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

Mariusz Lamentowicz,* Kazimierz Tobolski and Edward A.D. Mitchell

(1) Department of Biogeography and Palaeoecology, Adam Mickiewicz University, Dziegielowa 27, 61–680 Poznań, Poland; 2 WSL, Swiss Federal Institute for Forest, Snow and Landscape Research, Ecosystem Boundaries Research Unit, Wetlands Research Group, Station 2, CH-1015 Lausanne, Switzerland; 3 École 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 over-harvesting 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
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

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

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Figure 1 Study site location. (A) Poland and Tuchola Pinewoods; (B) Jelenia Wyspa mire. 1, Stażki Main Basin; 2, Jelenia Wyspa mire; 3, Sampling site.
and the southern part of the Tuchola Landscape Park. The bog is part of the ‘Bagna nad Stążką’ Reserve (Stążka 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 fluvo-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 oxyccocos. 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 Vaccinium oxycoccos. Hemlock appears natural, with no visible human impact.

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**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 a field following the Troels-Smith method (Troels-Smith, 1955). The entire peat sequence, as well as the top of the limnic sediments, 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 Habrotrocha 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

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**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 estimated 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 biorstratigraphic 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 (WA-tol) 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 Jacknife crossvalidation procedure (Crowley, 1992). For DWT the model with the lowest RMSEP was WA-tol, with a maximum prediction bias of 0.5 pH units and a RMSEP 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 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

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

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

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

Jelenia Wyspa was a lake until 300 cm depth (outside the range of our δ13C chronology but probably around 4000 cal. yr BP), as attested by the presence of algae (Pediasstrum 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 Chusa 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 limnic 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 Drepanoclados sendnieri, Mesia triquetra and Calliergon giganteum. Other important peat-forming minerotrophic plants include Menyanthes trifoliata and 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 Polystrichum 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 Limprichia cossontia) 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 Cupsidata) 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.

<table>
<thead>
<tr>
<th>Zone</th>
<th>Depth</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>JWB8</td>
<td>(0–9 cm)</td>
<td>The last, top zone is characterized by dominance of three taxa: Arcella discoides, Physochila griseola type and Nebela militaris. Diffugia leidyi and D. pulex present in low percentage. Hyalosphenia elegans reaches its maximum increasing in abundance along with Hyalosphenia papilo</td>
</tr>
<tr>
<td>JWB7</td>
<td>(9–16 cm)</td>
<td>Arcella discoides and Euglypha tuberculata type dominate in this zone. Simultaneously, Assulina muscorum culminates here and Hyalosphenia papilo, Nebela militaris and Centropyxis aculeata increase. Arcella vulgaris decreases. Low percentage of Physochila griseola type increasing in the top of this zone</td>
</tr>
<tr>
<td>JWB6</td>
<td>(16–26 cm)</td>
<td>The zone begins with the maximum of Trigomopyxis arcula. Heleopera sylvaticus dominates (40%). Gradual disappearance of Archerella flavum. Nebela militaris increases (over 20%). Diffugia leidyi, Arcella discoides and Assulina muscorum reach their maximum</td>
</tr>
<tr>
<td>JWB5</td>
<td>(26–46 cm)</td>
<td>This zone is characterized by two peaks of Archerella flavum and Hyalosphenia papilo. Arcella discoides and Cyclopyxis arcelloides increase. Maximum of Nebela minor as well as Euglypha rotunda type. Physochila griseola is recorded for the first time. The rotifer Habrotricha angusticollis reaches maximum (over 20%). Spermaphotopes of Copepoda disappear</td>
</tr>
<tr>
<td>JWB4</td>
<td>(46–67 cm)</td>
<td>Centropyxis aerophila type peaks at over 40% at 65 cm. Increase of Archerella flavum, Cyclopyxis arcelloides, Hyalosphenia papilo and Copepoda. Nebela militaris, Nebela minor and Arcella discoides appear</td>
</tr>
<tr>
<td>JWB3</td>
<td>(67–92.5 cm)</td>
<td>This zone begins with the maximum for Trigomopyxis arcula (35%). Simultaneously Archerella flavum and Hyalosphenia papilo decrease. Arcella discoides, Arcella vulgaris, Nebela tincta, Nebela minor, N. militaris and Cyclopyxis arcelloides increase. Abrupt increase of Centropyxis aculeata and Habrotricha angusticollis</td>
</tr>
<tr>
<td>JWB2</td>
<td>(107.5–92.5 cm)</td>
<td>Archerella flavum dominates achieving 40%. Hyalosphenia papilo culminates at 110 cm and then gradually decreases. At 105 cm Assulina muscorum, Cyclopyxis arcelloides and Trigomopyxis arcula increase. Nebela militaris and Nebela tincta increase slightly. Centropyxis aculeata, Centropyxis aerophila, Arcella catinus and Centropyxis sp. decrease. At 95 cm Habrotricha angusticollis increases, along with the dominance of Archerella flavum and decreasing percentage of Trigomopyxis arcula</td>
</tr>
<tr>
<td>JWB1</td>
<td>(107.5–125 cm)</td>
<td>Centropyxis aculeata, Hyalosphenia papilo and Archerella flavum dominate. Assulina muscorum, Centropyxis aerophila, Heleopera sphagni, Heleopera petricola, Nebela tincta, the rotifer Habrotricha angusticollis and Copepoda spermaphotopes recorded in lower percentage (&lt;10%)</td>
</tr>
</tbody>
</table>
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 arcula*, *Nebela militaris* and *Heleopera sylvatica* were rare except for one sample (c. 600 cal. yr BP or 90 cm), where *I. arcula* 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 Stażk river area (Kowalewski et al., 2002; Lamentowicz, 2005a) and more generally in Europe (Timmermann and Siczewicz, 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 gyttja 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 (Zurek 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 Polyphodiaceae 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 Latalowa, 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 (Hajek 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 (Wilmshurst 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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