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PII: S0048-9697(22)02882-0

DOI: <https://doi.org/10.1016/j.scitotenv.2022.155785>

Reference: STOTEN 155785

To appear in: *Science of the Total Environment*

Received date: 2 March 2021

Revised date: 13 April 2022

Accepted date: 4 May 2022

Please cite this article as: M. Karpińska-Kołaczek, P. Kołaczek, S. Czerwiński, et al., Anthropocene history of rich fen acidification in W Poland — Causes and indicators of change, *Science of the Total Environment* (2021), <https://doi.org/10.1016/j.scitotenv.2022.155785>

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Anthropocene history of rich fen acidification in W Poland – causes and indicators of change

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Abstract

In the time of the global climate crisis, it is vital to protect and restore peatlands to maintain their functioning as carbon sinks. Otherwise, their transformations may trigger a shift to a carbon source state and further contribute to global warming. In this study, we focused on eutrophication, which resulted in its transition from rich fen to poor fen conditions. The prior aim was to decipher how i) climate, ii) human, and iii) autogenic processes influenced the pathway of peatland changes in the last ca. 250 years. We applied a high-resolution palaeoecological analysis, based mainly on testate amoebae (TA) and plant macroremains. Our results imply that before ca. 1950 CE, dry shifts on the Kálmánie fen were generally climate-induced. Later, autogenic processes, human pressure and climate warming synergistically affected the fen, contributing to its transition to poor fen within ca. 30 years. Its establishment not only caused changes in vegetation but also altered TA taxonomic content and resulted in a lower diversity of TA. According to our research *M. patella* is an incredibly sensitive testate amoeba that after ca. 200 years of presence, disappeared within 2 years due to changes in water and nutrient conditions. As a whole, our study provides a long-term background that is desired in modern conservation studies and might be used to define future restoration targets. It also confirms the already described negative consequences connected with the Anthropocene and not sustainable exploitation of nature.

Keywords: testate amoebae, peatland degradation, global warming, human impact, rich fen, Central Europe

1. Introduction

Peatlands are ecosystems that accumulate organic matter which decomposes slowly thanks to anoxic conditions, resulting in carbon sequestration (Rydin and Jeglum, 2013; Mitsch and Gosselink, 2015). Their efficiency is not to be underestimated because even

though they cover, depending on the source, about 3-8 % of the land surface (Mitsch and Gosselink, 2015; Loisel et al., 2021), they are responsible for holding 20-30% of soil carbon (Lal, 2008; Xu et al., 2018). Hence, in the time of global climate crisis, it is vital to protect those areas and restore them, if possible, to maintain their functioning as carbon sinks (e.g. Fennessy and Lei, 2018; Moomaw et al., 2018). Otherwise, their transformations may trigger a shift to a carbon source state (Payne et al., 2016), as happened in the case of many European peatlands (e.g. Wheeler et al., 1995; Jassej et al., 2019; Swenson et al., 2019; Swindles et al., 2019), and further contribute to the global warming. Nowadays, the most threatening changes involve the drying of peatlands. The phenomenon of drying, has been recognized throughout the whole of Europe, even at the sites considered the less disturbed (Swindles et al., 2019). The water tables started to decrease abruptly ca. 200 years ago (Swindles et al., 2019), as an effect of global climate changes and human activities, such as peat cutting, burning and draining of peatlands, and afforestation (see Joosten and Clarke, 2002). Lower water tables lead to enhanced decomposition and increase the probability of wildfires, which results in the release of peat carbon into the atmosphere (Turetsky et al., 2015). They also affect local vegetation (e.g. Breeuwer et al., 2009) and microbial communities (e.g. Reczuga et al., 2018), and thus peatland functionality (Chaudhary et al., 2018) and growth (Charman et al., 2013).

Other changes, affecting mostly fens, involve acidification, which is a part of autogenic peatland processes (Gorham et al., 1987) but might be an effect of human activity (Lamers et al., 2015), and eutrophication. The acidification is connected to the gradual loss of contact with the mineral-rich water due to the accumulation of peat above the water level, which leads to succession from rich fen to poor fen (Rydin and Jeglum, 2013, Lamers et al., 2015). However, in the contemporary epoch of Anthropocene, determined by severe human-induced changes affecting synchronously „key physical, chemical, and biological processes at the planetary scale” (Zalasiewicz et al., 2011; Waters et al., 2018), the process might

accelerate (Kooijman and Paulissen, 2006; Lamers et al., 2015). Acid rain, air pollution, the use of fertilizers, and artificial drainage promote fen acidification (Gorham et al., 1984; Lamers et al., 2015). Acidification results in a loss of ecosystem services and biodiversity (Lamers et al., 2015) that applies to testate amoebae (Heal 1961, 1964), mosses and vascular plants (Glaser et al., 1996; Hájek et al., 2006). Although, sometimes, the diversity of the latter does not change (Lamentowicz et al., 2010). The causes of peatland eutrophication include the input of nutrient-rich surface and groundwaters, and/or increased deposition of nutrients from the atmosphere (Bragazza, 2006; Lamers et al., 2015). The source might be fertilizers, water and air pollution, and forestry practices (e.g. Bragazza, 2006). The result is lower species diversity due to the replacement of slowly growing fen vegetation by fast-growing highly productive species (van Diggelen et al., 2015) and acidification of the environment due to the establishment of *Sphagnum* species (Kooijman et al., 2012). Eutrophication also hampers later restoration efforts, making them a challenging and often expensive venture (Lamers et al., 2015).

In this study, we focused on the Kazanie fen, situated ca. 25 km from Poznań. The analyzed peat section developed in the last 250 years (Czerwiński et al., 2021), which encompasses the Anthropocene (*sensu* Waters et al., 2018). This calcareous fen, like many others in Poland, is listed among the Natura 2000 protected areas (code: 7210, Polish site code PLH300030). However, in the last ca. 50 years, as most of the alkaline peatlands in Europe, it has been drained and experienced both acidification and eutrophication (Czerwiński et al., 2021). Hence, the detailed study regarding palaeoecology of baseline conditions and further fen degradation should contribute to the already implemented environmental management/restoration plans for this fen, as well as others in Central Europe. Testate amoebae (TA) and plant macrofossils might be used for biomonitoring programmes and conservation management of peatlands (Lavoie et al., 2001) because these palaeoecological

proxies supplement each other well (both respond to local environment changes but not necessarily the same factors; Mitchell et al., 2008a). However, TA response to environmental changes, due to short life cycles, should be faster than that of plants.

The prior aim of our study was to decipher how i) climate, ii) human, and iii) autogenic processes influenced the pathway of peatland changes in the last ca. 250 years. Hence, we applied a high-resolution palaeoecological analysis, based mainly on testate amoebae (TA) and plant macrofossils. The second aim of our study was to explore the indicative value of TA concerning rapid trophic fen transformations. Even if knowledge about Central European TA (palaeo-)ecology is growing systematically (van Bellen and Larivière, 2020), the studies on TA communities from rich fens are still substantially deficient (Hájková et al., 2012; Lamentowicz et al., 2011, Lamentowicz et al., 2013; Marcisz et al., 2020, 2021). The reason might be the much higher taxonomic diversity of TA on rich fens in comparison with bogs (e.g. Lamentowicz et al., 2011; Janssey et al., 2014), which makes such studies more time-consuming. Moreover, the high decomposition of peat material accumulated by rich fens prevents efficient TA analysis, as some shells are selectively dissolved (Marcisz et al., 2020). Fortunately, the profile from the Kazanie fen revealed exceptionally well-preserved TA shells, which makes this site unique in terms of long-term TA ecology on rich fens.

2. Material and methods

2.1. State of art

2.1.1. Study site

Kazanie fen (ca. 3 ha) is of limnogenic origin and is located in western Poland, 25 km northeast of Poznań. The fen is classified as calcareous (chalk-bed) fen (Natura 2000 code: 7210) and is situated in ‘Ostoja Promna’, the Natura 2000 area (Polish site code PLH300030). The peat deposits thickness reaches 3 m, under which gyttja, sands, and lacustrine clays are

present (Miętkowicz and Sydow, 1999). The surrounding land relief that originated during the last glaciation (Marks 2012) is dominated by morainic hills and small depressions filled with water or overgrown with wetland vegetation (Laskowicz et al., 2015). The fen is surrounded by the riparian woodlands in the north and east, and wastelands, arable fields and households in the south and west. Farther, mixed forests with *Pinus sylvestris*, *Quercus robur*, *Carpinus betulus*, and *Betula pendula* are present in the landscape (Forest Data Bank). Vegetation from the ass. *Thelypteridi-Phragmiteteum* dominates now on the fen. However, in the past, the Kazanie fen harboured the population of threatened orchid *Liparis loeselii* and other rare species, e.g. *Drosera anglica* and *D. rotundifolia*. Moreover, in small water bodies, *Chara vulgaris*, *Utricularia minor* and *U. minor* were present (Michałowska and Rymon-Lipińska, 2008). In 2017, poor fen patches from the *Scheuchzeria-Caricetea* class were designated for protection (Regionalna Dyrekcja Ochrony Środowiska w Poznaniu, 2017). As our study was focused on the rich to poor fen transformation, we selected a site on the border of two habitats – *Sphagnum fallax* patch surrounded by progressively expanding reed bed communities dominated by *Phragmites australis*, *Typha latifolia* and *Cladium mariscus*.

The climate is typical of the temperate zone and is influenced mostly by the Atlantic air masses. The mean July temperature is 18°C, whereas that of January is -2°C. The annual precipitation is 507 mm, whereas the growing season lasts for 215-227 days (Laskowicz et al., 2005).

2.1.2. Core retrieval and chronology

A 91-cm long profile was collected from the *Sphagnum* lawn, at the margins of the Kazanie rich fen, in June 2017 (52°27'32.4"N, 17°17'45.2"E), using a Wardenaar sampler (dimensions 100x10x10 cm). Ten AMS (Accelerator Mass Spectrometry) ¹⁴C dates, obtained in the Poznan Radiocarbon Laboratory (Poland; laboratory code – Poz), are the basis for profile chronology. The dated material was carefully selected and consisted of terrestrial plant

remains (Supplementary Data 1a). The absolute chronology was inferred from the Bayesian age-depth model, constructed using the OxCal v. 4.2 software, by applying the *P_Sequence* function (Bronk Ramsey, 1995; Bronk Ramsey, 2008; Supplementary Data 1 b). The IntCal13 (Reimer et al., 2013) and post-bomb NH1 (Hua et al., 2013) atmospheric curves were the calibration set.

The top 49.5 cm of the model was validated by ^{210}Pb dates (Supplementary Data 1 b and c). The activity of ^{210}Pb was determined as an activity of its daughter radionuclide ^{210}Po (half-life 138 days) from 59 peat samples from the top of the profile (each 1-cm thick). The laboratory treatment and measurements were carried out in the Institute of Nuclear Physics, Polish Academy of Sciences, Kraków (for details see: Czerwiński et al., 2021). The excess of ^{210}Pb (unsupported) was calculated as the difference between the total ^{210}Pb activity and the supported ^{210}Pb activity. The supported level was calculated from the mean ^{210}Pb activity for the bottom layers (27 ± 2 Bq/kg). Constant Rate of Supply (CRS) and Constant Flux/Constant Sedimentation (CF/CS) models were applied to estimate the age-depth relationships in this part of the core (Appleby, 2002; Sanchez-Cabeza and Ruíz-Fernandez, 2012). The total ^{210}Pb unsupported inventory was calculated and was equal to 6038 ± 63 Bq/m². Next, we corrected this value, based on the extrapolation of the exponential equation, to eliminate a systematic deviation of CRS dates toward erroneously old ages, i.e. the so-called “old-date error” (Binford, 1990; Tylmann et al., 2016). Most of the ^{210}Pb dates overlapped with dates retrieved from the Bayesian age-depth model. The maximum difference between the parallel dates was identified at a depth of 35.5 cm and ranged from ca. 4.5 to 11.5 years (^{210}Pb : ca. 1974 CE; ^{14}C : ca. 1982 CE; Supplementary Data 1 d).

The dates used in this paper, expressed as CE (Common Era), are the μ (mean) values retrieved from the model $\pm \sigma$ error (Supplementary Data 1).

2.1.3. Plant macrofossils

Plant macrofossils reflect the local vegetation and peatland development and describe past TA habitats (Mauquoy et al., 2010). The 1-cm contiguous slices of profile (10 cm³) were analysed to identify plant macrofossils. Plant macrofossil findings were previously published by Czerwiński et al. (2021), but the interpretation of these data focused mostly on the regional changes/forest communities. The identification of *Sphagnum* and brown mosses species was performed separately, with the use of specialistic literature (Hedenäs, 2003; Smith, 2004; Hölzer, 2010; Laine et al., 2011), to obtain reliable results. The volume percentages of unidentified plant remains and mosses were estimated and rounded to the nearest 5%. The plant taxonomic nomenclature follows Mirek et al. (2002) and Ochyra et al. (2003).

2.2. Testate amoebae (TA)

TA enable (i) quantitative estimation of changes of the depth to the water table (DWT) (Charman et al., 2007; Lamentowicz et al., 2011; Amesbury et al., 2016), i.e. potential evidence for climate humidity and/or human impact changes, (ii) reconstruction of pH changes and conductivity, i.e. insight into fen succession (Mitchell et al., 2013) and (iii) study on the microbial food webs (Reznicka et al., 2018). The 1-cm contiguous slices of profile (3–5 cm³), parallel to those selected for plant macrofossils, were analysed in search of TA. The material for testate amoebae analysis underwent standard treatment (Booth et al., 2010). The material was washed with distilled water on a sieve of 300-µm mesh size and the filtrate was used for microscopic analyses. Samples were counted under a light microscope at 400× magnification until a minimum of 150 tests was obtained (Booth et al., 2010; Payne and Mitchell, 2008). The exception was eight samples where such a number was difficult to obtain. Identification was done using literature on the subject and aimed at achieving the highest possible taxonomical resolution (e.g. Clarke, 2003; Mazei and Tsyganov, 2006; Meisterfeld, 2001; Ogden and Hedley, 1980).

2.3. Statistical analyses and visualization

The results of both analyses were drawn as diagrams, divided into zones based on CONISS (Grimm, 1987), using the TILIA Graph programme (Grimm, 1991). Depth to the water table (DWT) and conductivity (indicator of the presence of ions/minerogenic sediments) changes were reconstructed using the transfer function performed on the testate amoebae data from surface samples from Poland (DWT – Lamentowicz and Mitchell, 2005; conductivity – Lamentowicz et al., 2011). For the reconstruction of DWT, a weighted averaging (WA) tolerance down-weighting model (Lamentowicz et al., 2008) was applied, whereas for the conductivity WA inverse deshrinking model (Lamentowicz et al., 2013).

We performed non-metric multidimensional scaling (NMDS) to determine the correspondence between (i) TA and local peat-forming plants (those expressed as percentages based on peat volume) and (ii) TA and palynological data (human impact indicators and the most frequent arboreal pollen taxa). This analysis was performed using the R software, version 3.6.0 (R Core Team, 2018), with the *vegan* package (Oksanen et al., 2017). Plant macrofossil and palynological data were projected on the NMDS using the *envfit* function. NMDS was calculated using the Bray-Curtis distance. To assess the changes in TA biodiversity, we also used the Shannon diversity index (H) that was calculated and drawn along the stratigraphic order, using the PAST 4.0.3 software (Hammer et al., 2001).

3. Results and interpretation

Analysis of 90 peat samples revealed the presence of 113 testate amoebae (TA) taxa, whose patterns were linked with the fen vegetation (Figs 2-5). The results of the CONISS clustering revealed 2 distinct phases of TA-vegetation assemblages. These results pointed out the boundary between phases at 36 cm (plant macrofossils) or 35 cm (TA), so then we arbitrarily positioned the boundary at a depth of 35.5 cm (ca. 1982±3 CE).

3.1. Mire succession: plant macrofossils, testate amoebae, water table and conductivity

3.1.1. Phase I – rich fen; 91–35.5 cm; ca. 1767±45–1982±3 CE

The rich fen developed as a result of the lake terrestrialisation and was dominated by brown mosses, mostly *Scorpidium cossonii*, with the addition of *Pseudocalliergon trifarium* and *Meesia triquetra* (Fig. 2). The presence of these mosses indicates the rich fen conditions then (Hedenäs, 2003; Atherton et al., 2010; Rehell and Virtanen, 2015). In this phase, the most abundant TA genera were *Centropyxis*, *Cyclopyxis*, *Diffflugia*, and *Pyxidicula*, which were accompanied by *Arcella discoides*, *A. vulgaris*, *Cryptodiffugia crenulata*, *Heleopera petricola*, *Hyalosphenia platystoma*, *Microchlamys patella*, *Gibbocarina galeata*, and *Paraquadrula irregularis* (Fig. 3). The presence of *Centropyxi* species and *Arcella vulgaris* confirms a high pH level (Lamentowicz and Mitchell 2007), whereas wet conditions are proved by the occurrence of *Diffflugia* sp., *Pyxidicula* sp. (Jax, 1985), *Cryptodiffugia crenulata* (Bobrov and Mazei, 2017), *Microchlamys patella* (Anderson, 1988; Vincke et al., 2006), *Paraquadrula irregularis*, and *Arcella discoides* (Beyens et al., 1990). However, the last species is also considered an indicator of water level fluctuations, i.e. unstable hydrological conditions (Lamentowicz and Mitchell, 2005).

A slight change in the composition of plant macroremains starts at ca. 1955±7 CE when *S. cossonii* decreased, whereas *Bryum pseudotriquetrum*, *Calliergon cordifolium* and *Fissidens* sp. gained importance subsequently. At the same time, *Lycopus europaeus*, *Carex lasiocarpa*, *Comarum palustre*, and *Thelypteris palustris* appeared (Fig. 2; Czerwiński et al., 2021). Whereas all these moss taxa are typical of rich fens, the appearance of *C. lasiocarpa* and *C. palustre* points to slow acidification of the environment (Ellenberg and Leuschner, 2010) and the development of communities from the *Caricion lasiocarpae* alliance (Matuszkiewicz, 2007). A similar change is reflected in testate amoebae composition and slightly decreasing TA-inferred conductivity, pointing to gradual acidification. Some taxa disappeared or retreated around that time (Fig. 3). Among them were *Awerintzewia*

cyclostoma which prefers deep water bodies, according to Heckman (1998), or soils and soil mosses, as Bankov et al. (2018) claim. Although no deep water body was present at the coring spot then, this species occurred probably in shallow pools. Other taxa that withdrew back then were *Centropyxis aerophila sphagnicola*, *Centropyxis discoides*, *Heleopera petricola*, *Hyalosphenia platystoma* and *Pyxidicula* sp. *H. platystoma*, *C. discoides* and *Pyxidicula* sp. withdrew probably due to lowering of the water level and disappearance of microhabitats with long-lasting shallow water (cf. Siemensma, 2019; Šatkauskienė et al., 2014; Jax, 1985)). In the case of *H. petricola*, it was replaced by *Heleopera rosea* that despite preferring more alkaline conditions, may survive in drier habitat (Lamentovica and Mitchell, 2005). *Quadrullella symmetrica* that appeared little earlier, found optimal conditions for life, as indicated by its maximum values then.

The TA-inferred water table revealed strong fluctuations in that phase. The extrema were represented by values -4.1 ± 8.1 cm (open water) and 25.5 ± 7.9 cm (mean: 8.4 cm). The TA-inferred conductivity was relatively stable and ranged between 510 and 320 $\mu\text{S}/\text{cm}$ (mean: 420 $\mu\text{S}/\text{cm}$), which confirms the supplementation of fen with waters rich in ions. This phase was characterized by the highest TA biodiversity, as indicated by the Shannon diversity index (H) that oscillated around a value of 2.5.

3.1.2. Phase II – poor fen; 35.5–0 cm; ca. 1982±3–2017 CE

Together with the disappearance of brown mosses and the appearance of *Sphagnum*, the TA communities changed (Fig. 2 and 3). The progressing acidification is reflected in the drop of conductivity and the spread of *Sphagnum* (Figs 2 and 3). The dominance of *S. teres* confirms the further development of communities from the *Caricion lasiocarpae* alliance (Matuszkiewicz, 2007). The subsequent succession of *S. fallax* and then *S. fimbriatum* reflects the transition from minerotrophic to more oligotrophic conditions (Wilcox and Andrus, 1987), however not stable, as visible in the curves of both taxa (Fig. 2; Czerwiński et al., 2021).

Quasi-stable conditions were reached with the appearance of mesotrophic state indicator *S. centrale* (Laine et al., 2009) and the spread of *Betula* at the site (proved by macroremains). The development of a birch stand points to the progressive drying of the fen. Such conditions enabled probably the appearance of *S. palustre* that, among other habitats, occurs in drying mires, gradually colonized by trees (Melosik, 2006).

Among the TA, the most numerous were *Euglypha* sp. and *Nebela* sp., as well as *Assulina muscorum*, *Corythion dubium*, *Heleopera rosea*, cf. *Pseudodifflugia* sp., *Sphenoderia splendida*, and *Tracheleuglypha dentata*. The characteristic feature of this stage is an almost constant presence of *Arcella discoides* that may indicate fluctuations in the water table (Lamentowicz and Mitchell, 2005). Unstable conditions may have enabled the appearance of species characteristic of either dry microhabitats or tolerant of frequent moisture fluctuations. The former, such as *Nebela tincta*, *Heleopera rosea* and *Euglypha rotunda* (Koenig et al., 2017; Lamentowicz and Mitchell, 2005; Tolonen et al., 1992), are indeed well represented in the diagram. The latter, e.g. *Arcella catinus*, *Assulina muscorum*, *Corythion dubium* and *Ceratomyxis aerophila* (Couteaux, 1976, after Smith, 1992; Tolonen et al., 1992), seem to benefit as well. Moreover, within the *Euglypha* sp., the most abundant were spineless forms of *E. ciliata* and *E. compressa*. According to Bobrov et al. (2002), such forms prevail in drier habitats in comparison with their spined relatives. This phase is also characterized by the abundant occurrence of ubiquitous *Trinema lineare* and *T. enchelys*, and unidentified cf. *Pseudodifflugia* sp. In the period of the latter species dominance (1986±2–2012±2 CE), the prominent decline of TA diversity was recorded (Shannon diversity index (H)<1), probably the result of the cf. *Pseudodifflugia* sp. overrepresentation.

Toward the top, an expansion of some taxa is observed (Fig. 3). Among them were many species considered indicators of dry habitats, such as *Alabasta militaris*, *Cryptodifflugia oviformis* and *Nebela parvula* (Bobrov et al., 2002), and besides acid, e.g. *E. rotunda* and *E.*

strigosa (Lamentowicz and Mitchell, 2005). However, in the top layer (ca. 5 cm/ last 7–8 years), some of the rich fen taxa became again more abundant (e.g. *Centropyxis aerophila*, *Cyclopyxis eurystoma*) and the taxa connected with the higher water level, such as *Euglypha cristata*, *E. filifera*, *E. laevis*, and *Sphenoderia lenta* spread (Bobrov et al., 2002; Lamentowicz and Mitchell, 2005). This could have reflected the higher minerotrophy caused by the increase in the water level (Cusell et al. 2012), but the reconstructed DWT does not confirm it (Fig. 3). Nevertheless, the changes might be connected with the restoration efforts, undertaken in the last couple of years, which might result in the slow recovery of the rich fen.

The transition from rich fen to poor fen is also visible in TA-inferred conductivity that dropped and oscillated between 35.7 and 302.8 $\mu\text{S}/\text{cm}$ (mean: 192.6 $\mu\text{S}/\text{cm}$). Moreover, the values of the reconstructed water table decreased to the mean value of 19.8 cm but still fluctuated (7.4–33.2 cm).

3.2. Non-Metric Multidimensional Scaling (NMDS)

The results of NMDS carried out on TA and plant macrofossils revealed a clear division between TA communities related to rich and poor fen habitat (Fig. 4, Supplementary Data 2a). The highest statistical significance ($p < 0.001$), in relationships between plant macrofossils and TA, was revealed by *Sphagnum fallax*, *S. fimbriatum*, *S. centrale*, *Scorpidium cossoni*, and unidentified herbaceous plants. The strong significance ($0.001 < p < 0.01$) was characteristic of *Thelypteris palustris*, *Sphagnum teres*, *Pseudocalliergon trifarium*, and unidentified brown mosses. *Diffugia pulex* was strongly linked to *S. fimbriatum*, whereas *Nabela collaris* to *S. fallax*. In the case of brown mosses, the strongest link revealed (i) *Lesquereusia spiralis* and *S. cossoni*, and (ii) *Heleopera petricola* and herbs.

NMDS based on TA and regional/local vegetation, including human impact (derived from palynological data; Czerwiński et al., 2021), revealed the highest statistical significance ($p < 0.001$) in relationships between *Pinus sylvestris*, *Betula*, *Alnus*, *Salix*, the sum of ruderal taxa (major ruderals, i.e. these wind-pollinated), and cultivated taxa. A strong significance was recorded for the microscopic charcoal influx and coprophilous fungi (Fig. 5, Supplementary Data 2b). The most distinct and positive correlations occurred between cultivated taxa and *Quadrullella symmetrica*, *Diffflugia globulosa*, *Centropyxis platystoma*, and *Centropyxis aerophila*, whereas cultivated taxa were negatively correlated with *Arcella discoides* and *Diffflugia pulex* type. *Nebela* sp. was correlated with the increases in micro- and macrocharcoal. However, because it was not possible to identify this species to the lower taxonomic level, this might be a group of species and it should not be interpreted as a reliable indicator. *Heleopera rosea*, *Trinema lineare*, *Nebela parvula*, and *Sphenoderia splendida* revealed strong affinity to *Alnus*.

4. Discussion

4.1. An abrupt rich to poor fen transition – causes of change

The processes that lead to further succession stages are almost inevitable, it is usually a question of time (cf. Jabłońska et al., 2020). The vegetation reaches the level above which the contact with mineral-rich groundwater is limited (Rydin and Jeglum, 2013). At the same time, rich fens undergo natural acidification. This contributes to the spread of *Sphagnum* which accelerates the process and results in the vegetation shift and the development of poor fen (Rydin and Jeglum, 2013). The shift might be quite fast and irreversible when *Sphagnum* expands (cf. Granath et al., 2010; Faber et al., 2016). Moreover, Kooijman (2012) shows that in nutrient-rich fens, where *Calliergonella cuspidata* (a taxon of similar preferences to *C.*

cordifolium, Fig. 2) is a dominant species, the succession to poor fen conditions may progress faster. In the case of the Kazanie fen, from the rapid decline of *Scorpidium scorpioides* to the development of poor fen conditions, ca. 30 years passed (Fig. 2) and, at the end of the rich fen phase, *Calliergon cordifolium* was an important species. However, the transition was not synchronous on the entire surface, as *S. scorpioides* was still present in the central part 10 years ago. It disappeared a couple of years later due to a water table decrease and a succession of reeds and willows on the fen surface (cut in the process of restoration). Nevertheless, in the palaeoecological research, similar quick changes were attributed rather to extrinsic factors like climate and human activity (comp. Lamentowicz et al., 2007; Payne and Pates, 2008; Tahvanainen, 2011; Pedrotti et al., 2014).

The shifts in TA and vegetation started in 1955 ± 7 CE and they demonstrate slow acidification and decreasing conductivity (both TA-inferred; Fig. 3). At the same time, there were no sharp shifts in TA-inferred DWT (Fig. 3) that could indicate human intervention (drainage) or climate influence (drought; cf. Singer et al., 1996). However, Czerwiński et al. (2021) suggest that in the 1950's CE, the intensification of agriculture took place in the region. It could result in the increased deliveries of phosphorous (P) and nitrogen (N) to the fen because, in the second half of the 20th century CE, many agricultural areas became eutrophic and hypereutrophic due to the use of fertilizers and manure (Lamers et al., 2015). The eutrophication of the fen could accelerate its acidification and further transformation (Kooijman, 2012). Indeed, in 1955 ± 7 CE, the vegetation shift, connected with acidification, was observed (Fig. 2). Moreover, many authors (Bakker et al., 1994; Verhoeven and Bobbink, 2001; van Diggelen et al., 2015) stressed that the eutrophicated fens undergo a fast transformation, such as in the case of the Kazanie fen (Fig. 2 and 3). Besides, in the transient phase, the highest micro- and macrocharcoal accumulation rates were recorded (Czerwiński et al., 2021). It might have been a result of combined (i) severe winters that forced people to

burn more wood and fossil fuels, (ii) the grass burning that was a popular method of fertilization then, and (iii) increased frequency of droughts (Fig. 6) that contributed to local fires. Hence, most probably, the first changes might have been accelerated by the indirect human impact. The final transition to poor fen conditions took place at 1982 ± 3 CE and it progressed within less than one decade. Numerous TA species that occurred over the last two centuries disappeared (Fig. 3). These changes, judging by the magnitude of the sudden DWT increase, were an effect of digging a drainage ditch then (still present in 2008, Michałowska and Rymon-Lipińska, 2008). It successfully drained the area in the forthcoming years, contributing to the acidification process and changes in vegetation and microbial communities, revealing pronounced declines in TA diversity (Figs 2, 3 and 6).

Climate affects peatlands through the influence on their hydrology (Holden, 2006; Labadz et al., 2010). Moreover, it may indirectly enhance acidification because desiccation of peat leads to the production of acidifying H^+ ions (Lamers et al., 2015). Moreover, Laiho et al. (1999) report that after a drainage, the groundwater influx is limited and uptake of base cations by the advancing trees, together with the longer nutrient retention in the biomass, may further increase the acidity in the surface soil. Hence, climate-driven drying of peatlands results in desiccation, followed by oxidation and acidification of the environment (comp. Cusell et al., 2013). During the Holocene, many dry and wet shifts were recognized in peat profiles and linked with hydro-climatic events (e.g. Bond et al., 1997; Magny, 2004). Such climate shifts contributed to the changes in vegetation and trophic conditions at other sites (e.g. van der Knaap et al., 2011; Dobrowolski et al., 2016). The more recent influence of climate on mires has also been recognized (e.g. Payne and Pates, 2008). The early record of dry years in Poland, from 1851 to 1950 CE (Posucha IMGW, 2010), was reflected with quite a good accuracy in the reconstructed DWT, i.e. concurrent drier conditions on the Kazanie fen (Figs 3 and 6). However, in the last century, droughts became more common (cf. Lloyd-

Hughes and Saunders, 2002). In Poland, about 20 dry years were recorded from 1950 to 2020 CE (Kasprzak and Salamon, 2020). Some of them positively correspond with the TA-inferred DWT, but they seem to be more chaotic than those between 1851 ± 26 and 1950 ± 7 CE. Nevertheless, the general shift toward drier conditions, reconstructed from TA, started in the 1980's CE and was concurrent to the final transition from rich to poor fen. This may imply that before 1950 ± 7 CE, dry shifts on the Kazanie fen were generally climate-induced. Later, autogenic processes, human pressure and climate warming synergistically affected the fen. This is visible in some water table drops in Kazanie, simultaneous to the drought events. The beginning of the transition phase (1950 ± 7 – 1965 ± 5 CE) took place in the period of the increased number of meteorological droughts, when three extreme droughts per decade occurred (Przybylak et al., 2020, Fig. 6). This suggests that their frequency might have influenced the fen transformation as well. Prolonged droughts have a similar effect, as shown by the example of kettle hole mires, where peat mat expansion occurred rapidly, as a threshold response to extreme water-level fluctuations (Ireland and Booth, 2011). What is striking, in the case of Kazanie fen, the final switch into poor fen conditions (1982 ± 3 CE) occurred in the decade when the positive anomaly in annual temperatures in Poland began (Fig. 6). Since then, annual temperatures grow constantly (IPCC, 2019), but without the changes in the frequency of droughts in the decadal time window (Przybylak et al., 2020). Global warming that enhances evapotranspiration further limited the contact of the fen vegetation with the groundwater (Lamers et al., 2015). That way, the effect of the drainage ditch strengthened and sustained the path toward ombrotrophy.

Nowadays, the state of the mire is far from natural, despite being perceived that way due to *Sphagnum* occurrence. Hence, Kazanie fen should be classified as the anthropogenic ecosystem that is an effect of various overlapping processes, such as vegetation succession, climate changes, drainage, and eutrophication. Their combination contributed finally to the

transition from rich fen to poor fen conditions (comp. Czerwiński et al., 2021). Despite the complicated history, our study site provides a long-term background that is desired in modern conservation studies (Bowman et al., 2017) and might be used to define the restoration target (Roleček et al., 2020). However, due to global warming, water shortage and degradation of the fen, the target will not be easy to reach (Vellend et al., 2017).

4.2. Quality of testate amoebae indicators of the rich-poor fen transformation

Some testate amoebae reflect greater sensitivity to drying, acidification and probable eutrophication, making them potential indicators of such changes. According to our data, the most sensitive to the combined effect of probable nutrient enrichment and lowering of the water table are *Awerintzewia cyclostoma*, *Hyalosphaera platystoma*, *Pyxidicula cymbalum*, *P. operculata*, and *P. patens*. All these testate amoebae disappeared/retreated in 1970±4 CE, when the drop in the water level (DWT=15 cm; Fig. 3), an effect of the hydrological drought (Farat et al., 1998), was recorded. Their reaction is adequate to their ecological preferences for the aquatic or wet habitats (Heckmann, 1998; Jax, 1985; Lamentowicz et al., 2013b; Siemensema, 2019). However, the droughts were recorded earlier and none resulted in the disappearance of these TA taxa before. Hence, their retreat might be connected with the concurrent eutrophication of the adjacent area.

The acidification connected with the sudden shift in moss communities toward ones dominated by *Sphagna* might have been responsible for the disappearance of *Centropyxis aerophila sphagnicola*, *Centropyxis ecornis*, *Centropyxis gasparella*, and *Cyclopyxis kahli*. Representatives of *Centropyxis* genus are generally considered opportunistic tolerant to various trophic conditions and dust and heavy metal pollutions, but pH is a controlling factor in their distribution in lakes (Patterson and Kumar, 2000). It is true also for peatlands (Lamentowicz and Mitchell, 2005), including the Kazanie fen, where lowering of pH allowed *Sphagna* encroachment (cf. Lamers et al., 2015) that caused the disappearance of most of

Centropyxis representatives (Fig. 3). However, some of them, such as *C. discoides* and *C. delicatula*, seem to be more sensitive to progressing acidification, as they reacted faster than moss communities and retreated/disappeared earlier than *Sphagna* appeared, i.e. before 1940±8 CE. *Cyclopyxis kahli*, which is often considered indicative of oligotrophic conditions, responded similarly (Schönborn, 1967). Nevertheless, it can occur in mesotrophic and even eutrophic waters (Prentice et al., 2018), as well as in the soil (Warner, 1994). According to Opravilová and Hájek (2006), *C. kahli* has its optimum in calcareous fens dominated by brown mosses, so progressing acidification in the Kazanie fen seems to explain its withdrawal.

The group of amoebae that reacted to fen transformation consists of *Arcella vulgaris*, *Microchlamys patella* and *Quadrullella symmetrica*. These taxa relative abundance increased after the drought episodes in 1969 and 1970 CE but disappeared when the drainage ditch was probably dug ca. 1985 CE (Fig. 3). In earlier research, *Microchlamys patella* occurred in wet or even aquatic habitats (Vincke et al., 2004; 2006). Moreover, studies on the surface samples along a poor-rich gradient, done by Lamentowicz et al. (2011), revealed that *M. patella* is abundant in calcium-rich brown mosses habitats. However, this species expanded in the transition zone, where the water level was generally lower than before 1970±4 CE (Fig. 3). Simultaneously, the highest charcoal influx was recorded in the period of *M. patella* optimum (Fig. 6), which suggests that potential dust fallout (with calcium, cf. Lurdes Dinis and Gonçalves, 2020) was also present. It might have enriched the fen and compensated for the effect of limited supplies of calcium-rich groundwater. Its later disappearance, at the beginning of the poor fen section of the profile, happened due to the habitat transformation resulting in low pH and low water level. Hence, a probable explanation for the *M. patella* spread in the transition period is eutrophication (by dust). A pattern similar to *M. patella* was observed in the case of *Arcella vulgaris*. The research conducted in lakes in Mexico showed

that *A. vulgaris* might be indicative of stressful environmental conditions, as it was common in water with higher levels of heavy metal contamination (Regalado et al., 2018). The authors also suggested that this species has similar ecological preferences both in temperate and tropical regions (Regalado et al., 2018). It might be confirmed by Patterson and Kumar (2000), who also connected the occurrence of *A. vulgaris* with higher contamination with heavy metals in the research regarding Swan Lake in Canada. The link between contamination and eutrophication was provided by Su et al. (2014), who showed that the use of fertilizers contributes to soil contamination with heavy metals. Hence, the expansion of *A. vulgaris* at that time might have been linked with the increased application of fertilizers. Moreover, it also fits an explanation regarding increasing dust fallout indicated by micro- and macrocharcoal accumulation in peat (Fig. 6). The last taxon, *Quadrullella symmetrica*, confined its presence to the transition zone mostly. Čprávilová and Hájek (2006) link this species with calcareous fens dominated by brown mosses. In our study, *Quadrullella symmetrica* revealed a positive link with cultivated fields in the catchment (Fig. 5). This species also occurred during the spread of eutrophent *Calliergon cordifolium* (but it is not visible in NMDS analysis, Fig. 4) (Kooijman, 2012). Its expansion might have been connected with eutrophication induced by the use of fertilizers in the catchment area of the fen. Kooijman and Bakker (1993) found a relationship between increased nutrient levels and the replacement of *Scorpidium scorpioides* by *Calliergonella cuspidata* in fens, the latter occurs in similar habitats as *Calliergon cordifolium* (Kooijman, 2012; <https://cisfbr.org.uk/>). According to Kooijman and Bakker (1993), eutrophication seems to have little effect under wet conditions but might be important in a drier environment, such as in the case of the Kazanie site. The later research by Kooijman (2012) confirmed the link between the occurrence of *C. cuspidata* and nutrient enrichment. To sum up, not only a decrease in the water table during the rich to poor fen transition but also an increased application of fertilizers

and dust deposition might have contributed to the establishment of optimum habitat for *M. patella*, *A. vulgaris* and *Q. symmetrica*. Nonetheless, it must be stressed that the final turnover toward poor fen conditions was a very fast process and *M. patella* is the best example of how small might be the difference between optimal and intolerable habitat. After ca. 200 years of presence, *M. patella* disappeared within 2 years, which proves the high sensitivity of this species to changing conditions.

From 1982±3 to 2017 CE drought-tolerating TA taxa prevailed (Fig. 3, cf. Lamentowicz et al., 2011) in the studied area of the Kazanie fen. Even though TA-inferred DWT failed to reflect the occurrence of all droughts, as for the period before 1950±7 CE, it still indicated some of them (Fig. 3). A similar response was revealed by extensively drained peatlands in the Orawa-Nowy Targ Depression, where the potential impact of droughts was marked by TA communities of xerothermic species (cf. Kołaczek et al., 2018). The poor fen stage was characterized by rapid and recurrent events of domination of *Trinema lineare*, *Trinema enchelys*, and cf. *Pseudodiffugia* sp. These taxa were recorded earlier, during the rich fen stage, but they did not visibly influence the TA diversity (Fig. 3). *Trinema* sp. shells are not embedded with thick organic matter (Mitchell et al., 2008b; Aoki et al., 2007), which makes them less resistant to decomposition than other testate amoebae possessing agglutinated (e.g. *Centropyxis* sp., *Diffugia* sp.) or organic-coated idiosomic tests (e.g. *Assulina* sp.) (Payne et al., 2012; Marcisz et al., 2021). Hence, their preservation depends highly on the conditions of peat accumulation. The highest frequency of *Trinema* sp. shells occurs usually in the topmost sections of peat columns, as was recorded in other fens and bogs (e.g. Lamentowicz et al., 2013; Kołaczek et al., 2018). Moreover, even though there is still a deficiency of experimental studies regarding the rate of TA reproduction (Marcisz et al., 2020), such small species like *Trinema* and *Pseudodiffugia* reproduce faster than larger TA (Heal, 1964), which contributes to the rapid increases in their frequency. When we add that a

drier microhabitat, as in the case of poor fen stage at the Kazanie site, promotes TA of smaller body size (Marcisz et al., 2016; Marcisz et al., 2020), this all together leads to the smaller biodiversity of poor fens. Moreover, the alkaline conditions provided by brown mosses, as were at the site before 1982±3 CE, support a high diversity of TA in comparison with more acidic *Sphagnum*-dominated peat (Lizonová and Horsák, 2017). The study by Lizonová and Horsák (2017) also shows that the diversity of rich fen TA might have been underestimated due to the standard number of tests counted per sample (N=150). Hence, the differences in TA diversity between rich and poor fens might be even more substantial. Summing up, rapid decreases in the water table on the poor fen favours small TA that can reproduce fast, which contributes to the lower diversity of TA during dry spells. However, further experimental research on small TA reproduction rates is highly desirable for a better understanding of the mechanisms that influence TA diversity.

Conclusions

1. A high-resolution study on the transformation from rich to poor fen, based on testate amoebae (TA) and plant macrofossils, revealed the long-term resistance of rich fen habitats during the Industrial Period. The transformation into poor fen was linked with many coinciding factors, making the unambiguous culprit impossible to point. Climate warming, combined with autogenic processes (natural peat growth), led to the loss of contact between the groundwaters rich in calcium and the moss layer. The increased use of fertilizers in the fen vicinity probably stimulated eutrophication, which also contributed to faster fen transformation. Finally, melioration, linked with regularly occurring droughts (symptoms of global warming), settled poor fen conditions and a path toward ombrotrophy. The reversion of the process is difficult, as restoration efforts on degraded rich fens may be hampered by disturbed water balance and climate changes.

2. Our study revealed that transformation from rich to poor fen habitat leads to a decline in TA diversity. The transitional stage provided habitat for TA *Quadrullella symmetrica* and *Diffflugia globulosa*, which distinctly revealed optima at that time. Moreover, *Microchlamys patella* and *Arcella vulgaris*, taxa characteristic of brown mosses, also positively reacted to the fen transformation. Their sudden rises might be considered indicators of such changes. What is striking, *Microchlamys patella* disappeared (or it became too scarce to be detected in TA analysis) within 1-2 years after 250 years of regular and frequent occurrence. This shows that some TA taxa are very sensitive to environmental disturbances and might be a diagnostic tool for detecting rapid ecosystem changes in the era of the global climate crisis.
3. The establishment of poor fen conditions not only caused changes in vegetation but also altered TA taxonomic content and resulted in a lower diversity of TA. In general, drought-tolerant taxa dominated the TA assemblages. Among them, the most frequent were *Trinema lineare*, *Trinema enchelys*, cf. *Pseudodiffflugia*, *Nebela tinctoria*, and *Assulina muscorum*. However, even though these are taxa linked with low water tables, their record is one of the rapid and recurrent events of domination that might be connected with drought occurrences. This shows that even TA assemblages indicative of dry conditions may reveal susceptibility to droughts. The result might be the depletion of TA diversity due to the promotion of small size taxa.

Acknowledgements

We would like to thank the reviewers for their comments that helped us to improve the manuscript. MKK also thanks PhD K. Marcisz (AMU, Poznań) for her help with TA identification. This work was conducted within the project of the National Program of Development of Humanities (No. 2bH15015483), funded by the Polish Ministry of Science

and Higher Education, and the grant 2015/17/B/ST10/01656 funded by the National Science Centre (Poland).

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Fig. 1. The locality of the Kazanie fen. A – on the aerial photography. B – on the map of Poland.

Fig. 2. Plant macrofossils in the Kazanie fen (Czerwiński et al., 2021).

Fig. 3. Short percentage diagram of the most frequent testate amoebae (TA) in the Kazanie profile. The grey area reflects percentage values exaggerated 10 times. Red belts reflect periods of droughts (Kasprzak and Salamon, 2020; Nauka o Klimacie, 2016; Posucha IMGW, 2010).

Fig. 4. NMDS scatter plot showing the correspondence between peat-forming plants (reconstructed from plant macrofossils; Czerwiński et al. in review) and TA. Note that the thickness of lines expressing vectors reflects the p-values. TA abbreviations: arcsp – *Arcella* sp., arcart – *A. cf. artocrea*, arccat – *A. catinus*, arcon – *A. cf. conica*, arcre – *A. cf. crenulata*, arcden – *A. dentata*, arcdis – *A. discoides*, argib – *A. gibbosa*, archem – *A. hemispherica*, arcvul – *A. vulgaris*, argsp – *Argygnia* sp., argden – *A. dentistoma*, assmus – *Assulina muscorum*, assem – *A. seminulum*, awecyc – *Awerintzewia cyclostoma*, censp – *Centropyxis* sp., cenacu – *C. aculeata*, cenacuobl – *C. aculeata oblonga*, cenaer – *C. aerophila*, cenaersph – *C. aerophila sphagnicola*, cencas – *C. cassis*, cencon – *C. constricta*,

cendel – *C. delicatula*, cendis – *C. discoides*, ceneco – *C. ecornis*, cenecoqua – *C. ecornis*
quadripannosa, cengas – *C. gasparella*, cengib – *C. gibba*, cenorb – *C. orbicularis*, cenplg –
C. plagiostoma, cenplt – *C. platystoma*, censpi – *C. spinosa*, cycsp – *Cyclopyxis* sp., cyceur –
C. eurystoma, cyckah – *C. kahli*, cordub – *Corythion dubium*, crymin – *Cryptodiffugia* cf.
minuta, crycre – *C. crenulata*, cryovi – *C. oviformis*, difsp – *Diffugia* sp., difacc – *D.*
accuminata, difcap – *D.* cf. *capreolata*, difele – *D. elegans*, difgeo – *D.* cf. *geosphaira*, difgig
– *D. gigantea*, difglo – *D. globulosa*, difmam – *D.* cf. *mammillaris*, difmin – *D.* cf. *minuta*,
diflan – *D. lanceolata*, difluc – *D. lucida*, difobl – *D. oblonga*, difpnl – *D. pulex* type, difpyr –
D. cf. *pyriformis*, difrot – *D. rotunda*, difrub – *D. rubescens*, eugsp – *Euglypha* sp., eugcil –
E. ciliata, eugcilgla – *E. ciliata* glabra, eugcom – *E. compressa*, eugcomgla – *E. compressa*
glabra, eugcri – *E. cristata*, eugfil – *E. filifera*, euglac – *E. laevis*, eugrot – *E. rotunda*, eugstr
– *E. strigosa*, helsp – *Heleopera* sp., helpet – *H. petricola*, helros – *H. rosea*, helsph – *H.*
sphagni, helsyl – *H. sylvatica*, hyasp – *Hyalsphenia* sp., hyacun – *H. cuneata*, hyapap – *H.*
papilio, hyapla – *H. platystoma*, lagsph – *Lagenodiffugia* cf. *sphaeoroides*, lesspi –
Lesquereusia spiralis, lesepi – *L. episcopium*, micpat – *Microchlamys patella*, nebsp – *Nebela*
sp., nebali – *N. aliciae*, nebbok – *N. bohémica*, nebcoll – *N. collaris* type, nebgal – *N. galeata*,
nebmil – *Alabasta militaris*, nebpar – *Nebela parvula*, nebpen – *N. penardiana*, nebtin – *N.*
tincta, nebtinmaj – *N. tincta* major, netcor – *Netzelia* cf. *corona*, padlag – *Padaungiella*
lageniformis, parirr – *Paraquadrula irregularis*, parcy – *Parmulina cyatus*, parobt – *P.*
obtecta, phygri – *Physochila griseola*, psp – *Pseudodiffugia* sp., pyxsp – *Pyxidicula* sp.,
pyxym – *P. cymbalum*, pyxope – *P. operculata*, pyxpat – *P. patensquasym* – *Quadrullella*
symmetrica, sphfis – *Sphenoderia fissirostris*, sphlen – *S.* cf. *lenta*, sphspl – *S. splendida*,
traden – *Tracheleuglypha dentata*, triarc – *Trigonopyxis arcula*, trimin – *T. minuta*, tricom –
Trinema complanatum, trienc – *T. enchelys*, trilin – *T. lineare*. Other abbreviations: *Bryum*
pseudotr. – *Bryum pseudotriquetrum*, Herbs – unidentified herbs.

Fig. 5. NMDS scatter plot showing the correspondence between human activity and changes in woodlands (main taxa; reconstructed from palynological and micro- and macrocharcoal data; Czerwiński et al., in review) and TA. Note that the thickness of lines expressing vectors reflects the p-values. Abbreviations: copr. fungi – coprophilous fungi, MAC – macrocharcoal accumulation rate, MIC – microcharcoal accumulation rate. TA abbreviations as in Fig. 4.

Fig. 6. The rich to poor fen transformation in the light of TA indicators across climate and human impact changes.

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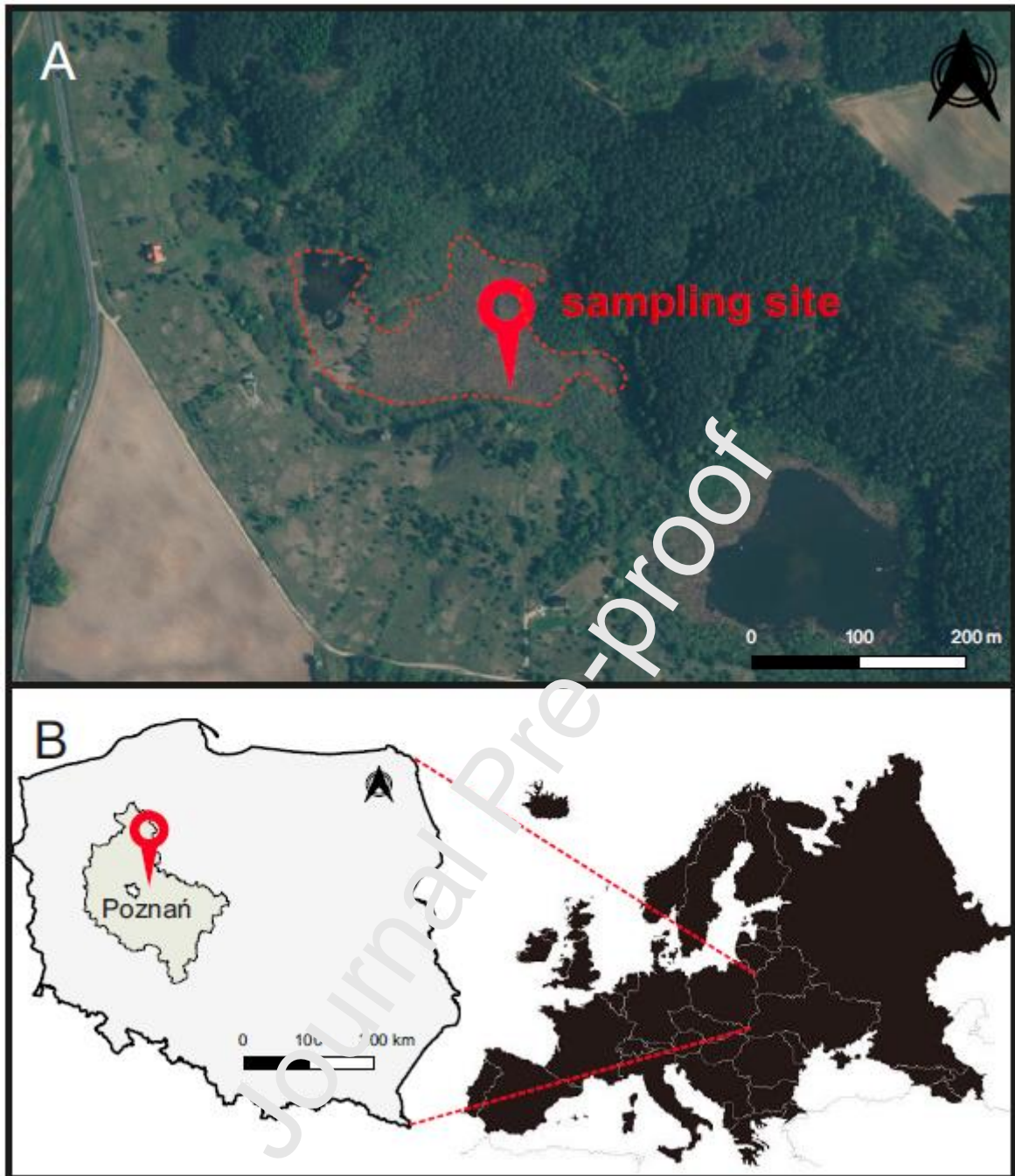


Figure 1

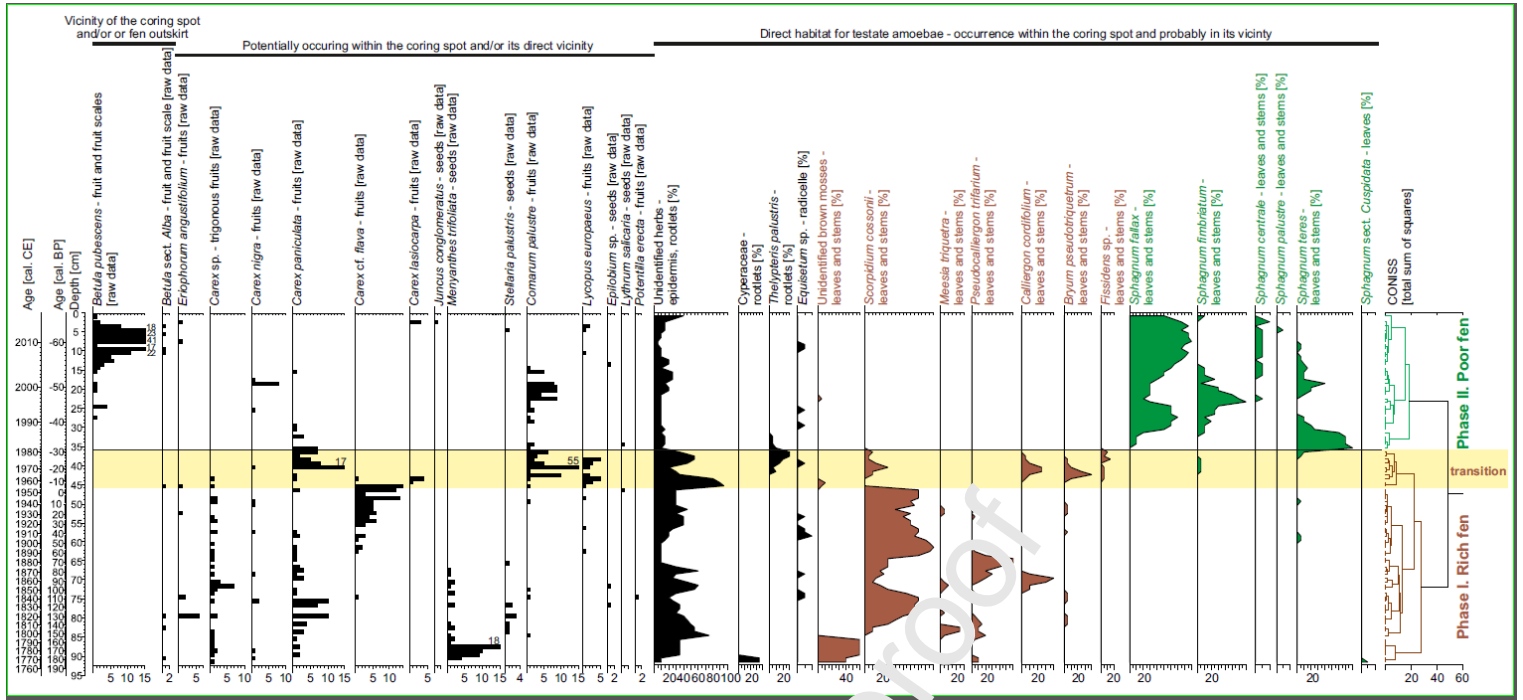


Figure 2

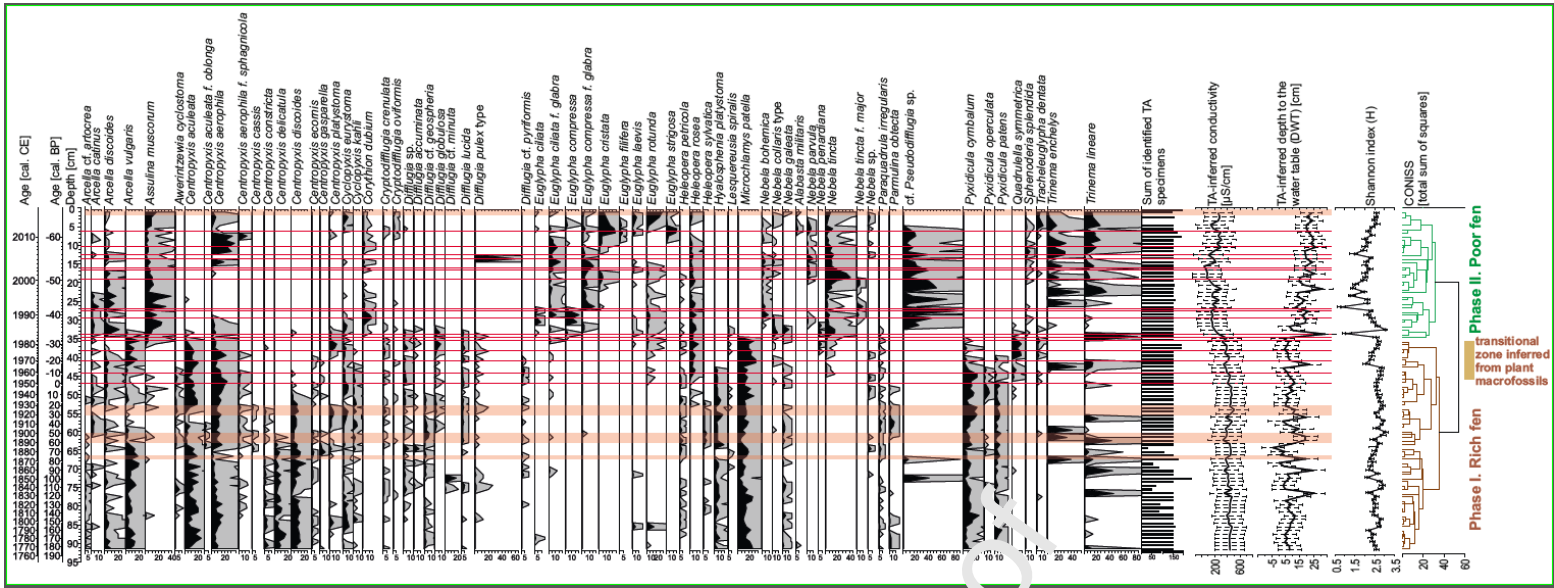


Figure 3

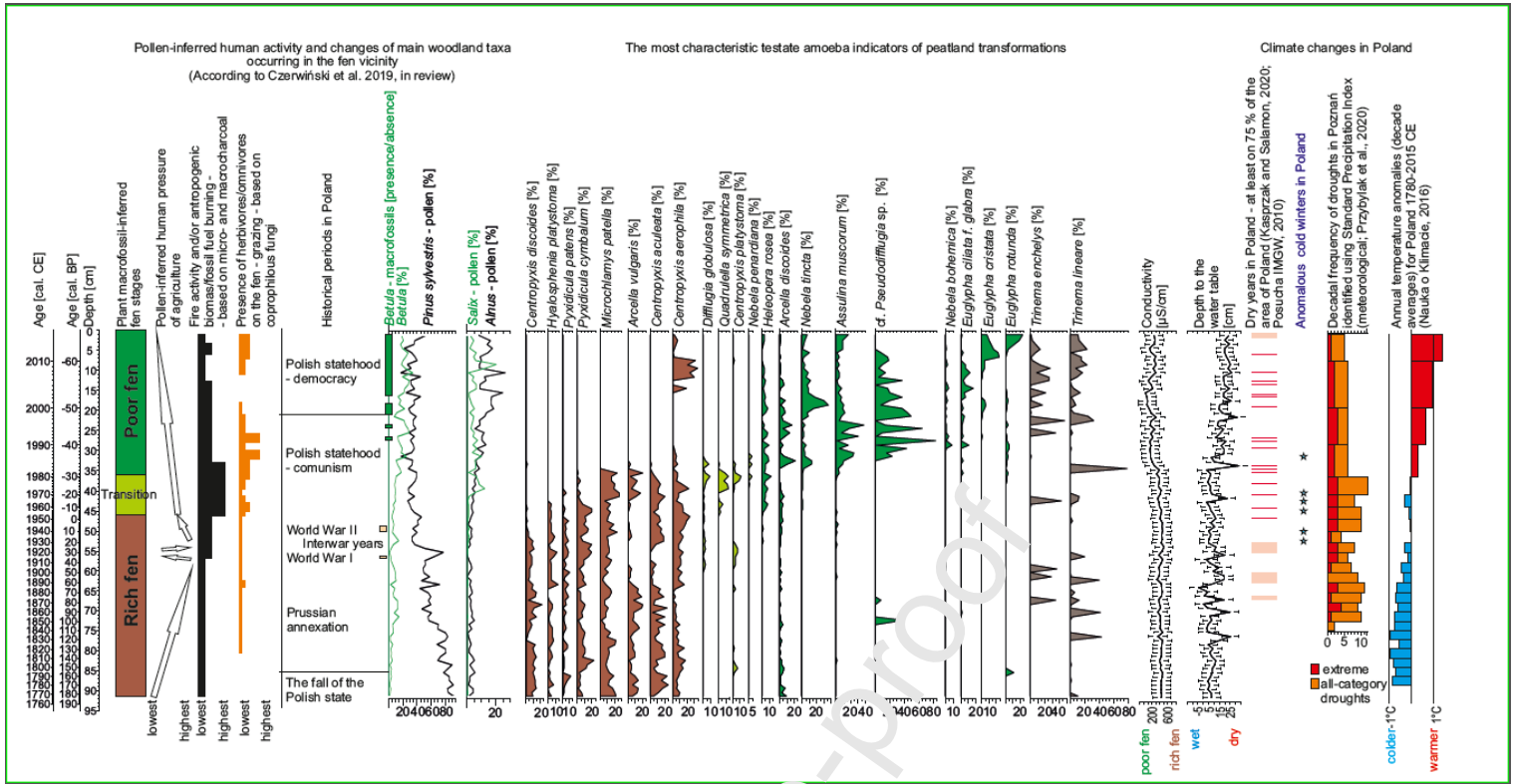


Figure 6

Author contributions: PK, MG and ML made the fieldwork, whereas SC subsampled the core; MKK performed the testate amoebae analysis; MG performed the plant macrofossil analysis; PK, SC and ML performed the statistical analyses; MKK wrote the draft version of the manuscript; MKK, PK, SC, MG and ML edited the final version of the manuscript. SC prepared Fig. 1, whereas PK and MKK prepared other figures and supplementary materials; PG provided funding for the research

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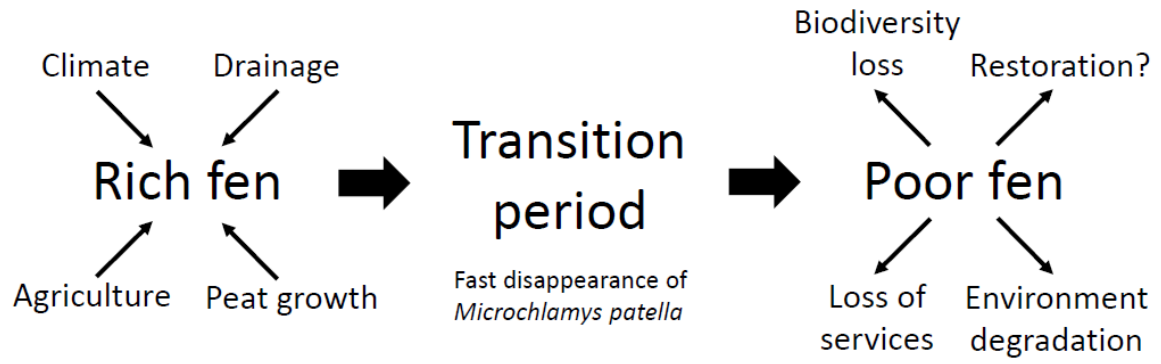
Declaration of interests

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests:

Mariusz Lamentowicz reports financial support was provided by National Science Centre.
Piotr Guzowski reports financial support was provided by Polish Ministry of Science and Higher Education.

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Graphical abstract

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Highlights

- Multi-proxy study on the rich fen - poor fen transition during the Anthropocene
- New high-resolution data on testate amoebae from fens in Central Europe
- Human activity and global warming as the main drivers of rich-fen loss
- Long-term palaeoecological record for ecological restoration
- Testate amoeba as susceptible indicators of rich fen degradation

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