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How far from a pristine state are the peatlands in the Białowieża Primeval Forest (CE Europe) – Palaeoecological insights on peatland and forest development from multi-proxy studies

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ABSTRACT

The Białowieża Primeval Forest is one of the most pristine forested and peatland areas in Europe, as recognized by its status as the World Biosphere Reserve. Palaeoecological analyzes offer the possibility of establishing a record of ecosystem change over time, and therefore setting reference conditions for their assessment, protection and restoration. To assess the impact of hydrological changes, fire and pollution (dust, metals from smelting) on peatland and forest ecosystems, we carried out high-resolution, multi-proxy palaeoecological investigations of two peat cores (50 cm long) from nearby locations at a peatland located in the protected area (nature reserve) of the Białowieża Forest (CE Poland). Our study revealed that: i) between about 1780 and 1920 CE high fire activity likely caused by humans led to a partly decline in dwarf shrubs at the sampling sites; ii) between about 1910 and 1930 CE distinctive changes in local and regional plant succession took place that can be considered as a sign of disturbance in the peatland ecosystems; iii) during the last three decades we recorded a recent decrease of trace metals and pollen indicating a decrease in human activity. These changes are synchronous with a decrease of industrial activity and curbing of emission through legislation as well as the ongoing depopulation of villages in E Poland that started in 1990.

Our data suggest that even well-preserved peatlands, located in protected areas might be far from their pristine state, predominantly due to disturbance effects from the past still lingering on. Nevertheless, the studied area remains one of the best-preserved forest ecosystems in Europe, despite the negative impact of human activity (deforestation, fires, hunting) over the past few centuries.

1. Introduction

The gradual development of agricultural and industrial activity since the Middle Ages in Europe was accompanied by a gradual decrease in forest areas and wetlands (Kaplan et al., 2009; O'Sullivan, 2013). The improvement of climatic conditions (increase of temperature) and changes in the organization of human communities (the tribe-to-state transition) in the Middle Ages led to the fragmentation of forest complexes, some of which were converted into agricultural lands (Hademann, 1939). Initially, only forests growing on fertile soils were cut down. As these fertile lands became scarcer, with the simultaneous growth of human population and demand for products obtained from forests (e.g. wood as a building material and charcoal, potash, tar, honey), as well as an increased demand for cereals, also drainage of less fertile areas including wetlands was taking place. As a result, in Central Europe only a few areas of the old grown forests dominated by

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deciduous trees (oak, beech and hornbeam) and swamps which most often developed in river valleys and fossil lakes (cf. terrestrialisation) have retained their pristine character.

The Białowieża Primeval Forest (BPF) located on the Polish-Belarusian border, despite some human disturbances over the last few centuries, can still be considered one of the best-preserved, near-pristine forest complexes in Europe (Faliński, 1986). Thus, Białowieża National Park was included in the World Biosphere Reserves of UNESCO in 1977. As shown by palaeobotanic studies carried out in various parts of eastern Poland, the development of the forest ecosystems in the BPF in the past (from the early Holocene to the Medieval Period) did not differ much from other forest complexes developed in the East-Central European Lowlands (Bałaga, 1990; Kuprianowicz, 2007, Milecka et al., 2009; Wacnik, 2009; Gałka et al., 2014, Latałowa et al., 2016). Former pollen studies (cf. Milecka et al., 2009; Mitchell & Cole 1998; Latałowa et al., 2016; Jaroszewicz et al., 2019) suggested that human activity has been limited in this area. Several historical factors have led to the preservation of this area. The first relates to the predominance of poor soils that hindered the development of major tribal populations and the transformation of this area into arable fields before the 15th century (Kossak, 2016). In contrast to other parts of western and central Poland (e.g. Greater Poland or Kuyavia), where deforestation took place before the 10th century (Czerwiński et al., 2021; Lamentowicz et al., 2019a), human pressure on ecosystems in eastern Poland started only in the 14th century or later (Wacnik et al., 2016; Kinder et al., 2019; Marcisz et al., 2020). The second factor is associated with the presence of a vast swamp and wetland area that was difficult to safely explore, drain and adapt for agriculture. Finally, the third factor for the good preservation of BPF area is its protection by the Polish kings since the 16th century as an area of military and recreational importance e.g., for hunting to obtain the meat for war campaigns and as an entertainment activity (Hademann, 1939). Hedemann (1939), Samojlik & Jędrzejewska (2004), and Kossak (2016) have revealed that in the period from the 16th to the end of the 19th century, despite many restrictions imposed on the use of the forest, activities were conducted in the form of logging, hay collection, grazing cattle and pigs, and hunting for animals. The first drainage works were carried out to transport wood via the local rivers e.g. since 1780 through the water trail: Narewka-Narew-Wisła-Gdańsk (Hedemann, 1939). Moreover, from the 16th century, the Białowieża Primeval Forest was detached from other forest complexes, such as Świslocka Forest, Czarnoloska Forest, Szerszewska Forest, and the Kamieniecka Forest, and was surrounded by villages and agricultural lands (Hedemann, 1939; Samojlik & Jędrzejewska, 2004). In the period from the 19th to the 20th century, when these areas were occupied by Russia (1797–1915) and Germany (1915–1919), the forest was subject to planned logging, including a railway line built for wood export. Since 1925, a part of the best-preserved forest was protected and the Białowieski National Park was created. Within this National Park framework, many areas were further protected as natural reserves. However, until now in most of the forests in the Białowieża Primeval Forest, the logging continues.

A vast area of the BPF is covered by peatlands that are suitable to serve as important archives of environmental and climate changes, as well as human activity (cf. Barber, 1981; van der Linden & van Geel, 2006). Palaeoecological analyzes offer the possibility of determining the state of ecosystems and setting reference conditions for their current assessment, protection and restoration (Chambers et al., 2013; McCarroll et al., 2017). Moreover, analyzing peat profiles allows for a better understanding of how peatland environments might respond to future climate change, human activity, and changing forest cover (Mauquoy & Yeloff, 2008), and thus define baselines for nature conservation planning and protection of those valuable ecosystems (Velsecchi et al., 2010; Hennebelle et al., 2018). Palaeoecological studies can also elucidate if the protected site, such as peatland, is close to its pristine state or if the protection status was established on an already disturbed/transformed site (Milecka et al., 2017; Czerwinski et al., 2021).

In our study, we applied high-resolution multi-proxy palaeoecological analysis to two peat cores from the Berezowo Nature Reserve (115 ha) in the BPF, to track the human impact on peatland and forest ecosystems and to determinate their ecological state. Unlike previous palaeoecological research (cf. Milecka et al., 2009; Mitchell & Cole, 1998; Latałowa et al., 2016), we took the peat cores outside the Białowieski National Park, in the south-eastern part of the BPF. Along the south-eastern border of the BPF, settlement activity was the most intense and from the 16th century many villages were located there (Hedemann, 1939). Because of this, we expect that the pressure on forest and wetlands ecosystems in this part of the BPF had been recorded in the peat stratigraphy. We hypothesize that increased human pressure included hydrological changes (decrease of water level depth with subsequent increase of decomposition), deposition of pollutants and increased fire activity across the peatland surface that caused changes in habitat conditions, which led to concomitant shifts in plant and testate amoeba populations. Specifically, we anticipate the appearance of moss species that may occur in minerotrophic habitats (e.g. *S. fallax*) and those associated with displacement of more ombrotrophic species (e.g. *Sphagnum medium*, in the past referred to as *Sphagnum magellanicum*, cf. Laine et al., 2018) following the habitat changes. Our aims are to: i) reconstruct local and regional vegetation changes during the last 250 years covering periods of increased human activity; ii) evaluate the influence of the pollution on the development of peatland communities, especially mosses; iii) explore fire activity and vegetation feedback to fire activity. To have better representativeness and insight into the succession of local vegetation, we analyzed two peat cores. Due to the highly decomposed lower peat layer, what might have led to selective preservation of plant and testate amoebae remains and consequently wrong paleoecological interpretations, we analyzed only upper 50 cm thick peat cores.

2. Materials and methods

2.1. Study site

The Berezewo reserve (115.26 ha, coordinates: 52°38′44″N 23°41′37″E) is located in W Poland and is included in the Białowieża Primeval Forest (Fig. 1). It was founded in 1995 to protect a fragment of the Białowieża Primeval Forest with specific habitats hosting a relict fauna of butterflies. Most of the reserve is a mixed forest with the dominance of *Picea abies, Pinus sylvestris, Tilia cordata, Carpinus betulus* and *Quercus robur*. The depressions of the terrain are filled with peat deposits up to 100 cm thick, highly decomposed in the lower part. As one of such peat deposits, the studied peatland is dominated by *Sphagnum fallax, Oxyccocus palustris, Eriophorum vaginatum* and *Pinus sylvestris*. The climate of the Białowieża Primeval Forest is classified as temperate continental, cool with the influence of Atlantic climate. The average annual air temperature (1991–2021) was 8.2 °C and the average amount of rainfall was ca. 710 mm per year (https://pl.climate-data.org/europa/polska/podlaskie-voivodeship/bia%c5%82owieza-215200/ accessed on June 23, 2022).

2.2. Core collection and chronology

Two peat cores Ber I and Ber II (each 100 cm long) were sampled using a Russian type peat corer (length 50 cm, diameter 10 cm) in autumn 2015. The replicate peat profiles were retrieved ca. 50 m apart in similar plant communities formed by *Sphagnum fallax* and *Eriophorum vaginatum*.

Eight AMS radiocarbon dates (four per each core) and ^{210}Pb analysis were used to establish age-depth models. Radiocarbon dating was obtained based on terrestrial plant macrofossils provided by the Poznań Radiocarbon Laboratory (Poland, Table 1). Lead dating was carried out at the University of Exeter laboratories. The absolute chronology is based on the Bayesian age-depth model based on combined ^{14}C and ^{210}Pb dates calculated using OxCal 4.2 software (Bronk Ramsey, 1995;

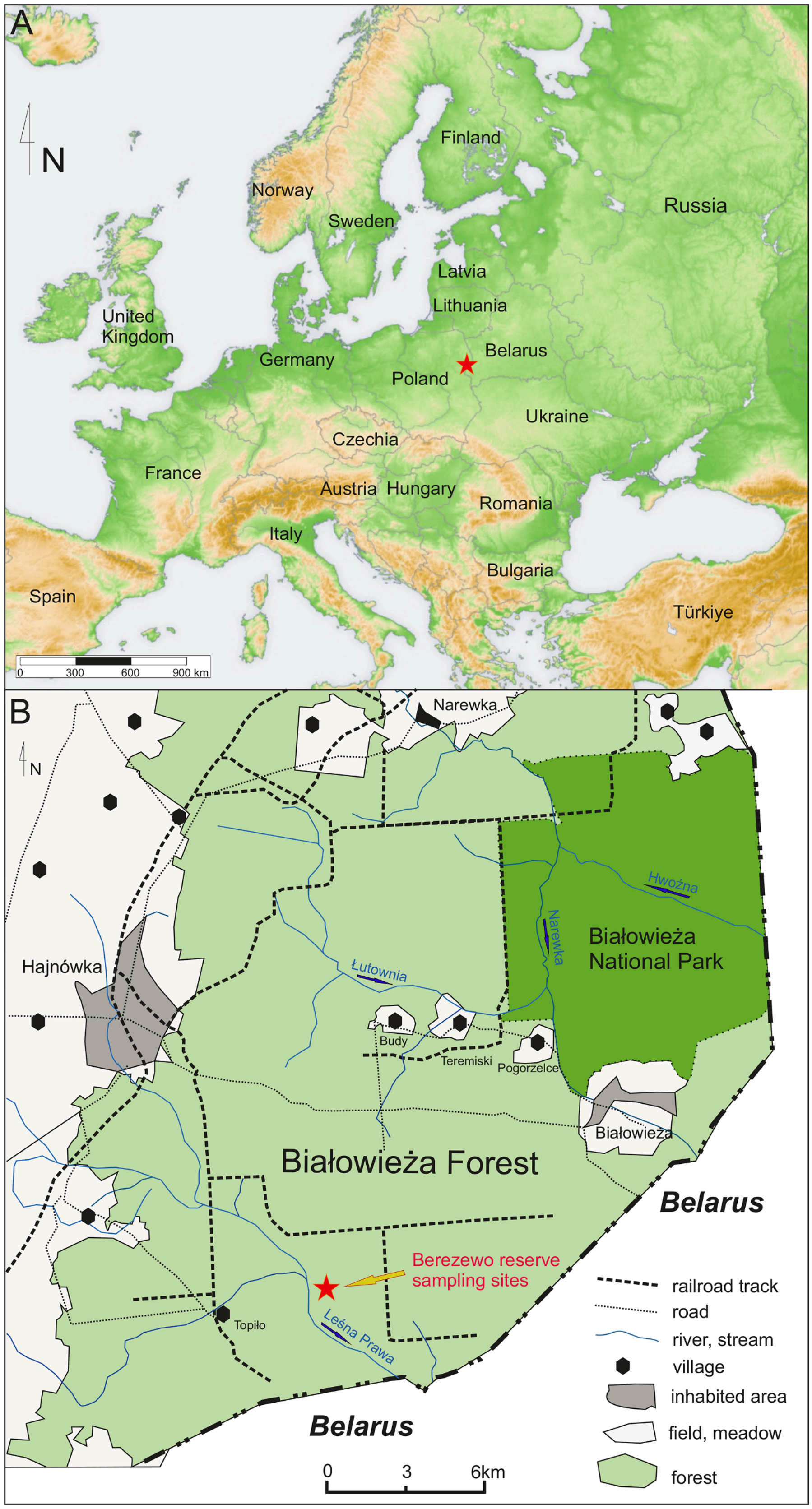

Fig. 1. Study site: A) site locations across Central Europe (source https://commons. wikimedia.org/wiki/File:Europe _topography_map.png Author: San Jose; modified); B) location map of the study site in Poland.

2008; *P_Sequence* function, model parameters: $k_0 = 1$, $log_{10}(k/k_0) = 2$, and *interpolation* = 1 cm). As the calibration set, we used IntCal20 (Reimer et al., 2020) and post-bomb NH1 (Hua et al., 2021) atmospheric curves. In the following sections of this article, μ (mean) values were selected to reflect the modelled age and was expressed as ca. date 'CE', in which 'CE' means 'Common Era'.

2.3. Vegetation development

2.3.1. Plant macrofossils analysis

The analysis of plant macrofossil remains provides a record of local plant communities and along time (Mauquoy et al., 2008; Gałka et al., 2015, 2017). Plant macrofossils were analyzed mainly contiguously at 1-cm intervals on cores BerI and BerII, resulting in total sum of 95 samples. Samples of 20 cm^3 volume were washed and sieved under a warm-water spray using a 0.20-mm mesh sieve. Initially, the entire sample was examined with a stereomicroscope to obtain volume percentages of individual subfossils of vascular plants and mosses. The subfossil carpological remains and vegetative fragments (leaves, rootlets, epidermis) were identified using identification keys (Smith and Smith, 2004; Mauquoy and van Geel, 2007). At some depths of the peat profile, *Sphagnum angustifolium* and *Sphagnum fallax,* as well as *S. medium* and *S. divinum,* were reported together due to the difficulty in separating these two species in the fossil state, which is caused by similar morphology of branch leaves and little presence of stem leaves (Hölzer, 2010).

2.3.2. Pollen analysis

Pollen analysis provides information on vegetation composition and abundance at a regional and local scale (Berglund & Ralska-Jasiewiczowa, 1996). The pollen analyses, on 45 samples from core BerII, was performed mostly at 1-cm resolution. Pollen were not counted in samples at depths: 0.5, 2.5, 4.5, 6.5, 8.5 cm. For the pollen studies, 1 cm^3 of peat were used. Each sample was acetolysed following the modified Erdtman method with an addition of hydrofluoric acid (Fægri & Iversen, 1989). Pollen grain and spores were identified with the use of specific keys and atlases, particularly Beug (2004). About 500 arboreal (AP) and non-arboreal pollen (NAP) taxa grains per sample were counted. Percentage values of pollen and spores in individual spectra were calculated based on particular taxa values concerning the total pollen number (TPS = AP + NAP), excluding local taxa (cryptogams, limnophytes, telmatophytes and Cyperaceae). Based on plant indicators we estimated human activity in the area. Summary curves were made for human activity (anthropogenic) indicators distinguished according to Behre (1981), as well as following van der Linden and van Geel (2006). The indicators of human activity include presence of *Artemisia, Centaurea cyanus,* Chenopodiaceae, *Plantago lanceolata, Rumex acetosa/acetosella* type, *Secale cereale*, *Triticum* type, *Fagopyrum esculentum* type and Cerealia type.

2.4. Macro-charcoal analysis

45 peat samples from core BerII were prepared for macroscopic charcoal analyses following standard methods described by Whitlock and Larsen (2001). Charcoal particles were analyzed using a stereomicroscope under a 40 magnification and divided into two size groups: 100–500 μm and > 500 μm. Macroscopic charcoal influx or accumulation rates (MAC, particles / cm^2 / year) were calculated by multiplying macroscopic charcoal concentrations by the peat accumulation rate (PAR; unit cm / year) inferred from the age-depth model. Macroscopic charcoal is a proxy for local fire activity (Conedera et al., 2009), especially particles > 600 μm provide best evidence for local fire occurrences (Adolf et al., 2018).

2.5. Testate amoebae

We used subfossil testate amoebae (Protists) on core BerII to examine hydrological changes through time (Mitchell et al., 2008). 26 samples from core BerII were analyzed. Peat samples were washed under 0.3-mm sieves following the method described by Booth et al. (2010). Testate amoebae were analyzed under a light microscope with 200 × and 400 × magnifications, aiming at a minimum of 150 tests per sample (Payne and Mitchell, 2009). Several keys and taxonomic monographs (i.e. Ogden and Hedley, 1980; Mazei and Tsyganov, 2006; Siemensma, 2021) were used to achieve the highest taxonomic resolution.

The results of the analysis were used to obtain a quantitative depth-to-water table (DWT) reconstruction. The results of the analysis were used to obtain a quantitative depth-to-water table (DWT) reconstruction expressed in cm below the ground. Quantitative palaeohydrological reconstruction was performed using the regional calibration data set (Lamentowicz and Mitchell, 2005) using the transfer function approach with the tolerance downweighted weighted averaging model (Juggins and Birks, 2012).

2.6. Geochemical analysis

Geochemical analyses of the peat samples at core BerI were used to reconstruct pollution and element input by atmospheric deposition (e.g. dust) and to quantify nutrient contents and peat decomposition (in terms of C/N ratios) over the last ca. 350 years. C and N concentrations as well as the stable isotopic composition were determined by elemental analysis coupled to an isotope ratio mass spectrometer (EA-IRMS; EA 3000, Eurovector, Pavia, Italy; NU Horizon, NU Instruments, Wrexham, UK). To this end, aliquots of 3–4 mg of bulk peat were weighed into tin capsules and analyzed via catalytic combustion. Calibration was done using certified standards and reference materials. Further peat sample total element concentrations (Al, Ba, Br, Ca, Cr, Cu, Fe, K, Mg, Mn, Na, P, Pb, Rb, S, Si, Sr, Ti, Zn) were determined on 500 mg of dried, ground bulk peat material (pressed to 13 mm sized pellets) through non-destructive X-ray fluorescence spectroscopy (ZSX Primus II wavelength dispersive X-ray fluorescence spectrometer, Rigaku, Tokyo, Japan), calibrated for peat and plant material using certified peat and plant reference materials.

2.7. Statistical analysis and data presentation

The results are presented in the form of diagrams of plant macroremains, pollen, testate amoebae and geochemical data (Figs. 2–5), which were prepared with the computer program *C*2 (Juggins, 2003). The quantitative reconstruction of water-table changes (DWT) based on testate amoebae was conducted with *C*2 software (Juggins, 2003) using the training set (containing 123 samples) developed for northern Poland by Lamentowicz and Mitchell (2005) and Lamentowicz et al. (2008). Non-metric Multidimensional Scaling (NMDS) was used to assess the relationship between local (based on plant macrofossils) and regional (based on pollen) vegetation change and water table changes (DWT) and fire activity (CHAR) in the BerII profile (App. 1). The analyses were performed in R Statistical Software (R Core Team, 2020) using the package 'vegan' (Oksanen et al., 2017).

3. Results

3.1. Chronology

The sequences of ^{14}C and ^{210}Pb dates revealed good agreement index opf model (fitness of modelled dates to calibrated ones) in both profiles (App.1, Fig. 2). No hiatus was detected in either peat core analyzed. Both age-depth models revealed reliable agreement indexes (A_{model}) i.e. higher than 60 % (cf. Bronk Ramsey, 2008; Fig. 2). Based on them the BerI core spans the last ca. 250 years (between 1780 ± 13 and 2015 CE)

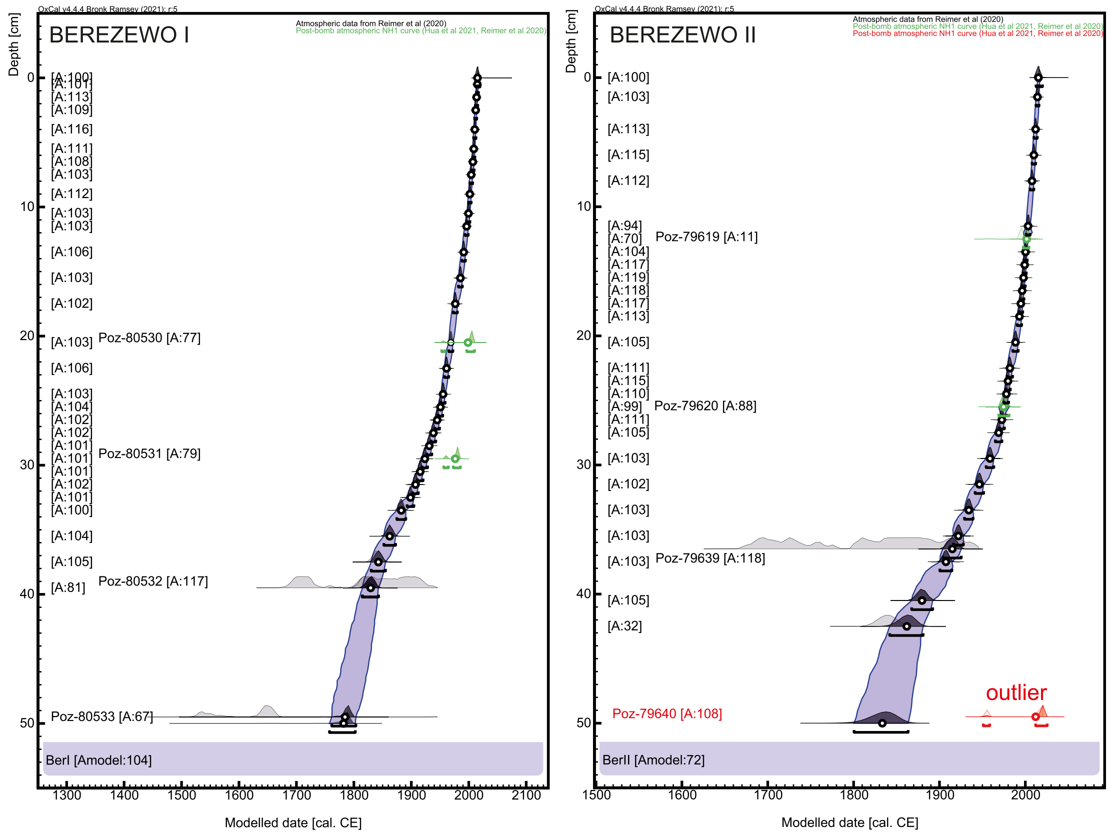

Fig. 2. Bayesian age-depth models for the peat profiles Ber I and Ber II.

and the core BerII spans the last ca. 200 years for (between 1830 ± 15 and 2015 CE).

3.2. Local plant succession

Analysis of both cores reveal a similar pattern of plan succession (Fig. 3A and 3B). In the most bottom part of peat profiles BerI and BerII *Sphagnum medium/S. divinum* and *Eriophorum vaginatum* are the dominant species. *Andromeda polifolia* is also present in both cores and *Pleurozium schreberii* in core BerII. From ca. 1900 *Sphagnum fallax* is a dominant species. Numerous *Pinus sylvestris* macroremains (needles, bud scales) are also present in both cores.

3.3. Macro-charcoal records

Numerous macro-charcoal pieces (also > 0.5 cm) were recorded in both cores between ca. 1780 and 1930 CE. Since ca. 1930 CE only limited macro-charcoal pieces were documented (Fig. 3B).

3.4. Forest succession and human impact indicators

Between ca. 1830 and 1920 CE *Pinus sylvestris* (up to 70 %) and *Betula* (up to 21 %) were dominant tree species based on abundant pollen (Fig. 4). Shares of *Picea abies* and *Quercus* pollen fluctuated slightly between 3.5 and 9 % and between > 1 and 3 %, respectively. During this period, the almost permanent presence of rye (*Secale cereale*) pollen and periodical presence of *Plantago lanceolata* and *Centaurea cyanus* pollen were recorded. The period between ca. 1920 and 1980 CE are characterized by the highest contribution of *P. abies* (up to 16 %) and *Quercus* (up to 4.3 %) pollen in the entire studied period. Moreover, *Triticum* type pollen appeared the first time and Ericaceae undiff., *Vaccinium* group, reached the highest pollen abundance (up to 2.6 %).

Between ca. 1920 and 2002 CE, a decrease of *Quercus, P. abies* and cultivated plants (*S. cereale, Triticum* type) pollen is documented. From ca. 2002 to 2015 CE the lowest counts of *Betula, Quercus, P. abies* as well as cultivated plants and local plants (mainly Ericaceae) were recorded.

3.5. Testate amoebae and hydrological changes

Between ca. 1830 and 1920 CE the water table level in the peatland was low (reaching a minimum at 32 cm below peatland surface) but with a rising trend (Fig. 5). The testate amoeba communities were dominated by dry indicator species (*Cryptodifflugia oviformis, Alabasta militaris, Nebela parvula*) and *Arcella discoides,* an indicator of hydrological instability (Lamentowicz and Mitchell, 2005).

Between ca. 1930 and 1970 CE water level stabilized at ca. 12 cm below the peatland surface with the highest abundance of *A. discoides, Assulina muscorum*, and *C. oviformis*. Stable water levels (ca. 10 cm below surface level) were also observed in the period between ca. 1970 and 2004 CE, when dominant testate amoebae were *A. discoides*, *C. oviformis, A. militaris, N. parvula, Heleopera sylvatica* and *Physochila griseola.* Since ca. 2004 CE, the dominant species *A. discoides* points to larger water table fluctuations. Water level depth in this phase first increased to 2 cm and then decreased again to 14 cm below ground, suggesting a rapid drying of the site.

3.6. Geochemical characterization

Geochemical data from core BerI were visually divided into four zones (Fig. 6). The zone between ca. 1780 and 1810 CE is characterized by low concentrations of Na, Si, S, Mn, and P. Between ca. 1810 and 1860 CE the highest concentrations of Na, Si, Cl, Al and Ti are recorded, coinciding with the low water table levels as derived from testate amoebae. The period between ca. 1860 and 2000 CE is distinguished by slight fluctuations in the concentrations of almost all elements and variations in stable isotopes N and C, along with more stable

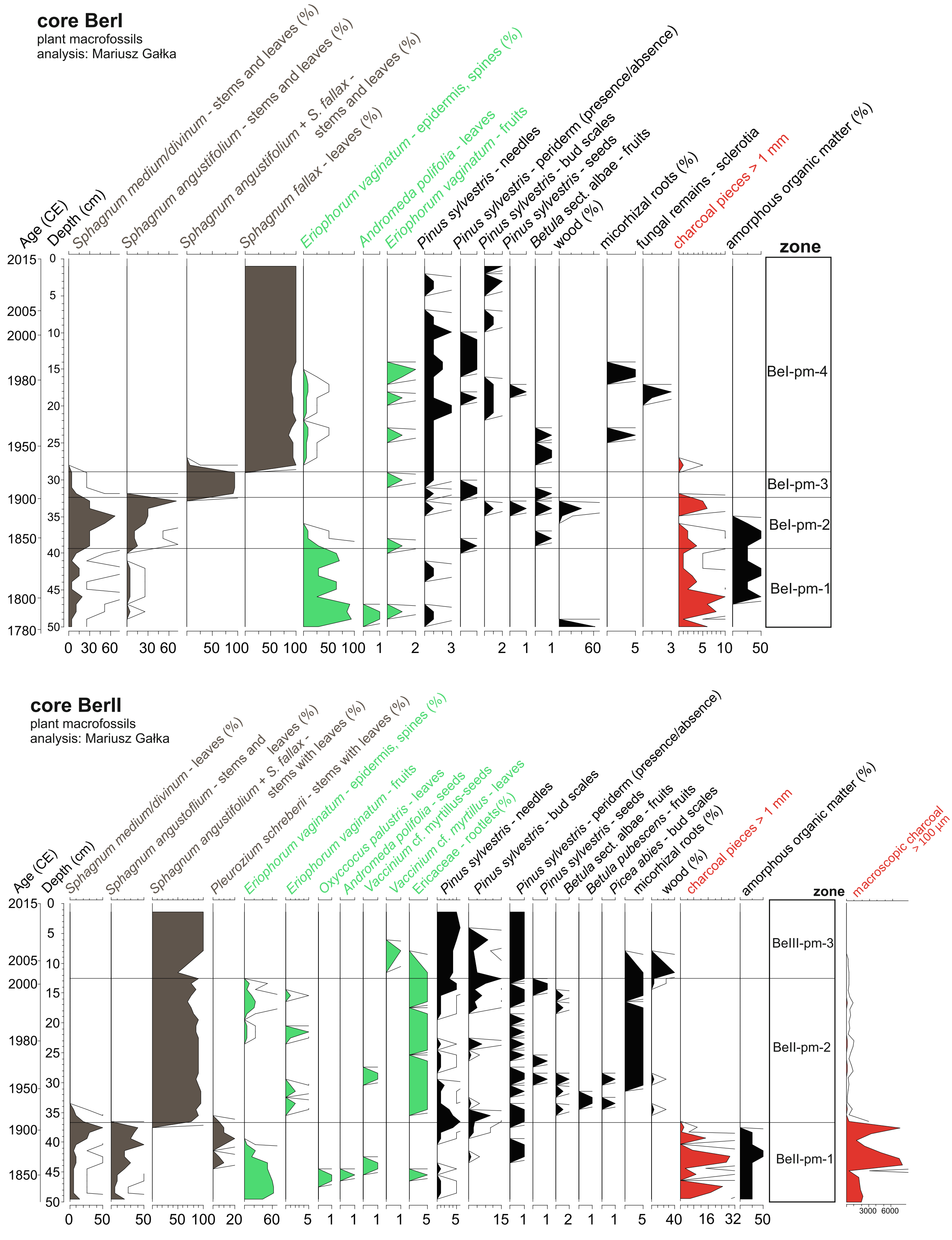

Fig. 3. Plant macrofossil diagram presenting local vegetation development in Berezewo peatland. Core Ber I and core Ber II. Taxa with '%' are estimated volume percentages, the others are counts (note scale differences on the x-axes). Core Ber II, macroscopic charcoal > 100 µm. The white areas outlined by curves represents percentage values magnified by 5.

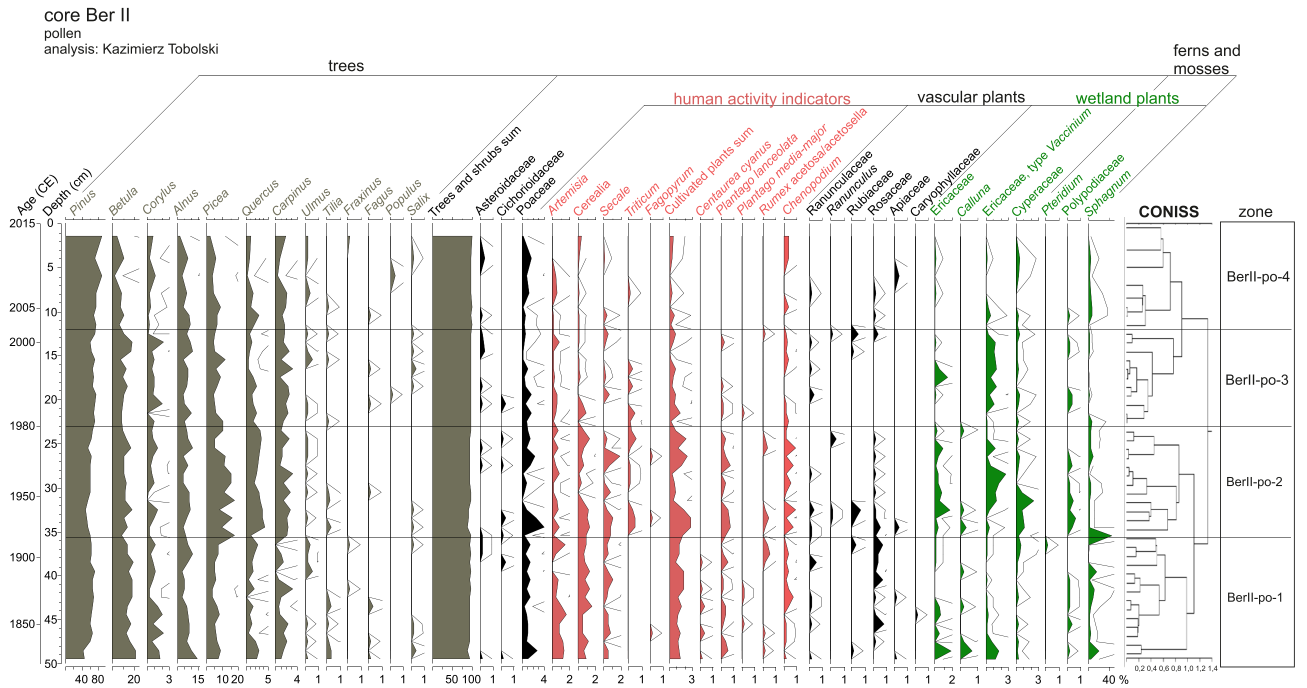

Fig. 4. Pollen diagram presenting regional and local plant succession, core BerII. The white areas outlined by curves represents percentage values magnified by 5.

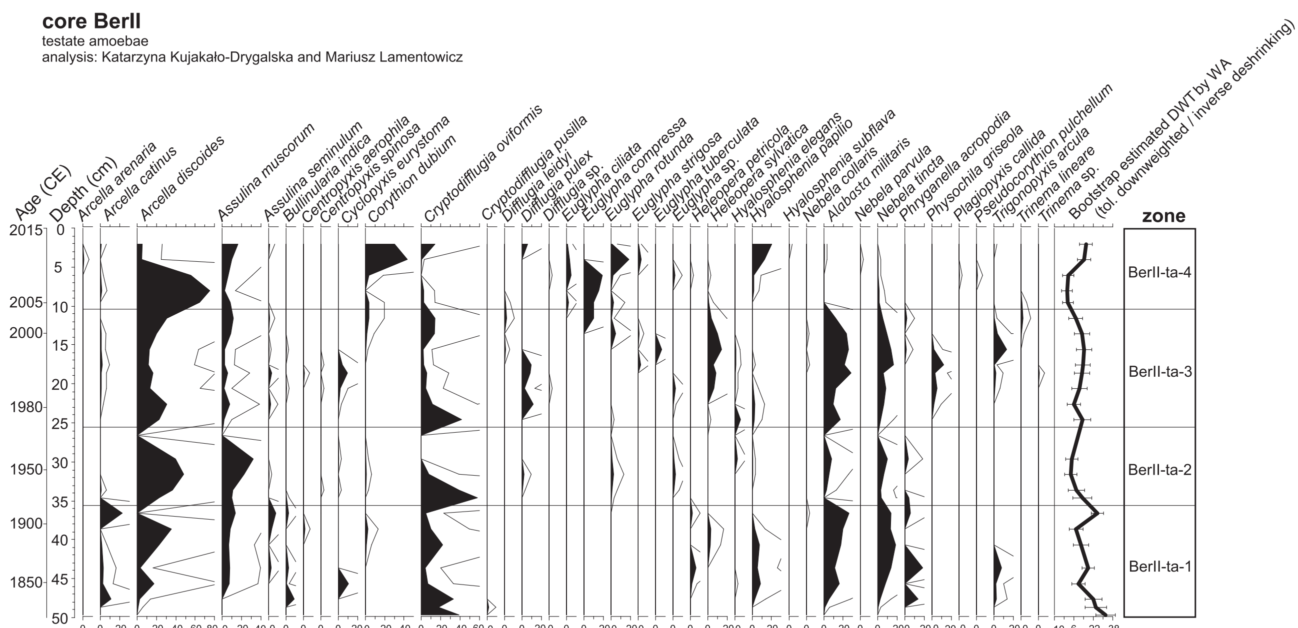

Fig. 5. Testate amoebae relative abundance from Berezewo peatland, core BerII. The white areas outlined by curves represents percentage values magnified by 5.

hydrological conditions.

Nevertheless, Fe, As, Pb reach highest levels in this period. The C/N ratio is overall decreasing with depth and low C/N ratios at greater depth correspond with the more decomposed peat at the basis and during phases of drought. Since ca. 2000 CE we record a decrease of trace metals such as Al, Pb, As, Fe and depletion of heavier stable isotopes of C and N (more negative values) as well as an increase of elements such as Ca, Mg, Mn, along with the most recent drying of the site. Also, C/N ratios tend to decrease again near the surface. N/P ratios consistently increase with depth, ranging from 11 to 12 in the uppermost depths to 30–38 at 40–50 cm depth.

3.7. Statistical analyses

Both non-metric multidimensional scaling analyses NMDS were computed using Bray-Curits distance and Wisconsin square root transformation. Both 2-dimensional solutions had low-stress values (see App. 2). Out of two analyzed disturbance variables, both regional and local vegetation changes were correlated to water table changes rather than to fire activity (App. 2). However, the effect of both water table changes and the fire was stronger for peatland vegetation (local) than for the forest composition (regional). Lower water tables and recorded fire activity (expressed in higher charcoal values) were related to habitats dominated by *S. medium/divinum* and *Pleurozium schreberi*. On the

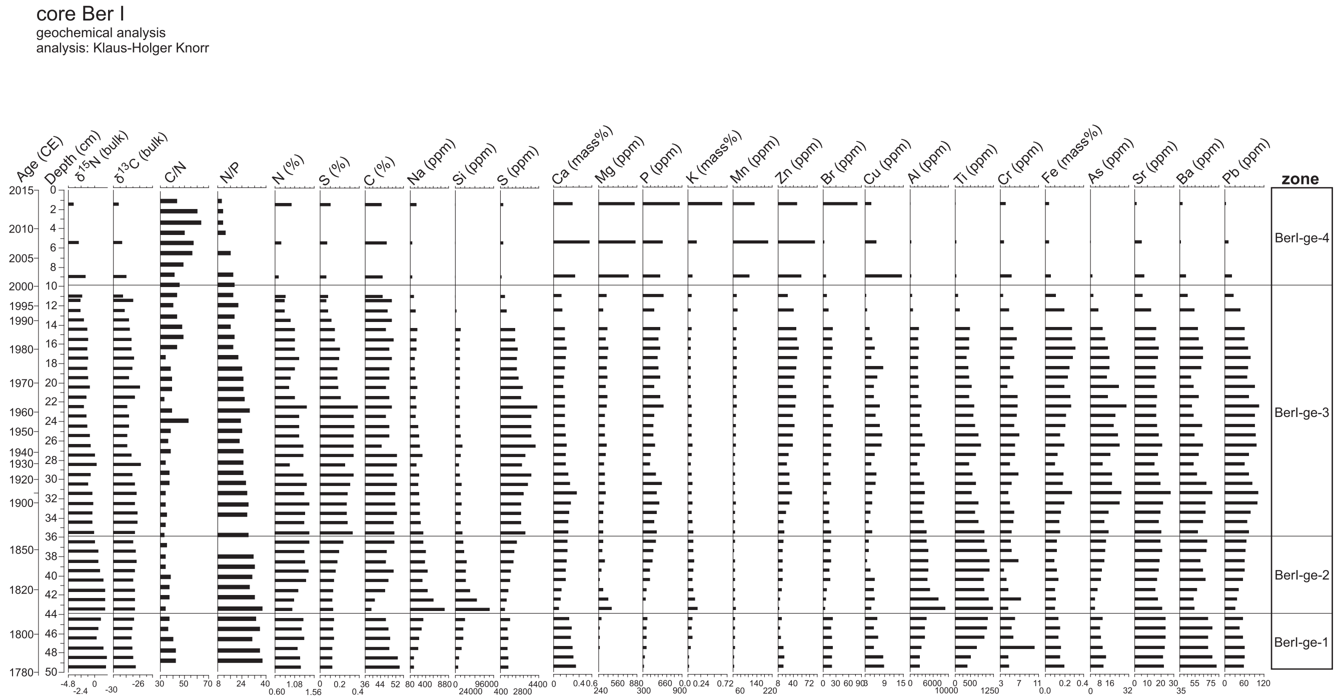

Fig. 6. Selected results of the geochemical analysis of Berezewo peatland, core Ber I.

regional scale, samples with higher charcoal sums were related to open habitats dominated by ruderals and cultivated land species (but these relations were statistically less significant than for the local taxa) (App. 2).

4. Discussion

4.1. Peatland and forest development vs human impact

Based on our palaeoecological studies two main stages of the peatland and the forest development in the Berezewo nature reserve were distinguished (Fig. 7).

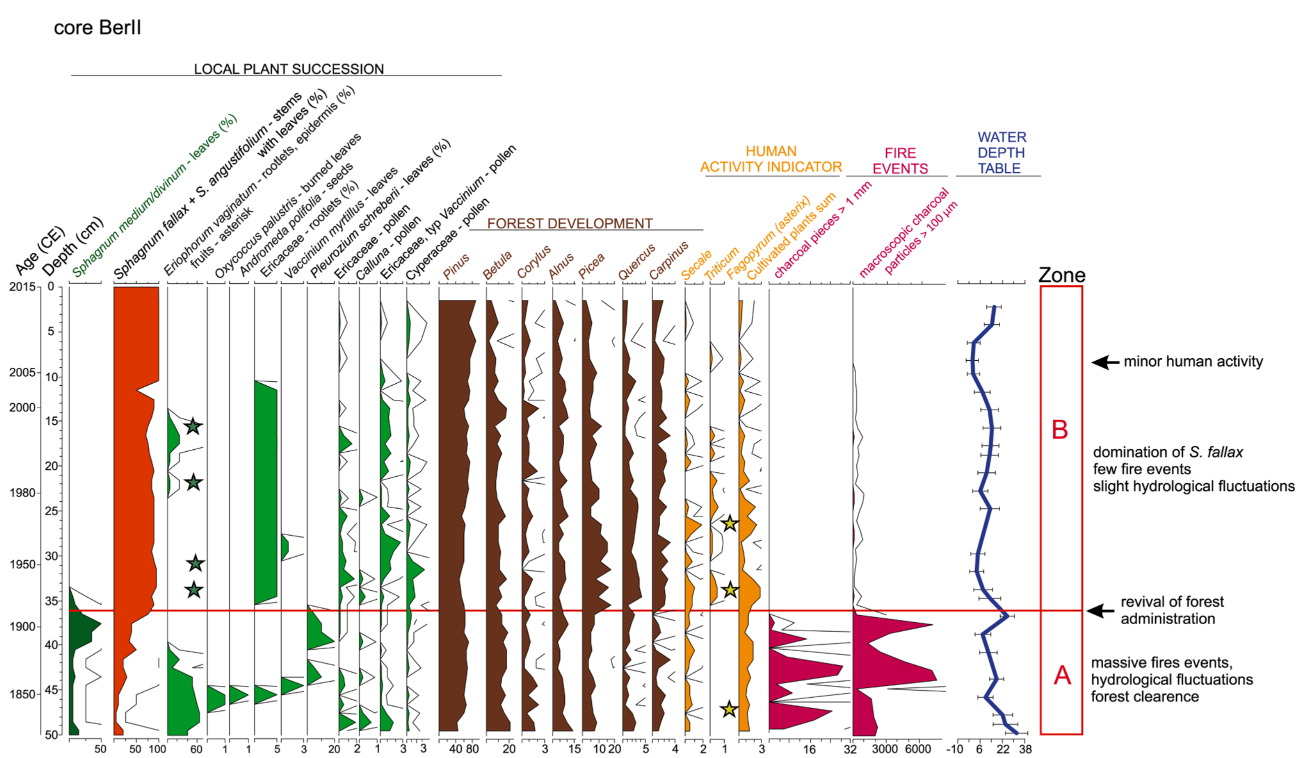

Fig. 7. Comparison of chosen taxa from plant macrofossils, pollen, water depth level, macrocharocal in the Berezewo peatland, core BerII.

4.1.1. Stage a (core BerI ca. 1780–1920 CE and core BerII ca. 1800–1920 CE).

At both sites, *Sphagnum medium/divinum* (*S. magellanicum*) along with *Sphagnum angustifolium* and *Eriophorum vaginatum* were the dominant species. The presence of these plant communities indicates oligotrophic conditions with only limited impact of minerogenic or nutrient-enriched water input. This is corroborated by low to moderate concentrations of minerogenic elements (Mg, Ca, P). In paleoecological records from CE Europe, *S. medium/divinum* and *S. angustifolium* are usually found in the transitional zone between rich-fens and bog ecosystems where they played a role as the main peat-forming species (Gałka et al., 2015, 2017). In addition, *E. vaginatum* usually expanded in the peatland during hydrological disturbances (usually lowering of water level) (Silvan et al., 2004; Lavoie et al., 2005; Gałka et al., 2016). At site BerII, we document water level fluctuations between ca. 1800 and 1920 CE that ranged between 8 and 32 cm below peatland surface (Figs. 4 and 6). Periodically dry hydrological conditions led to high decomposition of the peat. Such conditions are largely supported by observed C/N ratios, as lower ratios are indicative of more decomposed peat (Biester et al., 2014) also found at these depths. Such fluctuations of water table depth have often been an effect of human activities in the peatland, such as drainage or peat extraction (Marcisz et al., 2015; Kołaczek et al., 2018). In the case of the Białowieża Forest, fluctuations of the water table depth might have been caused by drainage works that began in the 18th century and have been conducted even up to the first half of the 20th century (Hedemann, 1939; Kossak, 2016).

Furthermore, massive macro-charcoal presence (pieces > 0.5 cm) at both sites suggest that large local fire events took place during stage A. Despite the protection and numerous royal prohibitions, the Bialowieza Primeval Forest was subjected to human pressure (cf. Mitchell & Cole 1998; Latałowa et al., 2016). For example, the 18th industrial settlements of Budy, Pogorzelce and Teremiski were established inside the Białowieża Primeval Forest, and people from Mazovia (central Poland) were specially brought to BPF to work in the forestry industry (Hedemann, 1939). Charcoal burning, honey harvesting, and pastoralism led to numerous wildfires. Fire events were enhanced by militant campaigns such as the November Uprising (1830–31), The January Uprising (1863–64), the First War World (1914–1918) and the Polish-Soviet War (1919–1921). Dense forests and wetlands in this area helped to protect insurgents and soldiers, while thanks to the presence of elk, deer and bison it was possible to obtain food. Fire events were a common phenomenon at the Berezewo peatland and they played a significant role in the bog plant succession, especially on dwarf shrubs. At both sites, there are visible plant changes (in both plant macrofossils and pollen data) related to WTD changes and fire events. For example, fire might led to a decline of *Andromeda polifolia* at ca. 1790 CE at BerI, and the disappearance of *A. polifolia, Oxycoccus palustris,* and *Calluna vulgaris* at BerII around ca. 1850 and ca. 1870 CE.

However, only minor fire impacts are observed on the moss population and *E. vaginatum* (Fig. 3, Fig. 7). This is most likely due to the adaptation of these plants to surface fire and high WTD, which burns only the above-ground parts of the plants allowing them to grow back. This is the case for both moss populations (Kuhry, 1994; Tuittila et al., 2007; Magnan et al., 2012; Gałka et al., 2019) and *E. vaginatum* (Kummerow et al., 1988). The resistance of *E. vaginatum* to fire events is documented by the fact, that the highest number of charcoal pieces was found in *E. vaginatum* peat, as also documented on Scandinavian and other Polish bogs (Tuittila et al., 2007; Väliranta et al., 2007; Marcisz et al., 2019).

A certain relationship between fire events and tree development is highlighted by our results. Periodically, a decrease of *Corylus avellana* pollen is related to the highest amount of macro-charcoal (Fig. 7). *C. avellana* occupied the understorey layer that was especially vulnerable to fires. However, it cannot be excluded that a decrease of *C. avellana* pollen during the last decades of the 19th was enhanced by the increase in the number of game animals (fallow deer, red deer, elk), which took place at that time (Kossak, 2016).

In contrary to other examples from European peatlands (cf. Karofeld, 1996; McClymont et al., 2008; Gałka et al., 2019), it seems that pollutant deposition played a limited role in the local plant succession at Berezewo peatland. Between ca. 1790 and 1850 CE we noticed a higher concentration of elements (Al, Si, and Ti) possibly related to dust input (Fig. 6, cf. Biester et al., 2012; Gałka et al., 2019), but it did not trigger changes among peat-forming species. In addition, quite high values of Ti are associated with fire events (Hölzer and Hölzer, 1998). An increase in dust inputs at that time could reflect the increase in the intensity of human activity in the Białowieża Forest. An additional source of deposition of pollutants might be related to iron smelting – factories were located at the Narewka River and Niemierzanka River. This could be reflected in elevated concentrations in S, Zn, Cu, As, and Pb (Fig. 6) (Biester et al., 2012).

4.1.2. Stage B (ca. 1920–2015 CE)

Around 1920–25 CE significant changes in the peatland and forest ecosystems took place. *S. medium/divinum* and *S. angustifolium* were gradually replaced by *Sphagnum fallax,* which has remained dominant ever since. The spread of the *S. fallax* is clearly associated with a decrease in macro-charcoal (Fig. 7). Such a sharp decrease in macro-charcoal is most likely related to forest management changes that were introduced after the takeover of control over this area by the Polish forest administration after the First World War and the Polish-Soviet War in 1920. The Białowieża Primeval Forest still served as a source of timber, but the new management did end wildfires. The spread of *S. fallax* was most likely triggered by an increase of water level depth, that rose sharply from ca. 22 (ca. 1915 CE) to 4 (ca. 1940 CE) cm below peatland surface. This increase in water table depth is possibly an effect of lower human pressure on the site and the abandonment of drainage ditches (that were blocked and were not maintained by the local population), yet it is not fully reflected in C/N ratios (remaining mostly around 40), yet several minerogenic elements show some decline in this phase of higher peat growth due to shallow water table levels. A statement that the water level depth fluctuations have been one of the main factors of changes in local plant succession at Berezewo peatland is supported by the fact that *E. vaginatum* reappeared ca. 1980 CE and disappeared again ca. 2000 CE. In addition, the decline of plants ca. 2005 CE, including the Ericaceae family took place, which is related to the increasing moisture trend (Fig. 7).

Some changes in forest ecosystems are also visible since ca. 1920–25 CE. Since that time, we noticed an increase in *Picea abies*, which played a most important role in the forest ecosystem because their contribution increased from 7 to 17.7 % (Fig. 7) (cf. Mitchell & Cole 1998).

During the last three decades, we recorded a decrease in trace metals such as Al, Pb, As, Ti and pollen-indicated human activity. These changes coincide with a decrease in industrial activity and depopulation of villages in E Poland since ca. 1990 CE. P concentrations tend to increase towards the surface, leading to a substantial decrease of N/P ratios towards the surface. Increase of P concentration is in agreement with other findings documented by Wang et al. 2015. Such relative enrichment of P near the surface due to intense recycling may thus not directly be related to the described recent environmental changes.

The drying trend observed since ca. 2005 CE at the Berezewo peatland suggests that the site is currently disturbed and may be in danger of crossing a hydrological tipping-point leading to a shift in peatland vegetation cover (Lamentowicz et al., 2019b), i.e. lower proportion of mosses and larger proportion of vascular plants. Peatland drying has been also observed in other European peatlands (Swindles et al., 2019). Furthermore, this may have a negative influence on peatland carbon stock (Rydin & Jeglum, 2013). Too low water tables could lead to carbon release to the atmosphere, but too high water tables can also lead to a slow of the carbon sink function (Evans et al., 2021). Several studies have suggested that a water level at ca. 10 cm may be the most suitable peatland restoration target (Lamentowicz et al., 2019b; Tanneberger et al., 2021; Evans et al., 2021).

4.2. *Sphagnum fallax* as an indicator of a degraded peatland ecosystem

Several studies from peatlands located in Poland (Gałka et al., 2015, 2017; Marcisz et al., 2015), Czechia (Šímová et al., 2019) and Wales (Milner et al., 2021) have documented the spread of *S. fallax* caused by hydrological disturbances (usually drying) and an increase of trophic levels (higher pH) (Gąbka & Lamentowicz, 2008). Furthermore, as indicated in several Baltic raised bog ecosystems located in Poland, this species was not found in sediments dated to the periods before human impact was recorded (Gałka et al., 2015, 2017; Lamentowicz et al., 2015a). Hence, we suggest that the presence of *S. fallax* indicates disturbed peatland ecosystems (cf. Limpens et al., 2003). Its common spreading in disturbed peatlands might be related to its ecological preferences. *S. fallax* is a weakly minerotrophic species, that occurs at poor to moderately rich fens and flushes in bogs, and it is commonly found with minerotrophic species such as *S. palustre, S. riparium,* and *S. papillosum* (Hölzer, 2010). As revealed by the bryological work on *Sphagnum* species distribution in the Białowieża Primeval Forest (Melosik, 2006), *S. fallax* belongs to the most common *Sphagnum* species that occupies wide range of habitats, that may suggest that development of some peatlands can be disturbed.

Although our study is the first such detailed palaeoecological investigation in this area, we suggest that most likely many peatlands in Białowieża Primeval Forest might have lost their pristine state. Further palaeoecological investigations are needed to assess the current state of peatlands in the Białowieża Primeval Forest. However, as shown by the results of palaeoecological analyzes (Gałka et al., 2015; Lamentowicz et al., 2015b), even peatlands hosted by valuable and protected plants have been transformed or created because of human activity.

5. Conclusions

In this study we present a detailed history of the peatland and forest ecosystem in the Białowieża Primeval Forest reconstructed by multi-proxy paleoecological analysis over the last 250 years. Our studies revealed that:

1. Numerous macro-charcoal particles between ca. 1780 and 1920 CE were found, indicating permanent high fire activity in this period. The fire had mainly an impact on the dwarf plants. The lack of major fire phenomena since around 1920 is associated with the revival of Polish forestry management and the beginning of partial protection of this area by the new forest administration.
2. Between ca.1910 and 1930 CE distinctive changes in local and regional plant succession took place. We documented the disappearance of *Sphagnum medium*/*S. divinum* in both cores that was replaced by *Sphagnum fallax*. Most likely it was triggered by hydrological disturbances, along with changes in peat decomposition and concentrations of minerogenic elements. At this time *Picea abies* played a more important role in the forest ecosystem.
3. Based on paleoecological data and present plant communities (domination of *Sphagnum fallax, Eriophorum vaginatum*) we suggest that the peatland ecosystems (or at least some of them) in the Białowieża Primeval Forest may have lost their pristine state due to human pressure.
4. During the last three decades we recorded a decrease in trace metals such as Al, Pb, As, Ti and pollen-indicated human activity. These changes coincide with a decrease in industrial activity and depopulation of villages in E Poland since 1990. Nevertheless, a strong enrichment of P near the surface was observed, shifting the system from N limited to P limited.
5. We suggest that the presence of *S. fallax* at peatlands may indicate disturbed hydrological conditions and we see strong indications for a recent drying of the site.

CRediT authorship contribution statement

Mariusz Gałka: Conceptualization, Methodology, Formal analysis, Investigation, Resources, Visualization, Funding acquisition, Supervision, Writing – original draft, Writing – review & editing. **Klaus-Holger Knorr:** Methodology, Formal analysis, Resources, Writing – original draft. **Kazimierz Tobolski:** Conceptualization, Formal analysis. **Angela Gallego-Sala:** Methodology, Formal analysis, Resources, Writing – original draft. **Piotr Kołaczek:** Methodology, Formal analysis, Resources, Writing – original draft. **Mariusz Lamentowicz:** Methodology, Formal analysis, Resources, Writing – original draft. **Katarzyna Kajukało-Drygalska:** Formal analysis. **Katarzyna Marcisz:** Formal analysis, Methodology, Writing - original draft, Writing – review & editing.

Declaration of Competing Interest

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.

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecolind.2022.109421.

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