve (E Estonia)</td>
<td>4500</td>
<td>4500</td>
<td>1.0</td>
<td>Sillasoo et al. 2007</td>
</tr>
<tr>
<td>Dosenmoor (N Germany)</td>
<td>4700</td>
<td>4250</td>
<td>1.1</td>
<td>Barber et al. 2004</td>
</tr>
<tr>
<td>Svanemose (S Danemark)</td>
<td>3000</td>
<td>3600</td>
<td>0.83</td>
<td>Barber et al. 2004</td>
</tr>
<tr>
<td>Kortlandamossen (S Sweden)</td>
<td>6400</td>
<td>9800</td>
<td>0.65</td>
<td>Borgmark 2005</td>
</tr>
</tbody>
</table>
Figure 1. Setting of the study site.
Figure 2. Age-depth model of the peat profiles in Mechacz Wielki: A - core MWI, B - core MWII
Figure 3. Plant macrofossils, core I

Mechacz Wielki, core MWI
Plant macrofossil analysis: M. Gałka

Figure 3. Plant macrofossils. Taxa with (%) are estimated volume percentages, others are counts (with X-axis scale labels; note scale differences) or presence/absence (no X-axis scale labels).
Figure 4. Plant macrofossils, core II. Taxa with (%) are estimated volume percentages, others are counts (with X-axis scale labels; note scale differences) or presence/absence (no X-axis scale labels).
Figure 5. A - Percentage testate amoebae diagram.
Figure 6. A - functional diversity and traits of testate amoebae - Mechacz Wielki, B - correlation matrix with histograms and scatter plots.
Shifts in vegetation composition due to autogenic changes (pH) (RDA axis 1)

$R^2 = 0.41$

$P < 0.001$

Shifts in vegetation composition due to allogenic changes (DWT) (RDA axis 1)

$R^2 = 0.14$

$P < 0.001$

Shifts in testate amoeba functionality due to allogenic changes (DWT) (RDA axis 1)

Shifts in testate amoeba functionality due to autogenic changes (pH) (RDA axis 1)

Figure 7. TA analysis statistics
Figure 8. Pollen, spores and palynomorphs. Percentages are shown in black, 5 times exaggeration in grey.
Figure 9. Wavelet analysis
Figure 10. Comparison
Fig. 11. Water table changes in bogs of S and E Baltic.
Highlights

- Long-term perspective of peatland palaeohydrology in C Europe

- Baltic raised bog development depended on climate and autogenic drivers

- Preserve the remains of pristine biodiversity despite drainage

- Rapid peat accumulation (2.7 mm/yr) in Mechacz Wielki bog

- Functional traits of testate amoebae reveal unusual ecosystem stability in the last 2k