

Palaeoecological evidence for anthropogenic acidification of a kettle-hole peatland in northern Poland

Mariusz Lamentowicz,^{1*} Kazimierz Tobolski¹ and Edward A.D. Mitchell^{2,3}

(¹Department of Biogeography and Palaeoecology, Adam Mickiewicz University, Dziegielowa 27, 61-680 Poznań, Poland; ²WSL, Swiss Federal Institute for Forest, Snow and Landscape Research, Ecosystem Boundaries Research Unit, Wetlands Research Group, Station 2, CH-1015 Lausanne, Switzerland; ³École Polytechnique Fédérale de Lausanne (EPFL), Laboratory of Ecological Systems (ECOS), Station 2, CH-1015 Lausanne, Switzerland)

Abstract: The Holocene developmental history of a small kettle-hole peatland in northern Poland was studied using radiocarbon dating and analyses of pollen, plant macrofossils and testate amoebae with the aim of sorting out the influences of climate change, autogenic succession and human impact. The mire followed the classical succession from lake to a *Sphagnum*-dominated peatland, but peat accumulation only started about 3000 cal. BP. A rapid shift to wetter conditions, lower pH and higher peat accumulation rate took place about 110–150 years before present, when the vegetation shifted to a *Sphagnum*-dominated poor fen with some bog plants. While the first shift to a peat-accumulating system was most likely driven by climate, the second one was probably caused by forest clearance around the mire. This shift towards a *Sphagnum*-dominated vegetation mirrors both in pattern and timing the changes observed in similar situations in North America and New Zealand. While human activities have overall caused the loss of vast expanses of peatlands worldwide in recent centuries, locally they may have also allowed the development of communities that are now ironically considered to have a high conservation value. However, in the case of the site studied the likely anthropogenic shift to bog vegetation was at the expense of a species-rich poor fen, which today has even higher conservation value than ombrotrophic bogs. Thus this study also illustrates the value of palaeoecology for peatland management and biodiversity conservation.

Key words: Holocene, Poland, peat record, human impact, hydrology, peat accumulation, vegetation succession, testate amoebae, forest management, *Sphagnum*, ecosystem resilience, threshold.

Introduction

Human activities increasingly influence the structure and functioning of ecosystems. This is even the case in natural ecosystems, which are affected by changes in local and global climate and pollution. Ecosystems differ in their sensitivity or resilience to these influences (Scheffer *et al.*, 2001). In most cases one can predict that ecosystems will first resist until a certain threshold is reached (Suding *et al.*, 2004). What happens next depends on the type of perturbation. Changes may be reversible (eg, in the case of overharvesting but without species extinction) or not (eg, in the case of severe erosion following forest clearance or the extinction of a

keystone species) (Boswell *et al.*, 1998). In most cases, however, it is impossible to track back in time how ecosystems have changed in response to human activities because of the lack of reliable records. Peatlands are one exception to this rule, because they preserve records of past communities in the peat itself. These records can be analysed by palaeoecological techniques, which can provide invaluable data to test ecological theories over time spans that are far beyond the range of even long-term experimental studies (Birks and Birks, 1980). The historical and palaeoecological perspective, however, is only rarely taken into account in the management of peatlands that aim to preserve biodiversity (Chambers *et al.*, 1999; Lavoie *et al.*, 2003).

The growth of peatlands depends to a large extent on surface moisture, which is determined by inputs (rainfall and in some

*Author for correspondence (e-mail: mariuszl@amu.edu.pl)

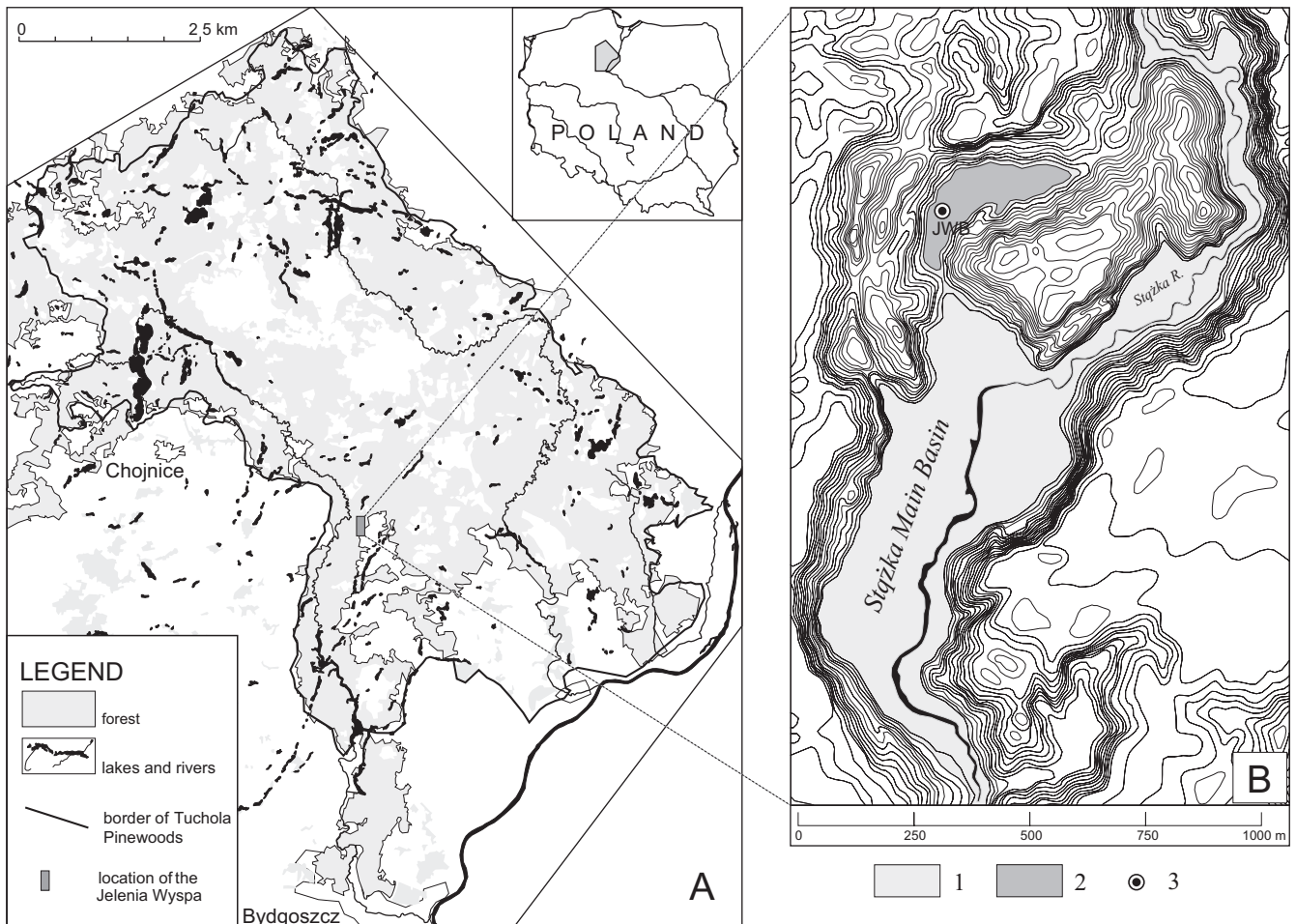


Figure 1 Study site location. (A) Poland and Tuchola Pinewoods; (B) Jelenia Wyspa mire. 1, Stążki Main Basin; 2, Jelenia Wyspa mire; 3, Sampling site

cases groundwater) and losses (evaporation and runoff). Not surprisingly these ecosystems are therefore very sensitive to shifts in climate between moister or drier conditions. In addition to climatic change, human activities can influence peatland development, be it direct in the case of peat extraction or restoration measures, or indirect in the case of drainage or land-use change in the surroundings (Blackford, 1993; Campbell *et al.*, 2003).

The aim of our study was to reconstruct the late-Holocene development of a *Sphagnum* mire in northern Poland, with special attention to (1) the local vegetation and land-use history (from local pollen, spores and macrofossils), (2) changes in micro-environmental conditions (water-table depth and pH inferred from testate amoebae) and (3) the rate of peat accumulation. Our broader and longer-term aims are to assess the relative influence of autogenic (ie, succession) and allogenic (change in land use and climate) factors in the development of the mire. We hypothesize that (1) changes in the mire vegetation and abiotic parameters could be

related to climatic change, autogenic succession and local or regional human impact; and (2) that these changes increased in frequency and magnitude through time in parallel with the increase in human impact in the catchment area. Accordingly, the likelihood of significant change in ecosystem structure (community structure) and function (peat accumulation rates) resulting from human activities was hypothesized to be highest in historical times.

Material and methods

Study site

Jelenia Wyspa mire is located in northern Poland (Figure 1) in the region of Tuchola Forest on the outwash plain of the Brda River, which formed during the Pomeranian phase of the Vistulian glaciation (Kondracki, 1998). Jelenia Wyspa Bog is located within the administration limits of the Tuchola Forest management area

Table 1 Radiocarbon (AMS) dates from Jelenia Wyspa mire

No.	Sample name	Depth (cm)	Age ^{14}C	Analysed material	Range of calibrated date BP 1s (1SD), 68% of probability 2s (2SD), 95% of probability	Middle point of 2 σ date
1	Poz-3131	35	70 \pm 25	Peat moss	1 σ 80–30 BP 2 σ 140–30 BP	85 BP
2	Poz-3132	68	205 \pm 30	Peat moss	1 σ 190–140 BP 2 σ 220–140 BP	180 BP
3	Poz-3133	127	1745 \pm 30	Brown moss	1 σ 1680–1610 BP 2 σ 1730–1550 BP	1640 BP
4	Poz-3134	190	2925 \pm 30	Wood	1 σ 3080–2990 BP 2 σ 3170–2960 BP	3065 BP

and the southern part of the Tuchola Landscape Park. The bog is part of the 'Bagna nad Stążką' Reserve (Stążką River Mires Reserve) (478.45 ha), where this complex of natural peatlands is under protection. Jelenia Wyspa bog is part of a mire complex that developed in a fluvio-glacial channel of the Stążka River. The 'Bagna nad Stążką' reserve is mostly composed of fens. There are also spring mires at the margins of the channel, as well as kettle-hole bogs scattered in the vicinity of the river. This whole ecosystem appears natural, with no visible human impact.

The vegetation of the peripheral part of the bog (lagg) is dominated by *Eriophorum vaginatum*, *Sphagnum fallax*, *S. cuspidatum* and *Juncus effusus*. The centre of the mire is open, and the vegetation is composed mainly of typical bog plants, such as *Eriophorum vaginatum*, *S. fallax*, *S. magellanicum* and *Vaccinium oxycoccus*. Hummocks are formed by *S. fuscum* and *Pleurozium schreberi* is locally present. Hollows and pools are colonized by *S. cuspidatum*, *Scheuchzeria palustris*, *Carex limosa*, *Rhynchospora alba*, *Drosera rotundifolia* and *S. fallax*. Around the central part is a zone with dwarf *Pinus sylvestris* and shrubs such as *Ledum palustre*, *Empetrum nigrum*, *Andromeda polifolia* and *Calluna vulgaris*. Wild boar (*Sus scrofa*) locally disturb the surface of the mire in search for roots, and these disturbed places represent good habitat for *Rhynchospora alba* and *Drosera* spp. The southwestern margin of the mire is covered by *Alnus glutinosa*, *Calla palustris*, *Juncus effusus* and *S. recurvum*.

The total average annual rainfall in the Tuchola Forest area is 600 mm (Sadowski, 1994; Wójcik and Marciniak, 1993). July is the wettest month (approximately 200 mm over the period 1981–1998), and August and September are the driest. The average annual temperature is 7°C. Averages for January and July are respectively –3°C and +17°C (KozBowska-Szczęśna, 1993). Poland is under the influence of both oceanic and continental climates, and this mixed influence results in a high variability of weather types (Woś, 1999).

Coring, dating and laboratory analyses

Core JWB was taken for palaeoecological analyses with a Russian corer (50 cm long and 5 cm in diameter). The upper 50 cm was sampled from a peat monolith. The sediments were described in the field following the Troels-Smith method (Troels-Smith, 1955). The entire peat sequence, as well as the top of the limnic sediments

(transition from lake to mire), was used for analyses of plant macrofossils and testate amoebae (upper 3 m) to reconstruct the full terrestrialization process and also for palynological dating.

Plant macrofossils were dated with the AMS radiocarbon method in Poznań Radiocarbon Laboratory (Table 1). Where possible, *Sphagnum* remains were used for AMS dating, as these have been shown to yield very precise dates (Nilsson *et al.*, 2001). The dates were calibrated with the OxCal 3.0 program (Bronk Ramsey, 2001). The calibration results are presented in two spans of standard deviation: 1 SD 68% of probability (1σ) and 2 SD 95% of probability (2σ). The middle date of the 2σ range was chosen to construct the calendar timescale. Average accumulation rates were calculated for the core based on the middle values of the calibrated dates.

Testate amoebae samples were prepared from 1 cm³ peat samples according to the sieving and back-sieving procedure described by Hendon and Charman (1997) at 2 cm intervals in the upper 50 cm and every 5 cm below this level. Testate amoebae were identified and counted to a total of 200 individuals at a magnification of 200–400×. One rotifer species *Habrotricha angusticollis* commonly found in *Sphagnum* peat was included in the counts.

From the JWB core, 1 cm³ volume was sampled at 5 cm intervals for pollen analysis. Samples were prepared according to standard methods (Berglund and Ralska-Jasiewiczowa, 1986). Before acetolysis, the peat was boiled for 40 min in 10% KOH. The residual was then sieved on a 200 µm mesh filter. Pollen of trees (AP) and shrubs were identified and counted to a total of 500 at a magnification of 400×. Algal remains, eg, *Pediastrum*, were included in the counts, but aquatic and telmatic plant spores were excluded from the calculation sum.

For plant macrofossils, the core was cut into 2 cm slices at 10 cm intervals. The material was rinsed on 0.25 and 0.5 mm mesh sieves. The residues were identified under the stereoscopic microscope at a magnification of 10–100×. In addition, two slides from each sample were examined under the light microscope at 200–400× magnification to determine the peat composition.

Numerical analyses and graphics

Percentage diagrams of plant macrofossils, pollen and testate amoebae were constructed with the software packages Tilia 2 and

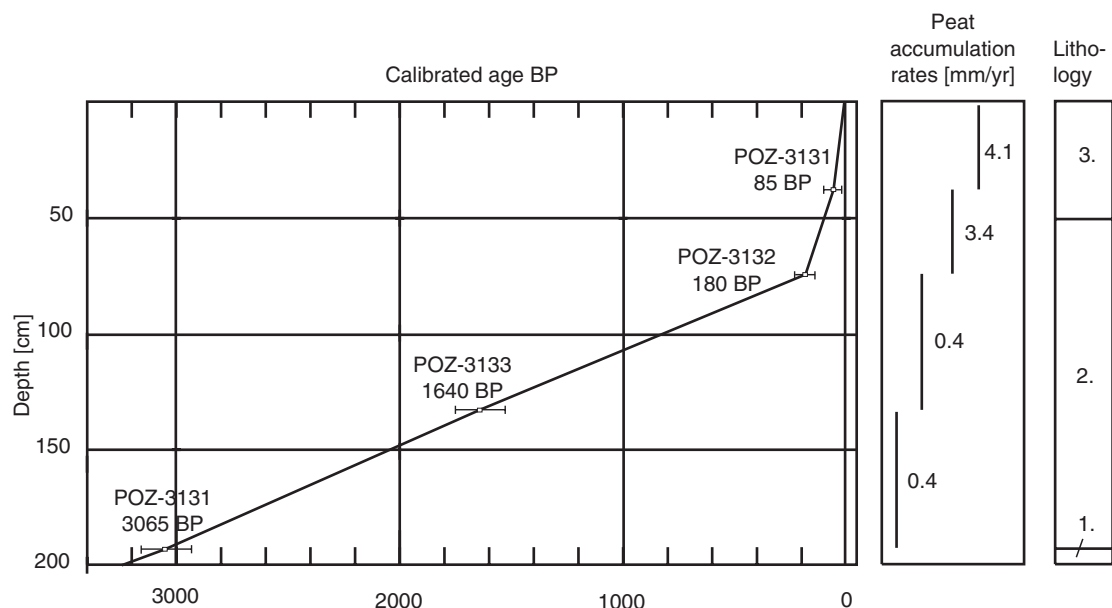


Figure 2 Age–depth model of Tuchola mire. Lithology: 1, brown moss peat; 2, mixed sedge-*Sphagnum* peat; 3, *Sphagnum* peat. The scale corresponds to calibrated dates

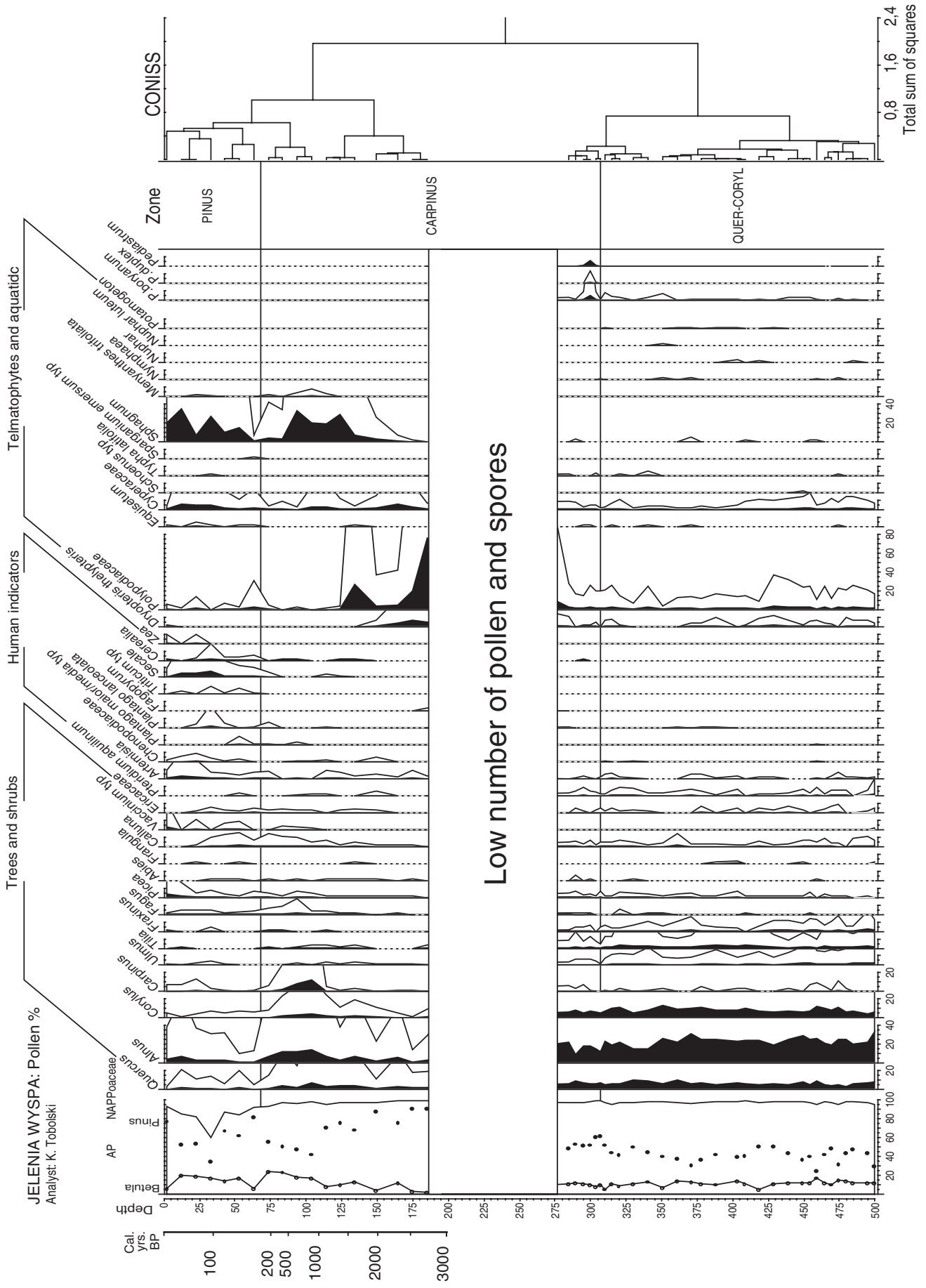


Figure 3 Percentage pollen diagram from Jelenia Wyspa mire

Tilia Graph (Grimm, 1992). The zonation was produced with CONISS (Grimm, 1992). The estimated percentage composition of particular macrofossils (eg, *Sphagnum* and brown moss species) is presented with a five-degree scale. Countable remains (eg, *Andromeda polifolia* seeds) are presented as absolute sums. Testate amoeba and pollen diagrams are based on percentage data. For each diagram we define biostratigraphic zones that represent a compromise between subjective and numerical approaches: LMAZ, Local Macrofossils Assemblage Zone; LPAZ, Local Pollen Assemblage Zones; TAZ, Testate amoeba Assemblage Zones.

We inferred past depth to water-table (DWT) and pH from the testate amoeba data with a transfer function based on Polish surface samples from the same region, which we are continuously expanding with the aim also of including samples from a broader range of environmental conditions (123 reliable surface samples were used here) (Lamentowicz and Mitchell, 2005; M. Lamentowicz, unpublished data, 2006). We tested the performance of four models by partial least squares (PLS), weighted averaging (WA), tolerance down-weighted averaging (WAtol) and weighted averaging partial least squares (WA-PLS) (Birks, 1995), using the software C2 (Juggins, 2003). The RMSEP (Root Mean Square Error of Prediction) was calculated with the Jackknife crossvalidation procedure (Crowley, 1992). For DWT the model with the lowest RMSEP was WA-tol, with a maximum prediction bias of 8.9 cm and a root mean square error of prediction (RMSEP_{jack}) of 4.3 cm. For pH, the best model as log-transformed WA-PLS, with a maximum prediction bias of 0.5 pH units and a RMSEP_{jack} of 0.41 pH units.

Results and interpretation

Lithology, radiocarbon dating and graphics

The lithological sequence follows a very classical terrestrialization sequence observed in many Northern Hemisphere bogs: (1) detritus gyttja from 300 to 275 cm depth, (2) moderately decomposed herbaceous peat from 275 to 250 cm, (3) weakly decomposed brown moss peat from 250 to 200 cm, (4) sedge peat from 200 to 50 cm, and finally almost pure *Sphagnum* peat for the top 50 cm. Four radiocarbon dates were obtained from the peat core (Table 1). The lowest dated level yielded an age of c. 3065 cal. yr BP. By linear interpolation the base of the peat record is estimated at approximately 3200 cal. yr BP. During the first c. 3000 years the peat-accumulation rate was relatively low at 0.4 mm/yr on average (Figure 2). By contrast, in the last c. 150 years (68 cm) peat (mostly *Sphagnum*) accumulated at the much higher average rate of 3 mm/yr. Although accumulation rates are likely to have varied within each of these two phases, and the upper peat is less compacted than the lower one, the average values are clearly different (almost 10×) and are also in agreement with the botanical composition of the peat.

The diagrams for pollen and spores, plant macrofossils and testate amoebae are presented in Figures 3, 4 and 5 and summarized in the three tables 2, 3 and 4. We separated pollen and spores into four categories: trees and shrubs, human indicators, telmatophytes (plants growing at the interface between aquatic and terrestrial habitats) and aquatics. Zones for pollen and spores are based on the dominant tree taxa and the relative importance of non-arboreal

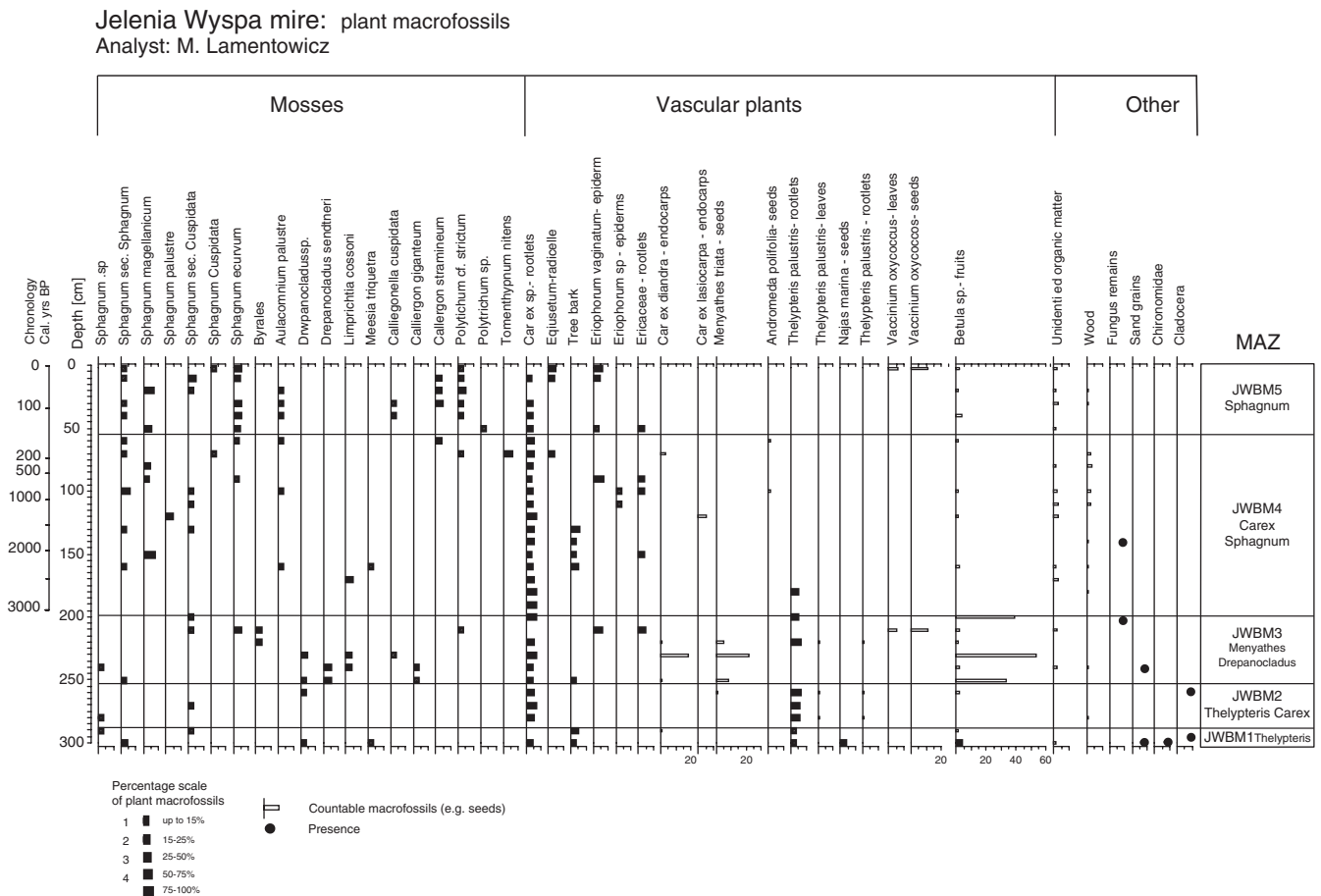


Figure 4 Plant macrofossils diagram from Jelenia Wyspa mire

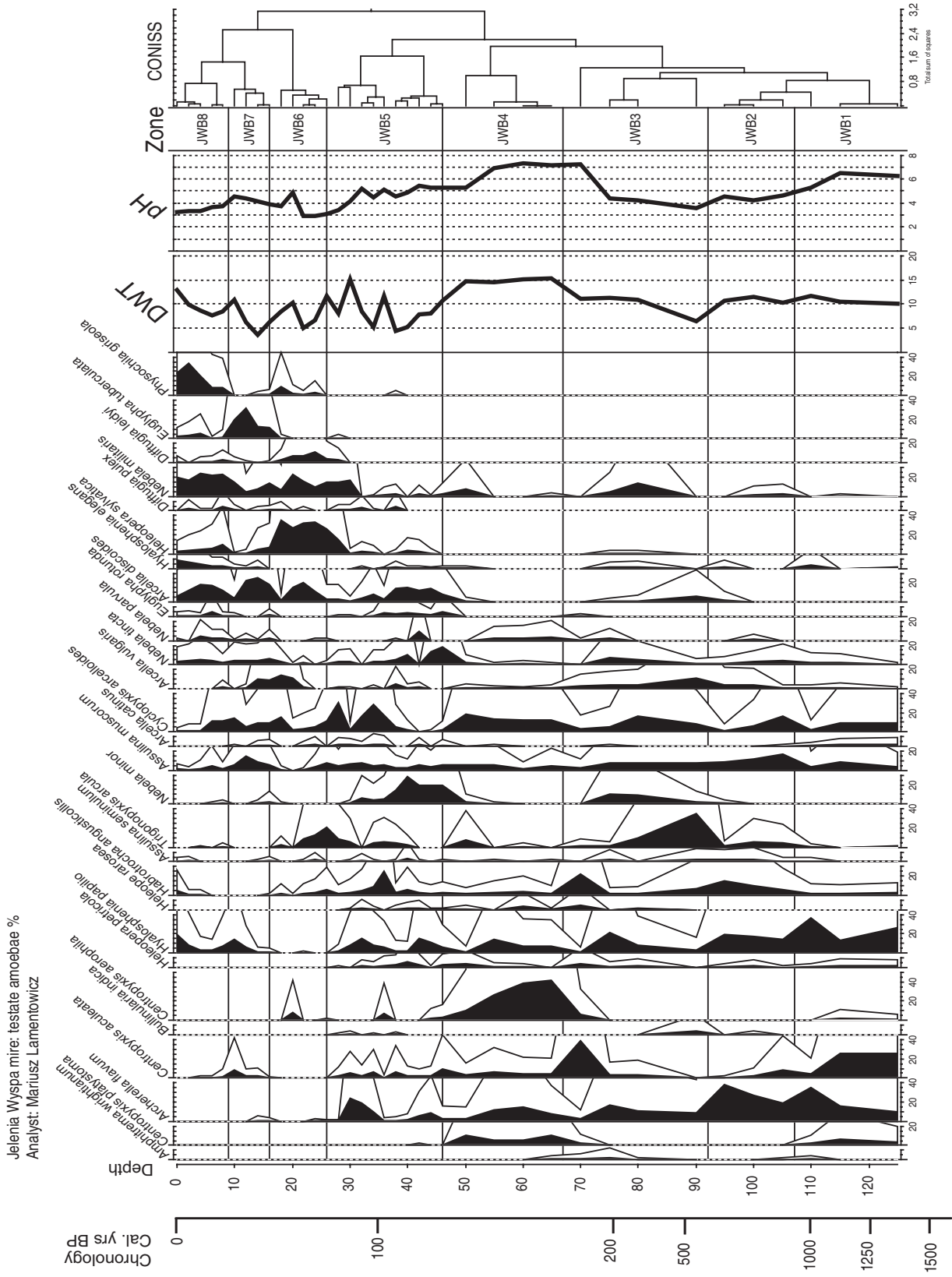


Figure 5 Testate amoebae percentage diagram from Jelenia Wyspa mire. The upper 50 cm was sampled at 2 cm intervals. Depth to water-table (DWT) and pH are inferred from testate amoebae (see text for details)

Table 2 Description of Local Pollen Assemblage Zones (LPAZ) from Jelenia Wyspa mire

Zone	Depth	Description
<i>Pinus</i> – NAP	(75–0 cm)	This zone is dominated by NAP. <i>Pinus</i> curve decreases as well as other tree species. <i>Alnus</i> and <i>Calluna</i> reach high abundance. The anthropogenic indicators are represented in majority by <i>Secale</i> (5%) and <i>Artemisia</i> (3%). <i>Zea</i> appears as a new taxon
<i>Carpinus</i>	(310–75 cm)	The lower boundary of this zone is difficult to determine because of low recoverable numbers of spores between 195 and 275 cm. From 195 cm <i>Pinus</i> decreases (to 40%) and <i>Betula</i> increases. <i>Corylus</i> reaches 5% and <i>Tilia</i> , <i>Quercus</i> and <i>Ulmus</i> have lower percentage. At 110 cm <i>Carpinus</i> achieves its maximum (13%) along with the culmination of <i>Fagus</i> and <i>Alnus</i> (to 15%). <i>Calluna</i> dominates the non-arboreal pollen spectrum. The number and percentage of anthropogenic indicators increases: <i>Chenopodiaceae</i> , <i>Artemisia</i> , <i>Urtica</i> , <i>Plantago lanceolata</i> , <i>Fagopyrum</i> , <i>Secale</i> and <i>Cerealialia</i> . From 195 to 130 cm spores of <i>Polypodiaceae</i> dominate the spectrum. <i>Cyperaceae</i> reach a high percentage and <i>Sphagnum</i> is increasing together with abrupt decrease of <i>Polypodiaceae</i>
<i>Quercus</i> – <i>Corylus</i>	(460–310 cm)	This zone is characterized by <i>Quercus</i> (approx. 10%) and <i>Corylus</i> (over 10%). <i>Alnus</i> increases. <i>Carpinus</i> is present in low numbers. <i>Corylus</i> reaches its maximum at 355 cm along with an abrupt decrease of <i>Alnus</i> . <i>Calluna</i> and <i>Pteridium aquilinum</i> dominate the non-arboreal pollen spectrum. The number of anthropogenic indicators increases: <i>Artemisia</i> , <i>Plantago lanceolata</i> , <i>Urtica</i> and <i>Chenopodiaceae</i> . <i>Pediastrum</i> occurs between 500 and 275 cm. Among aquatic plants, pollen of <i>Nuphar</i> , <i>Nymphaea</i> and <i>Potamogeton</i> are recorded, together the telmatophytes <i>Polypodiaceae</i> and <i>Dryopteris thelypteris</i> . Between 275 and 195 cm no significant number of spores was found.

Table 3 Description of Macrofossils Assemblage Zones (MAZ) from Jelenia Wyspa mire

Zone	Depth	Description
JWBM5 – <i>Sphagnum</i>	(0–54 cm)	This part of the core is characterized by the dominance of peat mosses, <i>Sphagnum recurvum</i> and <i>S. magellanicum</i> . From 30 cm depth <i>Cyperaceae</i> rootlets disappear. <i>Calliergon stramineum</i> and <i>Polytrichum strictum</i> are present. Roots of <i>Equisetum</i> and in the top of the zone epidermis of <i>Eriophorum vaginatum</i> as well as leaves and seeds of <i>Vaccinium oxycoccos</i> are present. Trees are represented by fruits of <i>Betula</i> sp. along with needles and bud scales of <i>Pinus sylvestris</i>
JWBM4 – <i>Carex</i> – <i>Sphagnum</i>	(54–194 cm)	The variability of macrofossils in this zone is considerable. <i>Limprichtia cossoni</i> was recorded at 170 cm depth. Above this level vegetative parts of <i>Cyperaceae</i> begin to dominate with a several peat mosses. At 150 cm <i>Sphagnum magellanicum</i> and rootlets of <i>Ericaceae</i> are present. Over this depth <i>Cyperaceae</i> and <i>Sphagnum palustre</i> dominate and endocarps of <i>Carex diandra</i> are recorded in one sample. Above, peat mosses from sections <i>Cuspidata</i> and <i>Sphagnum</i> are present as well as <i>Sphagnum magellanicum</i> , <i>S. recurvum</i> and <i>S. cuspidatum</i> . <i>Cyperaceae</i> rootlets still dominate together with the vegetative parts of <i>Ericaceae</i> and epidermis of <i>Eriophorum vaginatum</i> (at 80 cm reaching nearly 100% of the sediment volume). At 70 cm <i>Tomenthypnum nitens</i> dominates and occurs together with endocarps of <i>Carex diandra</i> . In the top of this zone leaves of <i>Calliergon stramineum</i> and <i>Sphagnum recurvum</i> were recorded, together with seeds of <i>Andromeda polifolia</i>
JWBM3 – <i>Menyanthes</i> – <i>Drepanocladus</i>	(197–252 cm)	Among mosses dominate: <i>Drepanocladus sendtneri</i> , <i>Limprichtia cossoni</i> as well as <i>Calliergonella cuspidata</i> and <i>Calliergon stramineum</i> . From depth 230 cm appear <i>Polytrichum strictum</i> and <i>Sphagnum recurvum</i> and peat moss <i>Cuspidata</i> section. Epiderms of <i>Eriophorum vaginatum</i> along with <i>Ericaceae</i> radicelli and seeds of <i>Vaccinium oxycoccos</i> are recorded. Vascular plants are represented by: endocarps of <i>Carex diandra</i> and seeds of <i>Menyanthes trifoliata</i> as well as considerable number of fruits of <i>Betula</i> are present. Pine is represented by needles and bud scales
JWBM2 – <i>Thelypteris</i> – <i>Carex</i>	(252–287 cm)	Roots and leaves of <i>Thelypteris palustris</i> comprise of 50% of the sediment volume, <i>Cyperaceae radicelli</i> are present. Mosses are represented by <i>Drepanocladus</i> sp. and peat moss <i>Cuspidata</i> section. Fruits of <i>Betula</i> sp. are recorded
JWBM1 – <i>Thelypteris</i>	(287–300 cm)	The characteristic taxa for this zone are <i>Dyopteris thelypteris</i> and <i>Chironomidae</i> . Seeds of <i>Najas marina</i> and <i>Andromeda polifolia</i> were recorded. Rootlets of <i>Cyperaceae</i> are present. Mosses are represented in small amount by <i>Meesia triquetra</i> , <i>Drepanocladus</i> sp., peat mosses from <i>Sphagnum</i> and <i>Cuspidata</i> sections

Table 4 Description of Testate amoebae Assemblage Zones (TAZ) from Jelenia Wyspa mire

Zone	Depth	Description
JWB8	(0–9 cm)	The last, top zone is characterized by dominance of three taxa: <i>Arcella discoides</i> , <i>Physochila griseola</i> type and <i>Nebela militaris</i> . <i>Diffugia leidy</i> and <i>D. pulex</i> present in low percentage. <i>Hyalosphenia elegans</i> reaches its maximum increasing in abundance along with <i>Hyalosphenia papilo</i>
JWB7	(9–16 cm)	<i>Arcella discoides</i> and <i>Euglypha tuberculata</i> type dominate in this zone. Simultaneously, <i>Assulina muscorum</i> culminates here and <i>Hyalosphenia papilo</i> , <i>Nebela militaris</i> and <i>Centropyxis aculeata</i> increase. <i>Arcella vulgaris</i> decreases. Low percentage of <i>Physochila griseola</i> type increasing in the top of this zone
JWB6	(16–26 cm)	The zone begins with the maximum of <i>Trigonopyxis arcula</i> . <i>Heleopera sylvatica</i> dominates (40%). Gradual disappearance of <i>Archerella flavum</i> . <i>Nebela militaris</i> increases (over 20%). <i>Diffugia leidy</i> , <i>Arcella discoides</i> and <i>Assulina muscorum</i> reach their maximum
JWB5	(26–46 cm)	This zone is characterized by two peaks of <i>Archerella flavum</i> and <i>Hyalosphenia papilo</i> . <i>Arcella discoides</i> and <i>Cyclopyxis arcelloides</i> increase. Maximum of <i>Nebela minor</i> as well as <i>Euglypha rotunda</i> type. <i>Physochila griseola</i> is recorded for the first time. The rotifer <i>Habrotricha angusticollis</i> reaches maximum (over 20%). Spermatophores of <i>Copepoda</i> disappear
JWB4	(46–67 cm)	<i>Centropyxis aerophila</i> type peaks at over 40% at 65 cm. Increase of <i>Archerella flavum</i> , <i>Cyclopyxis arcelloides</i> , <i>Hyalosphenia papilo</i> and <i>Copepoda</i> . <i>Nebela militaris</i> , <i>Nebela minor</i> and <i>Arcella discoides</i> appear
JWB3	(67–92.5 cm)	This zone begins with the maximum for <i>Trigonopyxis arcula</i> (35%). Simultaneously <i>Archerella flavum</i> and <i>Hyalosphenia papilo</i> decrease. <i>Arcella discoides</i> , <i>Arcella vulgaris</i> , <i>Nebela tinctoria</i> , <i>Nebela minor</i> , <i>N. militaris</i> and <i>Cyclopyxis arcelloides</i> increase. Abrupt increase of <i>Centropyxis aculeata</i> and <i>Habrotricha angusticollis</i>
JWB2	(107.5–92.5 cm)	<i>Archerella flavum</i> dominates achieving 40%. <i>Hyalosphenia papilo</i> culminates at 110 cm and then gradually decreases. At 105 cm <i>Assulina muscorum</i> , <i>Cyclopyxis arcelloides</i> and <i>Trigonopyxis arcula</i> increase. <i>Nebela militaris</i> and <i>Nebela tinctoria</i> increase slightly. <i>Centropyxis aculeata</i> , <i>Centropyxis aerophila</i> , <i>Arcella catinus</i> and <i>Centropyxis</i> sp. disappear. At 95 cm <i>Habrotricha angusticollis</i> increases, along with the dominance of <i>Archerella flavum</i> and decreasing percentage of <i>Trigonopyxis arcula</i>
JWB1	(107.5–125 cm)	<i>Centropyxis aculeata</i> , <i>Hyalosphenia papilo</i> and <i>Archerella flavum</i> dominate. <i>Assulina muscorum</i> , <i>Centropyxis aerophila</i> , <i>Heleopera sphagni</i> , <i>Heleopera petricola</i> , <i>Nebela tinctoria</i> , the rotifer <i>Habrotricha angusticollis</i> and <i>Copepoda</i> spermatophores recorded in lower percentage (<10%)

pollen (NAP) (Table 2). Macrofossils were divided into four categories: mosses, vascular plants, shrubs and others (Table 3).

Developmental history and hydrological changes

Based on the three proxies, the developmental history of Jelenia Wyspa mire is characterized by a classical succession from limnic to telmatic and then to terrestrial environments, the latter starting as a rich fen and then evolving into a *Sphagnum*-dominated poor fen with elements of bog vegetation.

Jelenia Wyspa was a lake until 300 cm depth (outside the range of our ¹⁴C chronology but probably around 4000 cal. yr BP), as attested by the lithology, the presence of algae (*Pediastrum* and *Botryococcus*) and faunal elements (Cladocera, Bryozoa, Chironomidae). The open water was colonized by macrophytes with floating leaves *Nymphaea*, *Nuphar*, *Potamogeton* spp., *Potamogeton alpinus* and *Najas marina*. Submersed *Chara* sp. grew on the lake bottom. *Dryopteris thelypteris* and Cyperaceae grew on the shore. Testate amoebae were either not abundant in this environment or poorly preserved in the peat.

The limnetic to telmatic transition was recorded between 300 and 250 cm depth (c. 4000 cal. yr BP). A dynamic terrestrialization is reflected in the macrofossil zones M1 and M2, where plants with a high peat-accumulating potential were found. An initial phase was marked by the dominance of *Dryopteris thelypteris* and Cyperaceae, which currently build a eutrophic floating mat in the main Stażka basin, where a water gap still exists below 2 m of peat. Underneath the mat, remains of vascular plants initially accumulated and then also moss remains. For unknown reasons between 275 and 185 cm depth very few pollen grains and spores were recorded, causing a gap in the pollen sequence (Figure 3).

The transition from rich fen to poor fen (zone M3) was completed by c. 3000 cal. yr BP (250–200 cm). This zone is dominated by brown mosses such as *Drepanocladus sendtneri*, *Meesia triquetra* and *Calliergon giganteum*. Other important peat-forming minerotrophic plants include *Menyanthes trifoliata* and Cyperaceae such as *Carex diandra*. Peat mosses were also present but not abundant. One of the pioneer species was *Sphagnum fallax*, which appeared together with *Vaccinium oxycoccos* and *Polytrichum strictum*. The considerable diversity of plant macrofossils probably suggests the presence of a mosaic of dynamic microhabitats.

The terrestrial phase began c. 3000 cal. yr BP. The abundance of *Sphagnum* mosses (reflected both in macrofossils and pollen) increased simultaneously (at least apparently, with the available temporal resolution) with the appearance of anthropogenic indicators as well as the first pine decline. Minerotrophic plant indicators (eg, *Dryopteris thelypteris* and *Limprichtia cossoni*) are present until c. 1500 cal. yr BP, at which time *Sphagnum* started to dominate. For, example, one sample (at a depth of 150 cm – c. 2000 cal. yr. BP) is composed almost entirely of *S. magellanicum*.

Two pine declines can be seen in the pollen diagram during the last 2000 years (Figures 3 and 6). The first one took place c. 1200 cal. yr BP (117 cm), when *Alnus*, *Carpinus* and *Quercus* reached their maximum relative abundance and *Carpinus* dominates the pollen spectrum. This was not associated with a decline in arboreal pollen (AP). The increase of *Alnus*, the presence of *Menyanthes* pollen, the decrease in *Dryopteris thelypteris* and the shift towards a community of *Sphagnum* (including the section *Cuspidata*) and *Eriophorum* indicates a wet phase in the history of the mire. The increase in *Sphagnum* took place c. 300 years before the pine decline and corresponds to the beginning of the period when testate amoebae could be recovered in significant numbers, making it possible to infer water-table depth

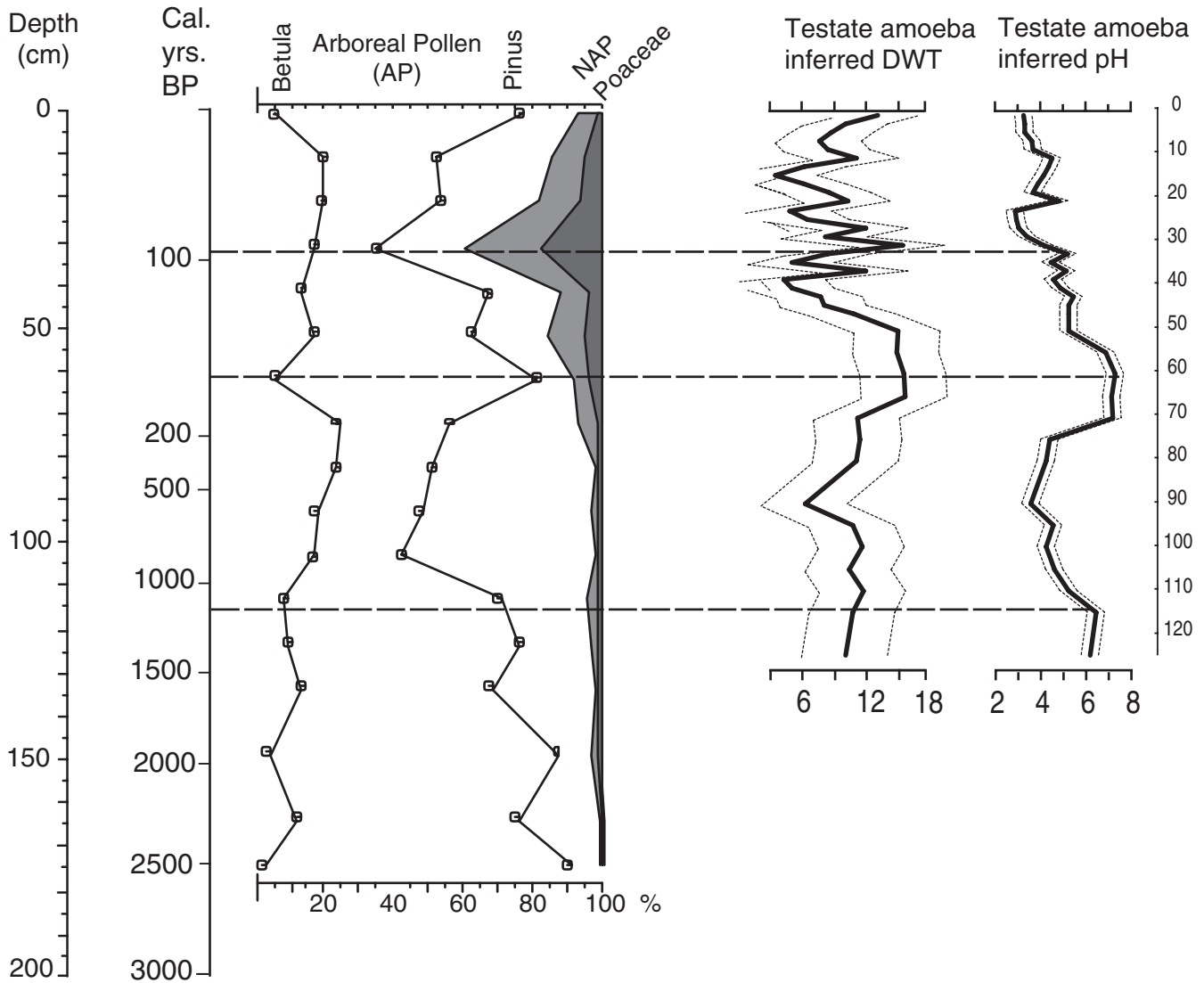


Figure 6 Hydrological and pH changes in Jelenia Wyspa mire inferred from testate amoebae, compared with the relative proportion of arboreal pollen (AP), non-arboreal pollen (NAP), *Pinus* (showing two pronounced decreases) and *Betula*. The thin dashed lines on either side of the lines of inferred values represent the Root Mean Squared Error of Prediction. The horizontal dashed lines indicate levels of low or high percentage of pine pollen

and pH changes quantitatively (Figures 5 and 6). Testate amoebae suggest that surface pH declined simultaneously with the first pine decline at *c.* 1200 cal. yr BP. In contrast, no significant change in water-table depth is associated with this event. *Archerella flavum* (= *Amphitrema flavum*) and *Hyalosphenia papilio*, which dominate the community, indicate relatively high (9–15 cm deep) water levels up to *c.* 700 cal. yr BP (95 cm) and to a lesser extent *c.* 200 cal. yr BP (70 cm) (Figures 3 and 6). Dry indicators such as *Trigonopyxis arcuata*, *Nebela militaris* and *Heleopera sylvatica* were rare except for one sample (*c.* 600 cal. yr BP or 90 cm), where *T. arcuata* was abundant, but the inferred water level was nevertheless high because of the presence of *Arcella* species (Figures 5 and 6). As pine pollen increased again between *c.* 200 and 150 cal. yr BP testate amoebae show a decrease in water-table and an increase in pH to its highest value for the entire record (>7).

The second decline in pine took place between *c.* 150 and 110 cal. yr BP (70 and 40 cm) and corresponds to increases in Poaceae and NAP. In parallel to the pine decline, testate amoebae again indicate a decrease in pH from about neutral to about 3.5 and increased water level (to its highest inferred position for the last 1500 yr) (Figure 6). Interestingly, in the most recent part of the record, as NAP and Poaceae sums declined again, the DWT

decreased again, while pH did not change much. As a result, while pH and DWT were positively correlated during the first part of the sequence ($r = 0.51$, $P < 0.01$), in the most recent part of the record (upper 20 cm) the two variables are negatively correlated ($r = -0.75$, $P < 0.01$).

Discussion

Classification and general peatland stratigraphy

Many small mesotrophic to oligotrophic *Sphagnum* bogs in northern Poland are difficult to characterize with the Polish ecological classification of peatlands. Bogs (raised and continental), transitional peatlands and fens are defined mostly on the basis of their present vegetation, while geological and stratigraphic criteria are usually not considered (Tobolski, 2004). On the basis of our data and following the hydrogenetic approach, Jelenia Wyspa should be classified as a kettle-hole mire (Timmermann and Succow, 2000). According to Hájek *et al.* (2006), in central Europe the bog–fen boundary is best determined not by pH but by a set of nutrient-requiring species that

avoid truly ombrotrophic conditions. Following this approach, because Jelenia Wyspa mire is dominated by *Sphagnum fallax* and other poor-fen indicators (eg, *Carex rostrata*), it should be classified as a poor fen that is not only dependent on precipitation, and this would also agree with the recent developmental history of the site. Small patches of relatively ombrotrophic vegetation types (eg, *Sphagnum fuscum* hummocks) occur in the central part of the mire but do not prove the ombrotrophy of the entire basin.

Developmental history of the mire and possible causes for the observed changes

The two major shifts that occurred in the developmental history of the mire were the onset of peat accumulation at *c.* 3200 cal. yr BP and the shift towards ombrotrophy *c.* 150 yr BP. Both correspond to the expected pattern of autogenic succession of kettle-hole peatlands, but the timing of these shifts may nevertheless have been controlled by allogenic factors, either climatic change or human impact on the hydrology of the catchment, or a combination of both. Alternatively, these external influences could also have prevented the shifts from taking place at an earlier time if they prevented autogenic succession to proceed.

First shift: onset of peat accumulation

Jelenia Wyspa mire followed the classical hydroseral succession of kettle-hole terrestrialization commonly observed in the Stążka river area (Kowalewski *et al.*, 2002; Lamentowicz, 2005a) and more generally in Europe (Timmermann and Succow, 2000) and North America (Damman and French, 1987). However, unlike many comparable peatlands in Poland, this site was a lake during most of its history (Tobolski, 1987). The lake gradually filled with peat until no open water remained approximately 3000 cal. yr BP. In the centre of the mire a water layer exists between gytja and the overlying 2 m of peat (Kowalewski *et al.*, 2002), and the peat is therefore less thick. At the onset of peat accumulation *c.* 3200 cal. yr BP there is no evidence for any increase in non-arboreal pollen or other indicators of significant anthropogenic influence on the landscape. Therefore a climatic shift is the most likely cause for the observed changes in the vegetation and the associated accumulation of peat. This period in time corresponds to dry phases or shifts in peatlands of eastern Poland (Żurek and Pazdur, 1999), lakes of northern Poland (Ralska-Jasiewiczowa, 1989), northern Britain (Charman *et al.*, 2006), Cumbria (Barber *et al.*, 2004) and the Jura Mountains (Magny, 2004). Our interpretation is therefore that low lake levels allowed the development of a rich fen at the coring site. After the shift from Polypodiaceae to *Sphagnum* in the local pollen record, testate amoebae indicate a relatively high water-table between *c.* 1300 and 750 cal. yr BP (125–95 cm). Plant macrofossils too indicate very wet conditions. This wet period agrees with previous palaeoecological studies indicating increasing water-tables (with some fluctuation) in lakes and mires of the region (Lamentowicz, 2005; Ralska-Jasiewiczowa and Latałowa, 1996; Tobolski, 1990).

Water-table depth (or surface moisture) is governed by the balance of temperature and precipitation, but it is often difficult to tell which of these two is responsible for past changes. Because Jelenia Wyspa is located at the interface between continental and oceanic climates, temperature may play a more important role in water-table fluctuation than in more oceanic regions. Indeed, Halas *et al.* (2007) showed that temperature, not precipitation, was responsible for water-table fluctuations in Linje mire, a small *Sphagnum* mire in central Poland 51 km SE of Jelenia Wyspa. Following the onset of peat accumulation, the gradually increasing land-use change could have contributed to water-table changes in Polish wetlands as much as, if not more than, climatic change. Unfortunately, few studies address the relationship between

climate and surface moisture for the late Holocene in Poland, because most palaeoclimatic reconstructions end at approximately 2500 yr BP.

Second shift: rich fen–poor fen

The vegetation at Jelenia Wyspa started to evolve through terrestrialization towards a bog-like community in the last *c.* 150 years, but as mentioned above the shift towards ombrotrophy is still not complete.

Our data may not allow us to pinpoint the exact cause of the observed changes in peat-accumulation rate and in plant and testate amoeba communities, because two allogenic factors could have been at play in addition to the autogenic succession. However, while the community succession and associated acidification could be regarded as a natural autogenic process, the pollen data suggests that human impact was likely responsible for the change. In the surroundings of Jelenia Wyspa mire a major change took place approximately *c.* 150 cal yr BP. The pollen record shows that the former mixed forest was cleared and replaced by a pine monoculture. Then the total arboreal pollen declined to its lowest level of the entire record. Furthermore, forestry-management maps of the region show evidence of deforestation *c.* 100 years ago around Jelenia Wyspa mire, and the oldest trees in the catchment of the mire are *c.* 130 years old. This change in land use could have strongly modified the hydrology of the catchment area, causing the groundwater level to increase as a result of reduced evapotranspiration and infiltration. Runoff water from this catchment might also have become more acidic owing to the difference in litter quality. These changes could in turn have affected the vegetation on the mire, allowing *Sphagnum* to expand, causing further acidification. According to this interpretation a change in the quantity and perhaps quality of water entering the mire was the cause for the shift. However, the timing of this shift also corresponds approximately to the end of the ‘Little Ice Age’, which would in any case have had an impact on the functioning of the ecosystem. Finally industrial development in Central Europe was also taking place at the time, and thus acid rain could also have contributed to the observed shift.

There seems to be a lag of about 30 years (10 cm between 60 and 50 cm) between forest clearance and the dominance of *Sphagnum* in the peat and the shift in the testate amoeba community. This suggests that the ecosystem was relatively resistant to the changing hydrological conditions. A possible cause may be the nutrient availability that allowed a rich fen to maintain itself for about three decades before *Sphagnum* finally took over the entire mire surface.

The reversal of the correlation between inferred water-table depth and pH observed at the transition leading to *Sphagnum* dominance suggests a change in the functioning of the ecosystem and a loss of the linkage between water-table depth and pH that had characterized the site between *c.* 1500 and 100 cal. yr BP. We interpret this change as a sign of the ongoing transition towards ombrotrophy. In ombrotrophic systems drier microhabitats are also more acidic, while in poor fens when the water-table declines vascular plants may take up mineral nutrients, including alkaline cations from deeper soil layers, thus possibly increasing the surface pH. However, the correlation between cations and pH is not straightforward, as examples of mires with high Ca content but low pH have been found (Hájek *et al.*, 2002).

Patterns and timing of succession similar to those observed in Jelenia Wyspa were reported from the eastern part of the region – Zabijak mire (M. Obremska, K. Tobolski, unpublished data, 2005) in New Zealand, where some of the *Sphagnum* mires appeared after European settlement expansion (Wilmschurst *et al.*, 2003), and in Ontario, where *Sphagnum* rapidly colonized the surface of

‘quaking bogs’ following forest clearance and creation of pasture by European immigrants (Warner *et al.*, 1989). It is interesting to note that comparable indirect effects of increasing human exploitation of the landscape on peatland development took place in very distant places in Europe, North America and New Zealand. Ombrotrophication, however, is not always associated with increased moisture. This can only happen in a geomorphic setting where the substrate is acidic and nutrient-poor. Elsewhere increased water levels would prevent rather than stimulate the growth of *Sphagnum*, while a lower water-table would cause nutrient leaching, leading to more oligotrophic or possibly even ombrotrophic conditions and allowing *Sphagnum* to become established (McNamara *et al.*, 1992).

Implications for management and conservation

Peatlands are very unusual ecosystems in that they keep a record of their developmental history as well as the history of past global and local events that might have affected their development. This and previous palaeoecological studies illustrate how land-use changes around peatlands (eg. deforestation for the creation of new pastures) can affect the vegetation of peatlands and peat-accumulation rates through changes in hydrology or local climate (Warner *et al.*, 1989; Heyerdahl and Card, 2000; Mitchell *et al.*, 2001; Sjögren and Lamentowicz, 2007). Changes in hydrology caused by deforestation, for example, can affect the surface moisture of a peatland, as well as its trophy status. Both of these will in turn affect the vegetation and peat composition and peat accumulation rate. This has two important implications for the conservation of peatlands: (1) the management of peatlands for conservation should take into account not only the peatland itself but also the surrounding area, and (2) conservation strategies could be greatly improved by knowing the developmental history of a peatland and how the peatland vegetation responded in the past to vegetation or land-use changes in the surroundings. From a conservation perspective, it is somewhat ironic that Jelenia Wyspa mire is generally perceived (locally) as nearly pristine and of high conservation value, while palaeoecological evidence suggests that the present vegetation likely developed as a result of human impact.

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