



From Alnus to Pinus: temperate peatland ecosystem

2 transformation triggered by human-driven landscape change

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Abstract. Peatlands are invaluable archives of palaeoenvironmental and climate dynamics, play a central role in the global carbon cycle and hydrological processes, preserve biological diversity, and act as climatic microrefugia. Over the millennia, these ecosystems have been heavily modified by human land use, including drainage, overgrazing or peat extraction, leading to their large-scale degradation in many regions. Knowledge of the long-term dynamics of peatlands is crucial for determining their conservation and restoration needs as well as for predicting their evolution, including response to climate change, community changes, carbon sequestration potential. Here we adopted an interdisciplinary approach to investigate the relationships between climate, vegetation, tree growth, hydrology, and human activities in a peatland ecosystem in one of the poorly explored regions of Central Europe, the Solska Forest in southeastern Poland. We used different types of proxy data from natural and human archives: long-term meteorological data (1792–2020), tree-ring data (1729–2022) from living peatland pines, palaeoecological data from the peat sediment (pollen, plant macrofossils, testate amoebae and charcoal data) and archival written and cartographic sources to reconstruct local ecosystem and landscape dynamics and assess possible climatic and anthropogenic impacts. Our results document a complete transition of a peatland ecosystem from black alder bog forest to Scots pine bog forest, most likely triggered by



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several factors, mainly land use change and associated fire activity, among others, in particular the landscape-scale expansion of the pine forests and the resulting environmental acidification that triggered *Sphagnum* encroachment. Our multi-proxy environmental reconstruction of the last >2,300 years also revealed considerable hydrological instability of the peatland and a complex interplay of different landscape shaping influences. In addition, certain advantages, challenges and limitations of multi-proxy studies of landscape history and ecosystem dynamics were highlighted, such as the different temporal resolution and coverage of the archives studied (including the problem of periods with no or very little data) or inconsistency of the quantitative and qualitative data. With this study, we have demonstrated the multifaceted interactions between different biotic and abiotic factors affecting both landscape and peatland ecosystems, confirmed the importance of long-term environmental records for conservation ecology and land management, and emphasized the continuing need for further research on peatland ecology, including past and current changes. Further, linking nature and human archives allowed us to gain a deeper understanding of a complex environmental system, with added value from combining different approaches.

1 Introduction

Peatland ecosystems are widely recognised as habitats crucial for a broad variety of species, important part of hydrological systems, paleoenvironmental archives, potential microrefugia and a long-term regulator of the global carbon cycle (McDonald et al., 2006; Yu, 2011; Leifeld and Menichetti, 2018; Amesbury et al., 2019; Słowińska et al., 2022). Despite their limited distribution (approx. 3% of the world's land surface), peatlands are the largest terrestrial carbon reservoir (Joosten et al., 2016). They belong to ecosystems strongly sensitive to climate change, which can substantially affect their carbon budget and in result transform them into carbon sources (Belyea and Malmer, 2004; Jassey et al., 2018). Like many other ecosystems worldwide, peatlands were significantly modified by human land-use for millennia, often involving activities of highly negative impacts such as overgrazing, peat extraction or drainage (Päivänen and Hånell, 2012; Joosten, 2016). Due to its high population density, long cultural history and climatic suitability for agriculture, Europe is currently a continent with the greatest proportional loss of peatlands – with 44% being degraded, i.e. no longer peat accumulating (Joosten, 2016). In many European countries intensive peatland drainage for both agriculture and forestry took place in the second half of the 20th century (Päivänen and Hånell, 2012; Joosten, 2016). Yet, the extraordinary value of peatland ecosystems has been acknowledged in the recent decades, resulting in broad conservation and restoration efforts across the continent (Andersen et al., 2017; Jurasinski et al., 2020). However, peatlands in the continental fen and bog region which covers a large part of the Eastern Europe (including eastern Poland, southern Belarus, northern Ukraine and substantial section in Central European Russia) are degraded to a high degree (52%) and still insufficiently protected (15%) (Tanneberger et al., 2021).

In Europe, peatland forests, in particular – bog woodlands, represent habitats of regional importance, legally protected by the European Union Habitats Directive (Annex I, habitat type code: 91D0) (Pawlaczyk, 2010; Anonymous, 2013; Grzybowski and Glińska-Lewczuk, 2020). In the continental biogeographical region of the European Union, nearly half of this habitat type is located in Poland (Anonymous, 2013–2018), making the country one of the conservation hotspots. However, environmental changes in peatland forests such as decreasing humidity, peat decay, increasing fertility, and decreasing acidity, which result in significant functional and structural changes have been recorded even in the best preserved woodlands (Czerepko, 2008; Yermokhin et al., 2021). Data on the long-term dynamics of peatland forests is thus urgently needed to provide important baseline information for conservation and management strategies of those highly valuable habitats (cf. Lindbladh et al., 2013; Tannenberger et al., 2021; Grzybowski and Glińska-Lewczuk, 2020).



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Forested or not, peatlands are driven by several hydrological feedbacks, regulating the response of these ecosystems to varying environmental factors, including seasonal water table depth fluctuations and various disturbances, which may cause profound changes in peatland functioning and structure, including vegetation, carbon budget, etc. (Waddington 2015). This specific feature of peatlands makes them very complex environments, where lag and feedback effects, together with interactive effects of different drivers, are common (Linderholm et al., 2002; Smiljanić et al., 2014; Janecka et al., 2025). Multi-proxy studies were proven to be valuable in broadening the understanding of the intricate peatland ecology and dynamics, including fire history (Niklasson et al., 2002; Šamonil et al., 2018), moisture dynamics (Edvardsson et al., 2019; Taminskas et al., 2019), anthropogenic impact (Lamentowicz et al., 2009; Edvardsson et al., 2018), vegetation and peatland development (Eckstein et al., 2009; Edvardsson et al., 2014; Šamonil et al., 2018; Stancikaitë et al., 2019), tree demography (Linderholm and Leine, 2004; Edvardsson et al., 2015a), and climate variability (Edvardsson et al., 2012, 2018). In Europe, the number of such studies substantially increased during the 21st century and resulted in several multi-proxy datasets covering much of northern Fennoscandia, Great Britain and the area around the southern Baltic Sea (southern Sweden, northern Germany, Lithuania, northern Poland). Yet, broad geographic areas are still underutilized in this respect, for example large sections of continental Europe, including Belgium, central Germany, Belarus, Ukraine, central and central-southern Poland (Edvardsson et al., 2022). Hence, a substantial share of European peatland ecosystems (Joosten, 2016) persists not thoroughly explored and understood.

Despite different time resolution between paleoecological and dendrochronological records (Edvardsson et al., 2022), tree ring data from both living (Niklasson et al., 2002; Edvardsson et al., 2019) and subfossil (Eckstein et al., 2009; Edvardsson et al., 2012) trees were often applied in multi-proxy studies of peatland ecosystems. Tree growth in peatlands is affected by both local water table fluctuations (Boggie, 1972; Smiljanić et al., 2014; Edvardsson et al., 2019) and meteorological parameters such as temperature or snow cover (Linderholm et al., 2002; Dauškane et al., 2011; Dinella et al., 2021). However, this complex and multifaceted relationship remains not fully recognised, mainly due to the already mentioned hydrological feedback (Waddington et al., 2015) and lag effects in peatland ecosystems (Linderholm et al., 2002; Edvardsson et al., 2015b, 2019; Dinella et al., 2019). Generally, high water table level may inhibit tree growth (Dang and Lieffers, 1989; Linderholm, 1999; Smiljanić et al., 2014; Edvardsson and Hansson, 2015) since waterlogged, anaerobic environment is strongly restricting root development or even leads to the dying of fine roots (Boggie, 1972; Laiho and Finér, 1996). Because of that, peatland trees: (1) often respond negatively (i.e., with reduced growth) to spring/summer precipitation (Linderholm, 1999; Linderholm et al., 2002; Dauškane et al., 2011; Edvardsson et al., 2015b; Blanchet et al., 2017) - just opposite to populations of the same species growing on mineral soils (Linderholm et al., 2002; Janecka et al., 2025), and (2) show a positive growth response to dry conditions (Potapov et al., 2019), for example as a result of peatland drainage (Linderholm, 1999; Potapov et al., 2019). On the other hand, prolonged periods of low water table level may cause water stress in peatland trees (Dang et al. 1991; Pepin et al., 2002). Hence, a contrasting, positive growth response to precipitation in the growing season can be also observed (Linderholm et al., 2002; Vitas and Erlickyte, 2007; Cedro and Lamentowicz, 2011; Ignatiev and Yermokhin, 2022). Such diversified data justify the need for further, multi-proxy studies, preferably with an interdisciplinary approach and high proxy number (Edvardsson et al., 2014, 2018, 2019; Stancikaitë et al., 2019; Bak et al. 2024). To date, such studies remain rather scarce and geographically limited (Edvardsson et al., 2022), especially in the case of studies using tree ring data from living peatland trees (Edvardsson et al., 2019; Taminskas et al., 2019).

Human impact on terrestrial ecosystems worldwide has spanned millennia (Leuschner and Ellenberg, 2017b; Ellis et al., 2021). Even before the industrial era human societies were modifying land cover, fire regimes, vegetation communities, and global carbon budget (Kaplan et al., 2011; McMichael and Bush, 2019; Sayedi et al., 2024). Increasing human population density and industrial development were followed by further substantial changes in disturbance





regimes, land use and land cover, including deforestation, rise of urban and cropland areas, and ecosystem transformation in effect of drainage (Ellis and Ramankutty, 2008; Kaplan et al., 2009; Joosten, 2016; Williams et al., 2020). Due to its duration and global extent, disentangling human impact from the other environmental factors shaping long-term landscape dynamics may be often challenging if not impossible, which calls for an integrative approach acknowledging the interconnection of environment and societies (Naveh, 1995; Bürgi and Russell, 2001; Dearing et al., 2015). However, human and nature archives differ heavily in terms of occurrence, time-span covered, objectivity, precision, spatial and temporal resolution, presence of quantitative information (Forman and Russell, 1983; Ruffner and Abrams, 1998) which makes long-term cross-disciplinary studies involving environmental sciences and humanities challenging and relatively infrequent (Verheyen et al., 1999; Dearing et al., 2008; Szabó, 2010; Lamentowicz et al., 2020; Bąk et al. 2024). Hence, broadening the knowledge on anthropogenic influence on different habitats and regions seems valuable for a full picture of the past, current and future trajectories of ecosystem processes (Dearing et al., 2015).

Since knowledge on the long-term dynamics of peatland ecosystems is important to aid predictions of their future development, including response to climate change, vegetation changes, carbon sequestration potential, restoration and conservation needs, etc. (Lindbladh et al., 2013), here we applied an interdisciplinary approach to explore interactions between tree growth, hydrology, climate and possible human impact in a peatland located in one of the unexplored regions of Central Europe – southeastern Poland (Edvardsson et al., 2022). Noteworthy, a unique feature of Poland is that, following the geopolitical changes of the late 18th century, different parts of its then territory were incorporated into distinct economic and administrative systems of the neighbouring Enlightenment-era monarchies: Prussia, Russia, and Austria (Davies, 2005; Lukowski and Zawadzki, 2006). This event significantly influenced local land management and in result the landscape of the Polish lands, including forests and peatlands (Broda, 2000; Jaszczak, 2008a, b, c; Bąk et al., 2024; Przybylski et al., 2025). Considering the above, in this study we aimed at (1) implementing a variety of proxy records from both, nature and human archives, to describe the long-term ecosystem dynamics enabling (2) an assessment of the peatland ecosystem stability and (3) an evaluation of the probable reasons for ecosystem transformation, including anthropogenic influence.

148149 2 Material and methods

2.1 Study area

151 2.1.1 Geography, vegetation and climate

Wielkie Bagno (Eng. *Great Swamp*) peatland is located near town Biłgoraj in the Solska Forest (50°31'N, 22°50'E) in south-eastern Poland, approx. 30 km west of the state border with Ukraine. Solska Forest is a large forest area covering over 1,400 km² in the Biłgoraj Plain, stretching from the Vistula River in the west up to the border of Ukraine in the east (50°48'N, 21°56'E–50°13'N, 23°26'E). Along with the neighbouring Roztocze region it is a globally important biodiversity hotspot due to its extraordinary ecosystem diversity, including forests, peatlands, meadows, steppe communities, and arable land. Solska Forest is a continuous woodland composed mainly of Scots pine (*Pinus sylvestris* L.) forests on mineral, mineral-organic and organic (i.e. peat) soils, varying from dry to moist, humid, and bog forest communities, including peatlands. Deciduous tree species such as European beech (*Fagus sylvatica* L.), oak (*Quercus* spp.), and black alder (*Alnus glutinosa* (L.) Gaertn.) occur in smaller patches, in majority in black alder bog forests (Chmielewski and Sowińska, 2008, 2011; Maciejewski and Szwagrzyk, 2011) (Fig. 1). Wielkie Bagno peatland is a large (approx. 250 ha) basin filled with peat and mud sediments, surrounded by fluvial sands of floodplain terraces and eolian sands, including eolian sands in dunes, overlying Pleistocene lacustrine silts, fluvial sands and gravels (including those with peat and mud layers) and Tertiary clays, sandy clays, and mudstones with sandstone interbeds (Popielski, 1992). The main part of the basin is generally flat (elevation of approx. 208–218 m a.s.l.), surrounded by dunes and with a dune





extending along a west-east axis across the southern section (Fig. 1c). Wielkie Bagno peatland and its immediate surroundings are covered by a network of ditches (Figs. 1 and S1).

The study area is located in the humid continental climate zone (Dfb) with warm summers and cold winters according to the Köppen-Geiger climate classification (1951–2000, Kottek et al., 2006). In the period 1951–2017, the mean annual air temperature in the study area was 7.2°C, with monthly mean air temperatures in January and July of 3.9°C and 17.9°C, respectively (Tomaszów Lubelski meteorological station, Institute of Meteorology and Water Management-National Research Institute, IMGW-PIB, 50°27'N, 23°24'E). The average annual precipitation total for the same period was 637.0 mm (Fig. 1d). Precipitation predominated in the warm half of the year (407.4 mm) compared to the cold half of the year (229.6 mm), which is typical for a continental climate. However, the climate of peatlands and Scots pine bog forests may be cooler than in the open areas where the usual weather stations are located (Olszewski, 1986; Słowińska et al., 2022).

Our sampling site was selected based on the subjective criteria: (1) presence of the old-growth tree populations, aged >180 years, (2) growing in a peatland area ensuring the possibility of peat sampling. Our tree ring (50°31'23.88"N, 22°51'56.52"E) and palaeoecological (50°31'31.08"N, 22°51'46.799"E) sampling within the Wielkie Bagno peatland (Fig. 1) took place in two neighboring pure pine stands on peat soil, which are 182 and 190 years old and represent a Scots pine bog forest (*Vaccinio uliginosi-Pinetum*, Leuschner and Ellenberg, 2017b) according to the forest inventory data available online in Forest Data Bank (Pol. *Bank Danych o Lasach*, https://www.bdl.lasy.gov.pl/portal/en). However, the pine populations of our study site should be described as multi-aged since several older trees were also present as confirmed by their crown and bark features typical for ancient conifers (Andersson and Niklasson, 2004). Ground layer was composed of *Vaccinium uliginosum*, *Ledum palustre*, *Eriophorum vaginatum*, *Molinia caerulea*, and *Vaccinium myrtillus*. Bottom layer was dominated by *Sphagnum* spp. mosses (Fig. S1).



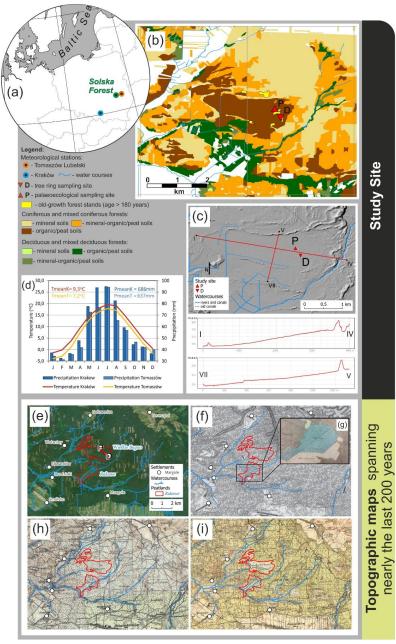


Figure 1. Our study site and its surroundings in different time periods. (a) location of the Solska Forest and meteorological stations (Kraków, Tomaszów Lubelski) that derived climate data used in this study; (b-c) study area and sampling sites presented on: (b) the forest type map (Forest Data Bank, Pol. Bank Danych o Lasach, https://www.bdl.lasy.gov.pl/portal/udostepnianie-en, accessed: 2024-04-19) and (c) the digital terrain model (GDAL/OGR contributors, GDAL - Geospatial Data Abstraction Library, Open Source Geospatial Foundation, https://gdal.org, accessed 2025-01-06); (d) average air temperature and total precipitation in Kraków and Tomaszów Lubelski in 1951-2017; (e) ortophotomap from June 2023 (© Google Maps 2023); (f) Topographical





Map of the Congress Kingdom, published in 1843; (g) archival map (APL, AOZ, IMK, sign. 3, sheet 421, archival source 15, AS15, full list of archival sources given prior to the reference list), published in the second half of the 19th century; (h) map of west Russia (Ger. *Karte des westchlichen Russlands*), published in approx. 1919; (i) map by the Military Geographical Institute (WIG), published in the 1930s. Hydrology data source: https://www.geoportal.gov.pl (accessed: 2024-04-19). Historical maps acquired from the public domain.

2.1.2 Regional historical background

Solska Forest is a remnant of a vast Sandomierz Forest that in the Middle Ages was directly neighbouring the Kievan Rus and was generally a settlement void (Buraczyński, 2008). After incorporating the area into the Polish Crown (second half of the 14th century) the settlement development was still slow. It intensified first at the end of the 16th century along with the foundation of an important trade route in the region (Szczygieł, 1985).

In the 16th–18th centuries, the landscape of Poland (Polish-Lithuanian Commonwealth) was characterised by large estates owned by very influential noble families. An important source of their power was the land, from which they earned enormous revenues. One of these families was the Zamoyski family. The estates belonging to the Zamoyski family were located in the south of the country and were called the Zamoyski Family Estate (Pol. *Ordynacja Zamoyskich*). These were agricultural estates, but they were also largely covered with forests, which gradually generated increasing income for their owners (Rajca, 1972). Solska Forest became part of the Zamoyski Family Estate already at the turn of the 16th and the 17th centuries. New owners started to intensify the settlement development in the area by building sawmills, creating seasonal forest production settlements (producing potash, ash, and wood tar), etc., especially at the end of the 17th century. After substantial decrease of the available forest resources, local inhabitants, called hutters (Pol. *budziarze*), had to modify their economy and land use. They lived by farming fields and meadows, cattle and sheep breeding, traditional forest beekeeping and limited exploitation of the surrounding forests, mainly production of wood tar. They were also hired as labor workers (Róg, 2021).

The late 18th century brought significant political and territorial changes in this part of Europe. The southern lands of the Polish-Lithuanian Commonwealth (which included the Zamoyski Family Estate and our study site) were incorporated into the Habsburg Monarchy in 1772 and subjected to Austrian legislation (Piller, 1782; Davies, 2005). As a result of the change of nationality, Austrian Galicia was subjected to intensive reforms as a new province. Land use rules which until 1772 depended only on the will of the private owner were modified. In terms of forest management, the changes involved the introduction of the Enlightenment management model (based on the German silviculture model, Hölzl, 2010). At the same time, the region was subjected to several economic reforms (Jones, 2015; Carvalho, 2018).

The beginning of the 19th century was marked by further geopolitical changes which were affecting our study area. The defeat of Napoleon and the resolutions of the Congress of Vienna in 1815 established both a new political order for the following decades and the arrangement of the borders of the Central European monarchies at the time. The Polish lands – originally incorporated by Austria in 1795 – by the end of the first decade of the 19th century landed within the borders of the Duchy of Warsaw, created by Napoleon in 1807. However, under the decisions made in Vienna in 1815, the Duchy was abolished and its lands came (including the extensive Zamoyski Family Estate and our study site, Wielkie Bagno peatland) under the rule of the Russian tsars. The change of governmental belonging brought new legal and administrative rules, including a management system for income-generating properties such as forests (Grodziski, 1971; Jewuła et al., 2015).

The 20th century brought further historical challenges. After World War I, some forest areas had to be sold to cover the costs of rebuilding the estate after the war. In the 1920s, the increasing demand for timber led to considerable logging. Rational forest management was introduced in the mid-1930s (Kozaczka, 2002). During World War II, the entire





Zamoyski Family Estate was managed by the Nazi occupying forces (Klukowski, 1945–1947). The end of the Zamoyski Family Estate was brought by the change in the socio-political system in Poland in 1944, which took private estates (including both agricultural lands and forest areas) into public ownership. Since then the land forming the estate was not the property of the Zamoyski family anymore (Kozaczka, 2003; Jędrejek, 2012).

Currently, the study area is a part of the Tereszpol Municipality. Forests surrounding our study site Wielkie Bagno are still state-owned, belong to the Zwierzyniec Forest District (Forest Data Bank, https://www.bdl.lasy.gov.pl/portal/mapy, accessed: 2024-04-19), and are used for forest management.

246 2.2 Climate data

To assess the long-term climate fluctuations in the region and the long-term climate-tree growth relationships at the study site, the average monthly, seasonal and annual values of air temperature (1792–2020) and atmospheric precipitation (1811–2020) from a meteorological station of the Department of Climatology of the Jagiellonian University in Kraków was used. The meteorological station is located in the city centre, in the Botanical Garden of the Jagiellonian University (50°04'N, 19°58'E, 220 m a.s.l.), and its location has not changed for 230 years. Sensors are installed at a height of 12 m above ground. Meteorological data from Kraków are one of the longest instrumental weather series in Europe and have been widely used in numerous scientific studies as they well represent the climatic conditions of Central European lowlands within a radius of 300 km (Hess, 1974; Kożuchowski et al., 1994; Trepińska et al., 1997; Trepińska, 2000), including our study site, located approximately 280 km to the east. To verify the representativeness of the Kraków data for our study area, we compared air temperature and precipitation data from Kraków and Tomaszów Lubelski (IMGW-PIB), the nearest weather station to our study site (Fig. 1a), for the overlapping period of 1951–2017 (67 years). We assessed the significance of differences between the two stations in monthly temperature (T) values (mean, minimum, and maximum) and precipitation (P) totals across various periods (monthly, seasonal, warm and cold half-years, and annual) using the Mann–Whitney U test. The statistical analyses were conducted using the nlme package (Pinheiro and R Core Team, 2025) of the R software (R, Version 3.1-167).

A percentile (quantile) classification of thermal and pluvial conditions was made for months, seasons and years in Kraków and Tomaszów Lubelski. The classification allowed for the assessment of mean air temperature values and precipitation totals for the specified period in comparison to the reference period (Miętus et al., 2002; Czarnecki and Miętus 2011). In our case, we assumed a common period for both stations, i.e. 1951–2017. The empirical percentiles were determined in 20% increments, ranging from 20% to 80%. Subsequently, the complete range of temperature and precipitation variability over a specified period and at a given station was divided into five percentile intervals. The following categories for temperature were assigned: <20% very cold (-2); 20.01–40% cold (-1); 40.01–60% normal (0); 60.01–80% warm; >80% very warm. In regard to precipitation, they were as follows: <20% very dry (-2); 20.01–40% dry (-1); 40.01–60% normal (0); 60.01–80% wet; >80% very wet (Figs. 3 and S2). Such classifications are used, among others, by the IPCC (2007) to assess climate change in specific time periods.

2.3 Dendrochronology

2.3.1 Fieldwork, sample preparation and chronology building

To reduce individual growth variability, tree ring samples were collected from 21 Scots pine trees in June 2022, selected according to their biosocial (dominant or co-dominant trees), health (vital individuals without visible damage) and stand structure (avoidance of trees at the edge of gaps and stand margins) status. From each sample tree two increment cores were taken from two perpendicular directions using 5.15 mm diameter Pressler borers at a height of 1.3 m (Cook and Kairiukstis, 1990). After discarding samples too eroded for analysis, wood samples from 19 trees were mounted on



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wooden supports, sanded with a series of progressively finer sandpapers (grit size up to 1000) to improve the visibility of the tree ring boundaries and digitised at 2400 dpi (Epson Expression XL12000). Identification of the boundaries between annual rings was done with a binocular (80× magnification LEICA S8APO) to enable detection of false rings (due to intra-annual density fluctuations in the early wood), wedging rings, and missing rings. Cross dating was performed using standard dendrochronological approaches (Stokes and Smiley, 1968; Yamaguchi, 1991) and verified with 'CDendro' software (Larsson and Larsson, 2018) after annual ring widths were measured to an accuracy of 0.01 mm using 'CooRecorder' software (Larsson and Larsson, 2018; Maxwell and Larsson, 2021). Tree recruitment dates (i.e., tree age) were determined based on the pith dates at sampling height (Heyerdahl et al., 2014). In case of increment cores, where the pith was missing, distance to pith was estimated based on growth and curvature of the earliest observed rings in the sample during the ring width measuring procedure (Larsson and Larsson, 2018). Determination of pith date was possible for 13 sample trees which did not include inner rot precluding a reliable assessment of the distance to pith in reference to the ring curvature. Tree ring width series were detrended to remove any biological (age) trend and other low-frequency fluctuations caused by non-climatic factors (Cook and Peters, 1981; Speer, 2010). Individual tree series were detrended with a 30-year cubic smoothing spline with a frequency cut-off of 50% (Bunn, 2008). To remove the first-order autocorrelation in the dimensionless ring width index (RWI) series, we applied autoregressive modelling. Finally, a biweighted robust mean was applied to the pre-whitened series of individual trees to develop a mean stand chronology (Cook and Kairiukstis, 1990). The quality of the generated chronologies was checked with the so-called Ger. Gleichläufigkeit (GLK, i.e. the coherence coefficient) (Eckstein and Bauch, 1969; Buras and Wilmking, 2015) and the mean correlation between individual tree-ring series (mean rbt, an indicator of the strength of the common signal) (Wigley et al., 1984; Cook and Kairiukstis, 1990). To test the suitability of the constructed chronologies for climate-growth analyses, we applied subsample signal strength (SSS; Buras, 2017), first-order autocorrelation (AR1, an indicator of the effect of the previous year's conditions on the current year's growth) and signal-to-noise ratio (SNR, the proportion of explainable variation in the chronology due to climate divided by the unexplained variation) (Wilczyński and Kulej, 2013). A threshold value of more than 0.85 was used as an entry criterion for the SSS (see Fig. S4). These steps were completed with the dplR package (Bunn et al., 2020) of the R statistical software (R Core Team, 2021).

2.3.2 Climate-tree growth relationship

To assess how climate affects inter-annual growth variability of peatland trees in the study site, we used the climate data from Kraków meteorological station (see Section 2.2) and calculated the Pearson correlation coefficients between site ring width chronology and monthly climate variables: mean temperature, precipitation sum and standardized precipitation evapotranspiration index (SPEI), aggregated over three and six months. To calculate the SPEI indices, we estimated the water balance as the difference between monthly precipitation and potential evapotranspiration. Positive value of the index (SPEI > 0) reflects the positive water balance, higher precipitation than potential evapotranspiration (Vicente-Serrano et al., 2010) (cf. Fig. S3). To assess the lag effect of the negative water balance we aggregated the monthly SPEI over three and six months (SPEI3 and SPEI6, respectively). To calculate climate—growth correlation we used the monthly_response() function implemented in the R package dendroTools, considering all previous and current seasons from the previous January to the current December (Jevšenak and Levanič, 2018; Jevšenak, 2020). As the relationship between tree growth and external factors is non-linear (Wilmking et al., 2020), we tested the temporal variability of the relationship between climate and growth by systematically subsetting sub-periods of RWI values and climate variables from the total analysed period, using a 30-year running window with a one year offset. For each subset period, we calculated climate variable-growth correlations (Jevšenak and Levanič, 2018; Jevšenak, 2020).



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2.4 Paleoecology of the peat archive

2.4.1 Core collection, lithology, chronology and numerical analysis

In June of 2022, a peat core with a diameter of 5 cm and a length of 50 cm was collected with an Instorf corer. The extraction cores were placed in PVC tubes and then transported to the cold room of the Institute of Geography and Spatial Organization of the Polish Academy of Sciences, where they were stored at 4°C until subsampling. The organic sediment (peat) was cut into 1 cm thick slices, which were then analysed at a resolution of 1 cm. Of these samples, 50 were analysed for pollen, macrofossils, and charcoal, and 25 for testate amoebae. The lithology of the analysed peat core was as follows: (1) highly decomposed peat at a depth of 50 to 37 cm, and (2) weakly decomposed Sphagnum peat from the depth of 37 cm to the top. Eight radiocarbon dates were obtained from the peat core (Table 1). The chronology of the profile was established from these eight dates. The age-depth model was constructed using OxCal (OxCal v4.4.4, 2023) (Fig. 7). The IntCal20 (Reimer et al., 2020) and Bomb21NH1 (Hua et al., 2021) atmospheric curves were used to calibrate the dates. To present variation in biological assemblages across the peat sediment layers, non-metric multidimensional scaling (NMDS) ordination on the Bray-Curtis dissimilarity (Ricotta and Podani, 2017) was applied on the dataset using the vegan package (Oksanen et al., 2025) in R software (R Core Team, 2021). The NMDS was based on pollen data (only taxa that exceeded 1% of total pollen sum in at least one sample were selected), plant macrofossil data, and micro- and macrocharcoal influx. To identify assemblage groupings, we applied k-means clustering to the NMDS ordination scores (Hartigan and Wong, 1979). To determine the optimal number of clusters, we used the elbow method, which involves calculating the total within-cluster sum of squares (WSS) for a range of cluster numbers (k = 1 to 10). Based on this analysis, we selected k = 5 as the most optimal clustering solution. The NMDS results were plotted in R using ggplot2 package (Wickham, 2016) as the ordination plot to show variation among samples and as the stratigraphic plot of NMDS1 axis scores plotted against depth to show temporal changes.

Table 1. The list of radiocarbon dates from the Wielkie Bagno peatland (Solska Forest) with calibrations.

No.	Laboratory	Depth cm	¹⁴ C date (¹⁴ C BP)	Calibrated dates	Material dated
	code			(cal CE 2σ-95.4 %)	
1	Beta - 657100	4.5	$101.25 \pm 0.38 \text{ pMC}$	2016–2019 cal CE	Sphagnum stems
				1955 cal CE	
2	Beta - 657099	9.5	$115.82\pm0.43~pMC$	1988–1991 cal CE	Sphagnum stems
				1957–1958 cal CE	
3	Beta - 640210	13.5	$114.39 \pm 0.43 \ pMC$	1990–1992 cal CE	Sphagnum stems
				1957 cal CE	
4	Beta - 657098	19.5	$170 \pm 30 \; BP$	1720–1815 cal CE	Sphagnum stems
				1907–Post cal CE 1950	
				1660–1700 cal CE	
				1832–1890 cal CE	
5	Beta - 657097	24.5	$120\pm30\;BP$	1799–1940 cal CE	Sphagnum stems
				1680–1740 cal CE	
				1752–1764 cal CE	
6	Beta - 640211	36.5	$140 \pm 30 \; BP$	1797–1944 cal CE	Sphagnum stems
				1671–1779 cal CE	
7	Beta - 657095	38.5	$1080 \pm 30 \; BP$	940–1023 cal CE	Pollen (extracted)
,	Deta - 03/093	36.3	1000 ± 30 DF	940-1023 Cal CE	i onen (exu





892–933 cal CE

8 Beta - 657096 48.5 2160 ± 30 BP 233–97 cal BCE Pollen (extracted)

356–279 cal BCE
72–57 cal BCE
257–247 cal BCE

2.4.2 Pollen and microcharcoal analysis

Pollen samples (in total: 50 samples) were collected from the peat core with the resolution of 1 cm steps and prepared using standard laboratory procedures (Berglund and Ralska-Jasiewiczowa, 1986). To estimate concentration of palynomorphs, *Lycopodium* markers were used (Stockmarr, 1971). Pollen and spore identification was made using photographic reference collections and keys (Fægri et al., 1989; Moore et al., 1991; Beug, 2004). For each sample, at least 500 pollen grains of trees were counted. The percentage share of plant taxa was calculated on the basis of the sum of arboreal pollen (AP) and non-arboreal pollen (NAP), i.e. AP+NAP sum. Pollen grains and spores of local aquatic and telmatic plants were excluded from the sum. The zonation was confirmed by CONISS cluster analysis (Grimm, 1987). During analysis non-pollen palynomorphs and microscopic charcoal particles (size: > 10 µm) were also counted from the same slides as pollen. The curve of human indicators total (HIT) contained taxa: *Plantago media, Plantago major, Plantago lanceolata*-type, *Rumex acetosella, Rumex acetosa, Ambrosia*-type, *Matricaria-type, Artemisia,* Chenopodiaceae, *Urtica, Polygonum aviculare*-type, *Scleranthus, Spergularia*-type, *Centaurea cyanus, Fagopyrum, Cannabis sativa, Secale cereale, Triticum*-type, Cerealia undiff., and *Zea mays*.

2.4.3 Plant macrofossils analysis

Material for the plant macrofossils analysis was collected at 1 cm intervals from the peat core (0–50 cm). All macrofossil samples were washed on sieves with a mesh diameter of 0.2 mm and 0.125 mm (Birks, 2001). Five microscope slides were prepared from each sample. Each specimen was inspected under an Opta-tech MB 300 series optical microscope at 200× and 400× magnifications in five fields of view. Plant macrofossils were identified using several macrofossil taxonomic keys (Lubliner-Mianowska, 1951, 1957; Szafran, 1963; Dombrovskaya et al., 1959; Grosse-Brauckmann, 1972, 1974; Grosse-Brauckmann and Streitz, 1992; Tobolski, 2000; Birks, 2007).

2.4.4 Testate amoebae analysis

Testate amoebae analysis was used to reconstruct hydrological variability. Material for the analysis was collected at 2 cm intervals from the peat core. The 2 cm 3 of the peat were mixed in a 500 ml beaker, and next shaken in distilled water, and washed through a sieve with a mesh of 300 μ m (Booth et al., 2010; Payne and Mitchell, 2009). The sediment was investigated using light microscope Nicon eclipse 50i at a magnification of 200× and 400×. Tests were counted and identified to a minimal total of 100 individuals per sample using the available identification guides (Mazei and Tsyganov, 2006; Todorov and Bankov, 2019; Siemensma, 2019). The exception was the lower part of the core (from 37 to 48 cm), where the abundance of amoebas was extremely low (single test on one microscopic slide). Therefore, these samples were excluded from the analysis and excluded in the percentage diagram. To calculate zonation of testate amoebae a CONISS method (Grimm, 1987) was applied based on a stratigraphically constrained cluster analysis . The reconstruction of hydrological variability (depth to water table, DWT) of the peatland was carried out based on the European training set compiled by Amesbury et al. (2016) with C2 software (Juggins, 2003). The Shannon diversity and Dominance D = 1-Simpson index of the testate amoeba communities were calculated in the PAST program (Hammer et al., 2001).

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Community of testate amoebae was divided into four categories based on the amoeba test (i.e. shell) construction (idiosomic, organic-coated idiosomic, agglutinated and organic) according to Marcisz et al. (2021) and Mitchell et al. (2008). Mixotrophic testate amoeba species (*Hyalosphenia papilio*, *Amphitrema wrightianum*, *Heleopera sphagni*, *Placocista spinosa* and *Archerella flavum*) were also summed up.

2.4.5 Macrocharcoal analysis

The record of macrocharcoal distribution was obtained from 50 samples (each 2 cm $^{-3}$) taken at 1 cm vertical intervals in peat profile. The collected samples were first bleached (Halsall et al., 2018; Hawthorne et al., 2018) and sieved through a 500 and 150 mm mesh. Charcoal particles with a size of >100 μ m were counted using a stereomicroscope at 200× and 400× magnifications. To account for variations in sedimentation in the sequence (Davis and Deevey, 1964), the macrocharcoal data were transformed into charcoal accumulation rate (i.e., charcoal influx, CHAR, particles cm $^{-2}$ yr $^{-1}$) by multiplying the concentrations of charcoal (CHAC, particles cm $^{-3}$) with the sediment accumulation rates (cm yr $^{-1}$). In addition, based on their sizes, macrocharcoal particles were divided into two groups: 150–500 μ m and >500 μ m. The subdivision of macrocharcoal particles can provide information on the potential distance of fires from the studied site (e.g., Clark, 1988; Vannière et al., 2008; Conedera et al., 2009).

2.5 Historical sources - Cartography and written evidences

To assess human impact, archives were searched for any archival sources such as documents, historical maps and printed archival sources, with information on land use, demography (including settlement development), economy, etc. of our study site and its surroundings. In search of the archival data, we focused on information from economic inventories that would depict the economic processes, the dynamics of environmental change, demography and the transformation of settlement structures in the Solska Forest. We also searched the rich cartographic archives for plans and maps of the Wielkie Bagno peatland which could visualise the above mentioned processes. The searches were conducted at the Central Archives of Historical Records in Warsaw (AGAD) and the State Archives in Lublin (APL). In the latter one, particular emphasis was placed on the Archives of the Zamoyski Family Estate (Pol. Archivum Ordynacji Zamoyskich, AOZ). In addition, we also searched and critically reviewed the existing historical studies on the Solska Forest.

3 Results

3.1 Temporal resolution of multi-proxy records provided by different archives

The peat archive allowed reconstruction of the peatland ecosystem dynamics during the periods of 330 BCE–1400 CE and 1830–2022 CE. The clear changes in the peat core based on the analysis of several palaeoecological proxies documented the two main phases development and transformation of the Wielkie Bagno peatland: (1) WB-1, 49–37 cm (time period: 330 BCE–1400 CE) and (2) WB-2, 37–0 cm (time period: 1830–2022 CE). Three subphases are distinguished in phase (2a) WB-2a, 37–16 cm (time period: 1830–1947 CE), (2b) WB-2b, 16–7 cm (time period: 1947–2004 CE), and (2c) WB-2c, 7–0 cm (time period: 2004–2022 CE). The tree ring archive covered the period of 1729–2022 CE, extending the paleoecological record back a century further in one of the above parts and broadening the picture of the period between the two main phases (WB-1 and WB-2). The climate records covered the period of 1792–2020 CE for temperature and 1812–2020 CE for precipitation. The human archives covered periods that overlapped with the nature archives. However, they provided more scattered data (Fig. 2). Most of the historical data covered the period from the mid-18th to the early 20th century and complemented the nature archives (Fig. 2, Tables S3 and S4).





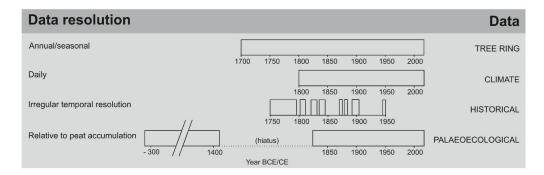


Figure 2. Resolution and time span of multi-proxy records provided by different archives and data types used in this study.

3.1 Climate conditions

3.1.1 Comparison of climatic data from Kraków and Tomaszów Lubelski

A statistically significant thermal contrast was observed between Tomaszów Lubelski and Kraków. From 1951 to 2017, the mean temperature in Tomaszów Lubelski was approximately 2°C lower than that of Kraków (Fig. 1d). However, the correlation between the air temperature values (monthly, annual, and seasonal) at the meteorological stations in Kraków and Tomaszów Lubelski was found to be highly significant (correlation coefficients >0.8–0.9). In contrast, the annual precipitation total, as well as the precipitation totals for the winter, spring, and autumn months, did not exhibit statistically significant differences. The correlation between precipitation data and the meteorological stations in Tomaszów Lubelski and Kraków was notably weaker than that observed for temperature data, particularly in the spring and summer months. However, in many instances, the values were statistically significant at the 0.05 level (Table S1).

3.1.2 Classification of thermal and pluvial conditions in Kraków and Tomaszów Lubelski

The classification of thermal and pluvial conditions carried out for each month, season and year in the analysed datasets (Section 2.2) revealed values within the norm and deviations from it, both positive and negative. For air temperature, the increasing frequency of warm and very warm periods since the end of the 1980s and of cool and very cold periods in the years 1826–1920 can be clearly seen by the increased frequency of occurrence. Wet months and seasons occurred more frequently in the years: 1829–1849, 1896–1910, 1962–1966, 1996–1997 and 2010. Dry and very dry summer months have occurred more frequently since the 1980s. If we compare the classification results for the data from Kraków and Tomaszów Lubelski, we can see that there are no very clear differences between the values, both in terms of air temperature and precipitation (Figs. 3 and S2).





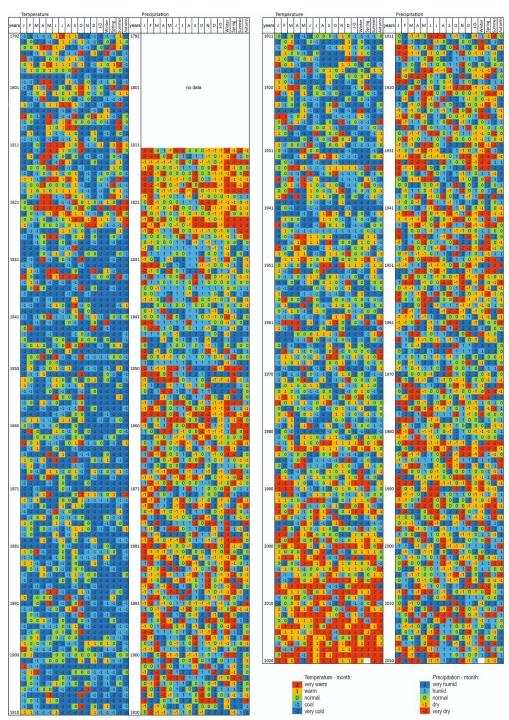


Figure 3. Classification of thermal and pluvial conditions in Kraków in each month (January–December: J, F, M, A, M, J, J, A, S, O, N, D), season (Winter, Spring, Summer, Autumn) and year (J–D) in the period 1792–2020 (base period 1951–2017).

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3.2 Tree ring data

3.2.1 Site chronology

Scots pine ring-width chronology covered the period 1729–2022 (GLK=0.685; Rbar=0.491; AR1=0.775; EPS= 0.948; SNR=18.334; SSS=0.959) (Fig. 4). The annual ring widths ranged from 0.06 mm to 6.96 mm, with an average of 0.81 mm. Peatland pine chronology revealed the following pointer years that agreed with data from other study sites in the region (NE Poland, Lithuania, Latvia; Cedro and Lamentowicz, 2008; Dauškane et al., 2011; Edvardsson et al., 2015b, 2019; E. Zin, K. Pilch, M. Klisz, unpubl. data): (1) positive: 1851, 1864, 1919, 1924, 1926, 1953, 1968, 1977, 1988, and (2) negative: 1928, 1930–1931, 1937, 1952, 1956, 1963, 1965. Sampled pine population recruited in two different time periods. Tree establishment data (at sampling height of 1.3 m) revealed continuous pine regeneration in the 18th century (during 1720s–1770s) and a cohort originating from the first half of the 19th century (1823–1827). One of the sample trees had a fire scar in the middle earlywood of 1830 indicating a fire which occurred during the season of cambial activity (Baisan and Swetnam, 1990). This fire was recorded by other pines as a post-fire growth reaction in the form of a short-term growth depression (1–5 years) that was often combined with fire-induced disturbances in tree ring morphology (Niklasson and Granstrom, 2000; Zin et al., 2015).

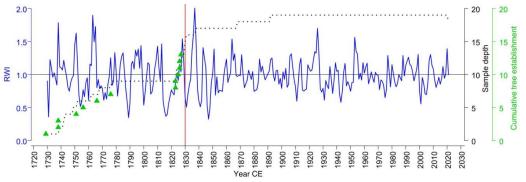


Figure 4. Scots pine (*Pinus sylvestris* L.) chronology (blue line) and tree recruitment dates (green triangles) of living peatland trees in Wielkie Bagno, Solska Forest. RWI – ring width index. Sample depth is denoted by a dotted line and fire date recorded in the tree ring material by red vertical line.

3.2.2 Climate sensitivity of peatland pines

Climate—growth analyses revealed the dominant effect of the aggregated drought indices (both SPEI3 and SPEI6) of the second half of the current year (June—December), demonstrating the growth-promoting lagged effect of the wet conditions. The influence of temperature on growth of peatland trees was more diverse, documenting the significant effect of the current year conditions. Higher early spring temperatures (February—March) induced tree growth while warmer conditions in the latter period (May—December) had the opposite, growth inhibiting effect. Precipitation showed the weakest influence on tree growth. The pluvial conditions of the current season had a dominant, growth-promoting effect. Precipitation in the previous year November and the current October showed positive correlation with tree growth, while precipitation in July of the previous year evidenced an opposite, negative correlation (Fig. 5).



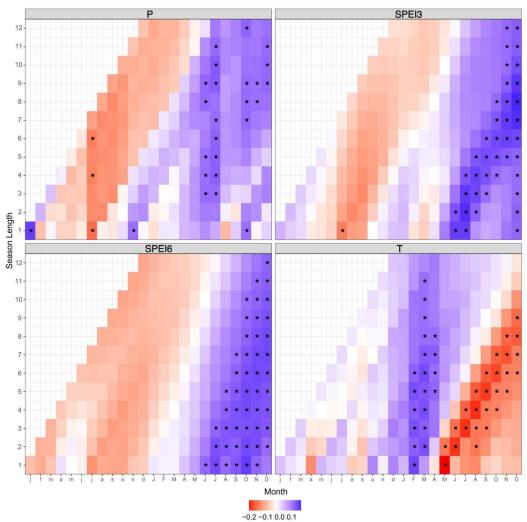


Figure 5. Correlation between indexed tree ring width (RWI) of peatland pines and monthly precipitation sum (P), mean monthly temperature (T) and standardized precipitation evapotranspiration indices aggregated over three (SPEI3) and six (SPEI6) months, calculated for the period from January of the previous year (horizontal axis, lowercase letters) to December of the current year (horizontal axis, uppercase letters). Asterisks (*) indicate the correlation significance level (p < 0.05).

3.2.3 Temporal variation of the climate-growth relationship

The growth-accelerating effect of the positive water balance (SPEI3, SPEI 6) in spring—summer of the current season observed until the 1980s of the 20th century was inverted to a growth-limiting, however, statistically insignificant effect in the recent decades. This was paired with a clear growth enhancing effect of the positive water balance of the autumn months (October—November). Interestingly, a positive influence of wet early summer conditions was also noted in the earliest period, i.e. in the first half of the 19th century (Fig. S5). A markedly similar trend of temporal changes in climate sensitivity was observed for the effect of precipitation (Fig. 6). The temperature influence on tree growth of peatland





pines revealed a more complex picture throughout the analysed period (1812–2022). The negative impact of high temperatures in spring–summer continued until the 1920s, where it changed towards the stronger effect of summer temperatures (August). In the recent decades, since the second half of the 20th century, negative correlation of growth with temperature was observed. Noteworthy, a comparable effect of temperature in autumn (October–November) was recorded in the second half of the 19th century (Fig. 6).

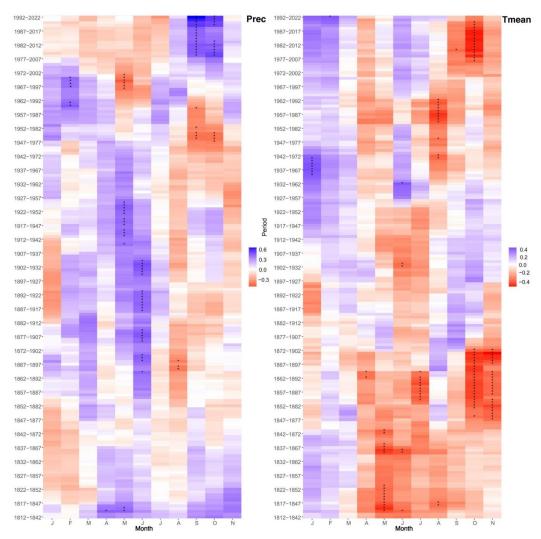


Figure 6. Correlation in the 30-year moving window during the period 1812-2022 between indexed tree ring width (RWI) of peatland pines and monthly precipitation sum (Prec), and mean monthly temperature (Tmean), calculated for the current year (January–November, J–N). Asterisks (*) indicate the significant correlations (p < 0.05).





3.3 Paleoecology

3.3.1 Age-depth model and sediment composition

In the peat core, the section between 50 and 37 cm was already very different from the other sections during drilling due to the degree of decomposition, the structure of the sediment and the macroscopic difference in the peat type. The heavily decomposed peat at a depth of 50 to 37 cm was characterised by a slow accumulation rate (about 170 years per cm), while the second part of the profile showed a markedly increased peat growth rate of about five years per centimeter (Fig. 7). Sediment accumulation was not continuous in this part of the Wielkie Bagno peatland. Between 1830 and 1396 CE, a hiatus was observed in the transition between the two lithological segments, in which increased amorphous matter and a pronounced horizon rich in macroscopic charcoal were present.

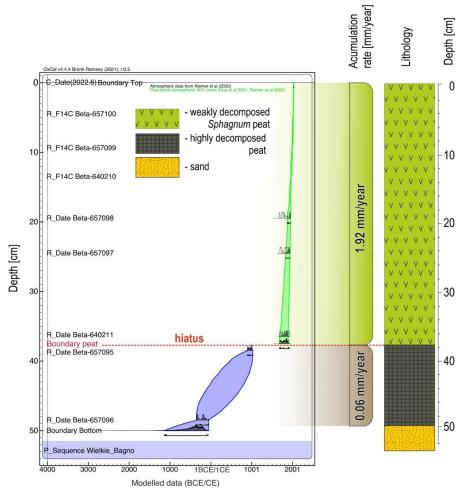


Figure 7. Age-depth model of the peat core from the Wielkie Bagno peatland, Solska Forest.

3.3.3 Pollen data (regional vegetation) and microcharcoal distribution

Based on changes in the percentage of taxa, three local pollen assemblage zones (LPAZ) were separated (Fig. 8), with two sub-phases in LPAZ-1 and two sub-phases in LPAZ-2:





- 525 (1) LPAZ-1: 50–37 cm, Carpinus
- 526 Level with a high proportion of Carpinus pollen grains (13.9–19%) in which two sub-phases were distinguished:
- 527 (1a) 50-44 cm, Quercus: percentages of Carpinus reached a maximum of 19%. Quercus content was between 6.2 and
- 528 8.1%. *Ulmus* curve was stable and reached values between 1.3 and 1.7%;
- 529 (1b) 44-37 cm, Fagus: Carpinus (7.9-12.6%) and Quercus (3.3-5.5%) percentages decreased. Fagus content was from
- 3 to 9%. The curve of *Ulmus* declined below 1%.
- The upper limit of the level LPAZ-1 was marked by a decrease in the *Carpinus* curve.
- 532 (2) LPAZ-2: 37–13 cm, *Pinus*–NAP
- Proportion of *Pinus* pollen grains gradually increased from 42% at the beginning of the phase to 63.6% at the top of the
- 534 level. NAP percentages were high, between 10.6% and 23.6%. Continuous curves of anthropogenic plant indicators
- 635 (Rumex, Plantago lanceolata-type, Cannabis sativa, Secale cereale, Cerealia undiff.) were present. Two subphases were
- 536 distinguished:
- 537 (2a) 37–22 cm, Carpinus-Fagus: the proportion of Carpinus and Fagus pollen grains was 2.9–7.2% for hornbeam and
- 538 2.5–6.1% for beech. High percentage of *Calluna* pollen grains was recorded (up to 7.4%). Proportion of anthropogenic
- indicators (HIT) reached 9.8%;
- 540 (2b) 22-13 cm, NAP: share of NAP was between 17.6 and 23.7% with predominance of anthropogenic indicators (up to
- 541 13.8%). The proportion of hornbeam and beech was less than 2%. *Calluna* did not exceed 2.7%.
- The upper limit of the level was determined by the decrease of the NAP.
- 543 (3) LPAZ-3: 13–0 cm, *Pinus*
- 544 Content of *Pinus* pollen grains was predominant and reached a maximum of 83.1%. NAP decreased to less than 10%.
- 545 HIT content gradually declined from 11% at the beginning of the LPAZ-3 to 1.3% in the top sample (Fig. 8).

The distribution of microcharcoal particles, both concentration and influx, showed considerable variation throughout the profile, with the highest values recorded at depths of approximately 45 cm, 40 cm, 35–30 cm, 25–20 cm, and 17–12 cm. The maximum concentration (over 70%) and the maximum influx (over 600 grains cm⁻³ yr⁻¹) were found at a depth of 33 cm. A decrease in the amount of microcharcoal was observed from a depth of approx. 12 cm (Fig. 8).

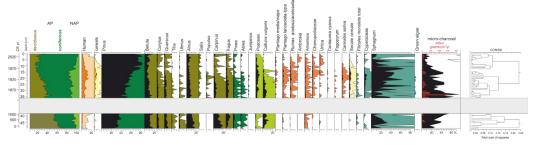


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Figure 8. Simplified percentage pollen diagram from the Wielkie Bagno peatland, with selected taxa, microscopic charcoal concentrations and influx presented. Pollen and microcharcoal percentages are shown in black, 10 times exaggeration is marked by colours, and charcoal influx is depicted as red bars.

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556 3.3.3 Plant macrofossil data (local vegetation)

- 557 As a result of the plant macrofossil analysis (Fig. 9), five local macrofossil assemblage zones (LMAZ) were determined:
- 558 (1) LMAZ-1, 50–37 cm: this phase was characterised by a high proportion of roots (from 35 to 76%) and a large number
- 559 of uncategorised parts. Throughout the entire section, Sphagnum (including Secc. Cuspidata and Secc. Palustria) occurred





at a level of 1–5%. In the roof part of this phase, there was a sharp increase in the share of *Eriophorum*, from 1 to 13%.

Remains of *Alnus* and *Pinus* bark were found throughout the entire section. However, their share was not large, only *Pinus* at a depth of 37–38 cm had a share of 18%.

(2) LMAZ-2, 37–18 cm: this phase began with a significant increase in the share of *Sphagnum* Secc. Cuspidata (increase from 12 to over 70%). Compared to the previous phase, there was a clear decrease in the share of roots and uncategorised parts. *Eriophorum*, which occurred along the entire length of this phase, was characterised by a significantly greater share in the initial and final phases. The share of *Eriophorum* was clearly smaller at a depth of 24–31 cm and then fell below 10%.

(3) LMAZ-3, 18–7 cm: the boundary of this phase at a depth of 18 cm was determined by a significant decrease in the share of *Eriophorum*, whose share in this phase dropped to 0–2% at subsequent depths. *Sphagnum* Secc. Cuspidata was still at a high level. Fragments of *Pinus* bark were found at all depths, with the maximum occurring at a depth of 14–15 cm (27%). At a depth of 11–12 cm, *Polytrichum commune* appeared. However, its share in this phase was still small (1–4%).

(4) LMAZ-4, 7–2 cm: this phase was characterised by a clear and sudden increase in the share of *Polytrichum commune* and the appearance of *Aulacomnium palustre* at the expense of *Sphagnum* Secc. Cuspidata, whose share dropped even below 10%. *Eriophorum* did not occur in this phase. In addition to *Pinus* bark, there were also numerous needles and a pine bud scale.

(5) LMAZ-5, 0–2 cm: again, *Sphagnum* Secc. Cuspidata had a share of over 70%. The presence of *Polytrichum commune* and *Aulacomnium palustre* decreased to 0%.

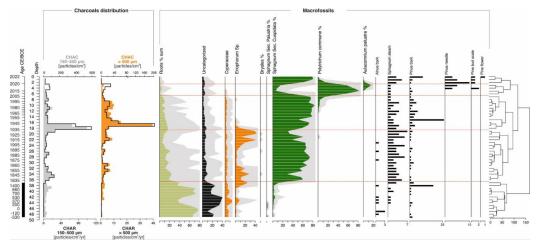


Figure 9. Macrofossil diagram and charcoal distribution: influx (CHAR, particles cm $^{-2}$ yr $^{-1}$) and concentration (CHAC, particles cm $^{-3}$) for macrocharcoal particles of two size classes, 150–500 µm (grey) and >500 µm (orange), from the Wielkie Bagno peatland. Red dashed lines indicate the boundaries between five local macrofossil assemblage zones (LMAZ).

3.3.4 Macrocharcoal data - long-term fire evidence

The period between approximately 330 BCE and 1400 CE was characterized by low and gradually increasing CHAR and CHAC values. The values of macro charcoal remains larger than 500 μ m ranged from 0.01 to 0.07 particles cm⁻² yr⁻¹ CHAR, while fragments in the 150–500 μ m range varied between 0.1 and 0.5 particles cm⁻² yr⁻¹ CHAR. A sudden shift





occurred immediately after the hiatus at a depth of 37 cm (\sim 1830 CE), where we observe a notable increase in fire activity, with macro charcoal remains increasing to 1.1–40 particles cm⁻² yr⁻¹ CHAR. In the 100–500 μ m fraction, values ranged from 0.1 to 108.5 particles cm⁻² yr⁻¹ CHAR. The peak concentration and influx of macro charcoal remains occurred at depths of 17 cm and 16 cm, corresponding to the years \sim 1941–1946 CE (Fig. 9).

3.3.5. Variation in biological assemblages across the peat sediment layers

The non-metric multidimensional scaling (NMDS) analysis based on pollen, plant macrofossil, and micro- and macrocharcoal influx data revealed clear compositional variation among biological assemblages across the peat sediment layers (Fig. 9). The k-means clustering approach identified five distinct clusters (Fig. 10a). Samples from cluster 4 and 1 stood out from the rest, representing, respectively, the oldest sediment layers below the hiatus, before ~1830 CE (37–50 cm), and the most recent surface layers after ~2015 CE (0–5 cm) (Fig. 10b). The remaining clusters were located closer to each other in the NMDS space, indicating higher similarity. However, cluster 2 stood out slightly from the others. Cluster 3 and 5 were the most similar, corresponding to the middle part of the record (~1830–1960 CE), with cluster 3 including samples just after the hiatus (~1830–1915 CE), and cluster 5 mainly representing samples after ~1915 CE. Samples in cluster 5 and 4 showed the highest internal similarity, with mean within-cluster Euclidean distances of 0.096 and 0.102, respectively. In contrast, the most modern samples from 0–12 cm depth (after ~1960 CE) were characterised by the highest internal compositional diversity of 0.202 (cluster 1) and 0.198 (cluster 2) (Fig. 10).



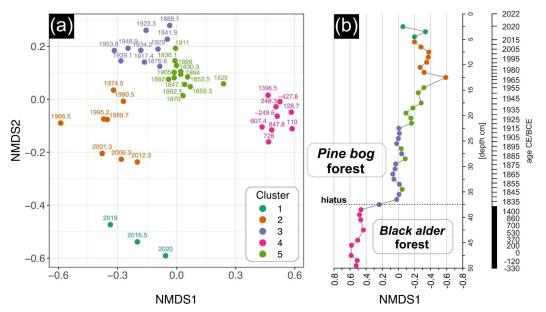


Figure 10. The non-metric multidimensional scaling (NMDS) and k-means clustering of biological assemblages across peat sediment layers from the Wielkie Bagno peatland (stress = 0.14). The analysis was based on pollen data (>1%), plant macrofossil data and micro- and macrocharcoal influx. (a) The NMDS ordination plot showing compositional variation among samples. Points are labeled by calibrated year (CE or BCE) and colored according to cluster group (k = 5). (b) Stratigraphic plot of NMDS1 axis scores by depth, illustrating temporal changes in biological assemblages' composition.





3.3.6 Hydrology reconstruction – testate amoebae data

Altogether, 43 species of testate amoebae were recorded in the peat core. The changes in the community of testate amoebae indicated four zones (Fig. 11):

TA-1, 48–36 cm: the lowest parts of the peat core were characterised by an extremely low concentration of testate amoebae. Single tests of *Cryptodifflugia oviformis*, *Amphitrema wrightianum*, *Archerella flavum*, *Centropyxis aculeata*-type and *Phryganella acropodia* were recorded.

TA-2, 36–16 cm: this zone was dominated by organic testate amoebae (around54–89%) and characterised by a strong dominance of one species – *Cryptodifflugia oviformis* (around 35–88% of the total number of testate amoeba tests). It was accompanied by *Galeripora discoides* (around 2–12%). The remaining community of testate amoebae was mainly constituted by *Amphitrema wrightianum*, *Archerella flavum*, *Centropyxis aculeata*-type, *Difflygia* sp. / *Netzelia*. *lithopila*, *Difflugia pulex*-type and *Phryganella acropodia*. The Shannon diversity index of the testate amoeba communities ranged between 0.5 and 2.5. Depth to the water table (DWT) was unstable and oscillated between around 17.2 cm and 32.1 cm. TA-3, 16–7 cm: in this zone the greatest change in the testate amoeba communities was observed. A rapid decrease of organic testate amoebae (around 35–68%) and a rapid increase of idiosomic testate amoebae to around 54% were recorded. *Cryptodifflugia oviformis* first decreased to around 23%, and next increased to around 66%. Its decline in the first half of the phase contrasted with an increase of *Galeripora discoides* to around 29%. The contribution of *Alabasta militaris* significantly increased to around 30%. The rest of the testate amoeba community was mainly constituted by *Difflugia leidyi*, *Euglypha ciliata*-type and *Euglypha compressa*. The Shannon diversity index of the communities ranged between around 1.2 and 2.2. A trend of a slight increase in the DWT was observed in this zone. DWT oscillated between around 17 cm and 32.1 cm.

TA-4, 7–0 cm: in the top layer of the peat core idiosomic testate amoebae were found to be dominant (around 86%), including species such as *Alabasta militaris* and *Nebela tincta*, accounting for around 33% and 27% of the total community, respectively. *Cryptodifflugia oviformis* disappeared in this zone, whereas the contribution of *Galeripora discoides* increased to around 24%. The Shannon diversity index was high, varying between 2.3 and 2.5, whereas the DWT increased slightly (oscillation between around 13.9 cm and 20.1 cm).

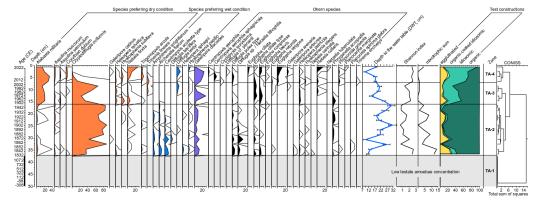


Figure 11. Testate amoebae percentage diagram for Wielkie Bagno peatland with 10 times exaggeration (presented as black lines) and with quantitative reconstructions of depths to water table (DWT), diversity (Shannon index), sum of mixotrophic species and divided into test constructions of testate amoebae.





3.4 Human archives

Query in archives evidenced 133 cartography and written sources relevant for our study area. The majority of historical data was related to land use/economy (Table S2). The most detailed quantitative data were found for the land use and settlement intensity in the second half of the 1700s in the direct surroundings of our study site, documenting an increase by over half (51.9%) in the rent paid for fields and meadows in the Tereszpol area between 1757 and 1775 (Table S3), as well as an increase in the number of hutters in both, the Zwierzyniec Key of the Zamoyski Family Estate (including Wielkie Bagno and Tereszpol) and in the vicinity of the Tereszpol village in the period 1759–1792 (Table S4). We recorded 20 historic maps depicting our study site and/or its direct surroundings (Fig. 1f–i).

4 Discussion

In this interdisciplinary study, data from nature (climate, peat sediment, tree rings from living peatland pines) and human archives (Fig. 2) allowed us to document a complete shift in a peatland ecosystem from *Alnus* to *Pinus* and *Sphagnum* dominance, which occurred on a time scale of over two millennia of our reconstruction. This transition from the alder bog forest (i.e., alder carr, alder swamp forest) to the Scots pine bog forest resulted in substantial changes in ecosystem's diversity and functioning (Figs. 7 and 10–11). To our knowledge, this is the first record of such a conversion in temperate Europe (cf. Barbier and Visset, 1997). Despite the challenges in unequivocal interpretations of certain aspects and some limitations of our data, we were able to demonstrate that the human impact on this transformation was undeniable.

4.1 Dynamics of the peatland ecosystem revealed by multiple archives

The archives we studied covered the last >2,300 years with different resolution and overlaps (Fig. 2). Based on the longest record from the peat archive and the associated palaeoecological proxies, coupled with data from the other archives, we distinguished three main periods of our environmental reconstruction: (1) the oldest period, covering approx. 1,700 years (330 BCE–1400 CE), (2) the transition period of approx. 430 years (1400–1830 CE), and (3) the last period of approx. 200 years (1830–2022 CE).

4.1.1 Alder (Alnus) bog forest (ca. 330 BCE-1400 CE)

The oldest period of our ecosystem dynamics reconstruction was only covered by the peat archive (Fig. 2). A 25 cm long section of heavily decomposed peat documents the beginning of the functioning of the Wielkie Bagno ecosystem in this part of the peatland basin. The very low peat accumulation rate of about 140 years per cm on average (0.06 mm yr⁻¹, Fig. 7) indicates that the conditions for organic matter accumulation were not favourable during this period of the ecosystem's history and that continuous decomposition was taking place. There are several indications that our study site was covered by an Alnus glutinosa bog woodland (i.e., alder carr, black alder swamp forest, black alder bog forest) during this oldest period (Fig. 2). Alder bog forest is characterised by wet soils and frequent fluctuations in water levels, which are closely related to the high groundwater table and seasonal fluctuations in the amount of stagnant water (Faliński, 1986; Solińska-Górnicka, 1987; Leuschner and Ellenberg, 2017a). The quantity of Alnus macrofossil remains was highest in this phase. Further, the aforementioned low peat accumulation rate, high occurrence of roots and uncategorised parts together with a low share of Sphagnum and substantial share of Cyperaceae (including Eriophorum) macrofossils documented unstable moisture conditions (Shaver et al., 1986; Rydin and Jeglum, 2013; cf. Pędziszewska and Latałowa, 2016) (Fig. 9). The palinological data reflected a substantial share of deciduous forests in the area. In addition to Alnus, Carpinus, Quercus, Fagus and Betula also had a relatively high (10–20%) proportion of pollen grains. Conifers in the surrounding landscape were represented by Abies, Picea and Pinus, with the latter accounting for the largest proportion (share of approx. 25-40%). This is consistent with historical accounts, revealing a diverse tree species composition and a high share of





deciduous tree taxa in the Solska Forest before the onset of intensive settlement and traditional forest industry development, which first began in the 16th century (Kubrak, 2010), so in the next period of our environmental reconstruction. Interestingly, the relatively high proportion of *Calluna* pollen as well as microcharcoal concentration (Fig. 8) indicate noticeable fire activity in the landscape around our study site during this phase of its history (Rösch, 2000; Pędziszewska and Latałowa, 2016). However, the very low macrocharcoal concentration (Fig. 9) clearly suggests low fire occurrence, which was probably related to the low flammability of the ecosystem at this time. Considering the large number of sand dunes surrounding the Wielkie Bagno peatland (Popielski, 1992; Fig. 1c), these were probably the sites most strongly associated with fire at this time. Although the region was still largely uninhabited during this period (Szczygieł, 1985; Buraczyński, 2008; Kubrak, 2010), the anthropogenic pollen indicators (*Artemisia, Plantago lanceolata*-type, cereals) in the profile proved the human presence in the landscape. *Urtica* pollen showed a slight increase at 44 cm (ca. 200–370 BCE), suggesting a probable rise in the peatland trophy (Behre, 1981; Zarzycki et al., 2002) (Fig. 8). This coincided with a small decrease in the share of roots and an increase of uncategorised parts, *Eriophorum* and *Cyperaceae*, indicating a possible drop in the peatland wetness and providing further evidence of the hydrological instability of the ecosystem.

4.1.2 Transition period (ca. 1400–1830 CE)

Due to the discontinuous sediment accumulation and the resulting hiatus, there is no peat sediment documenting this period (Figs. 2 and 7). However, the other archives have partially filled this gap in the stratigraphy, including annually resolved tree ring data for the last one hundred years of this phase, as well as mostly qualitative and often intermittent historical records encompassing mainly the period from the mid-18th to the mid-19th century. Information on earlier periods is limited (Fig. 2).

Yet, valuable records of the factors and processes that shaped the Solska Forest during the 16th-18th centuries are given by the historical study of Kubrak (2010), which demonstrated the crucial role of human activities during the transition period of our reconstruction. According to this study, settlement development in the Solska Forest increased from the second half of the 16th century as a result of the expansion of the manorial-serf economy and the gradual shift from the pastoral and beekeeping economies to agriculture. This was closely linked to the emergence of a very receptive market in Western Europe for grain, timber, and forest products such as ash, potash, and tar and led to significant deforestation in the area, initially (and especially) on the more fertile soils. In the late 1600s, large-scale deforestation occurred in the areas north of the Tanew River in the Księżpol area due to potash and charcoal production. At the end of the 17th century, the village of Tereszpol (approx. 5.8 km northwest of our study site) was founded. From the beginning of the 18th century, the Tereszpol area was intensively used for the production of ash and charcoal, as well as wood tar and wood shingles, which led to deforestation. Ash burning and potash production were the most destructive forms of forest utilisation. The strongest development of ash production in the Solska Forest took place from the second half of the 17th century. Further development of this type of forest industry took place in the late 18th century in connection with rapid settlement development in deforested areas. Existing settlements were enlarged and new villages were established. One of these was the village of Aleksandrów, located approx. 8 km south of our study site, which was settled in 1791 and where intensive ash production has taken place ever since. Forest utilisation was also intensified by the establishment of new towns and cities, including those close to our study site such as Biłgoraj, which was founded in 1578, and Józefów, which was settled in 1725. Along with the deforestation associated with settlement activity and the development of forest industry, as well as forest use by peasants and townspeople, the tree species composition in the Solska Forest changed. The mixed forests, which consisted of tree species such as fir, spruce, beech, oak, hornbeam, pine, birch, lime and yew, were gradually transformed as a result of selective use of certain taxa (e.g., oak, yew), whose wood was particularly



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preferred for various purposes (every-day objects, construction timber, etc.), of damage, especially to tree regeneration, caused by the grazing of domestic animals (e.g., sheep, cattle) in the forests, and of ash burning (exceptionally affecting beech, but also oak and hornbeam). In consequence, the proportion of deciduous tree species decreased and the degree of forest openness increased, which in turn favoured the advance of light-demanding taxa such as *Pinus*, *Betula*, and *Corylus*. The establishment of pine was particularly facilitated by fires, as it colonised burned areas faster than the other tree species. By the end of the 18th century, Scots pine was already predominant in the Solska Forest, while fir, beech, spruce, and hornbeam were only found locally (Kubrak, 2010).

Because of the hiatus in our peat archive (Fig. 2), we cannot corroborate this picture with pollen, macrofossil and sedimentary charcoal data, which are missing for this period of the ecosystem's history. However, our palaeoecological record for the neighbouring periods (Figs. 8-9), coupled with the tree ring archive covering the last hundred years of this phase (Fig. 4), support the findings from historical accounts (Kubrak, 2010), highlighting the value of both, archival sources, and interdisciplinary, multi-proxy studies. All of the Scots pine trees we sampled, established before the end of this period, documenting successful recruitment throughout the 1700s and in the 1820s (Fig. 4), which aligns with the phenomena discussed above (Kubrak, 2010). Further, the archival sources we studied confirmed both the increasing colonisation of the study area in the second half of the 18th century (archival source 1, AS1, full list of archival sources given prior to the reference list; Tables S3 and S4) and the dominance of pine with admixture of spruce and beech in the late 18th century as shown in the forest management maps of our study site (AS2; Janeczek et al., 2015). Particularly interesting data were supplied by the Austrian military survey map and its description from 1779 (actually the first description of the local environment of our study area), which documented our study site and its immediate surroundings as a very wet and marshy area interspersed with dense coniferous forests, pastures, and meadows. The high water level near the Wielkie Bagno peatland was reported as being maintained by the regularly overflowing Ratwica stream (Janeczek et al., 2015). During the surveying work carried out in the mid-1780s for the Austrian land cadastre (Ger. Josephinisches Lagebuch), the surroundings of our study site belonged to the cadastral village of Tereszpol. Its forests were divided into three main areas: Ratwica, Stoczyska, and Bukownica, with the Wielkie Bagno peatland located in the largest of these areas (Ger. Revier) Ratwica, which covered approximately 5,612 Austrian morgens (approx. 3,229 ha) (AS3). The creation of the cadastre resulted from the fact that the southern part of the Polish lands (including the Zamoyski Family Estate) was annexed to Austria in 1772 and was thus subject to new legislation (Piller, 1782; Davies, 2005) and farreaching economic reforms (Jones, 2015; Carvalho, 2018). In line with the land use recommendations of the Austrian Forest Act of 1782, the Enlightenment forest management model (Hölzl, 2010) was introduced. One of the first measures taken by the Austrian authorities was to secure their new areas with regard to military reconnaissance through accurate mapping, combined with a description of the manoeuvrability of military units and supply logistics under different geographical conditions (Janeczek et al., 2015). For each settlement in the newly acquired territories, detailed data on agriculture, taxes and forest management were collected and compiled in a cadastre. Its purpose was to estimate the value of productive land (including forests) and to standardise the taxation of real estates. In connection with the forest areas, precise estimates were made for each village, covering all aspects that could be of economic importance. The system of land use and economic utility of forests for the Tereszpol cadastral village was edited in 1786. During the survey, several hundred morgens were excluded from all forest areas in Tereszpol, as the waterlogged soils made economic activity unreasonable. The technical estimates of the individual areas showed that the Ratwica area (including our study site) was considered suitable for timber production in its entirety. The indicated area was classified as pine forest (softwood – Ger. weiches), with aspen in admixture. The forest stands were in good condition and suitable for utilisation over several decades. Based on tree ring samples taken from five different sites in the area, the approximate age of the stand was determined to be 31-55 years (Ger. Dermaliges Alter der Hölzer) (AS3). This means that the forests in the vicinity of the





Wielkie Bagno peatland recruited around 1730–1750, which also corresponds with our tree ring data (Fig. 3). The cadastral survey recommended an optimal tree felling age (Ger. *Schlagbar*) of 80 years for the Ratwica site. In addition, the characteristics of the terrain and the possibility of other economic activities in the area were described. The entire Ratwica area was generally classified as a plain with sandy soils. The pastures and forest clearings present in the area were given a low utilisation value (AS3).

The early 19th century is a period in which the number of proxies provided by the various archives analysed increases (Fig. 2). This phase of our environmental reconstruction evidenced a cohort regeneration of Scots pine as documented by the tree ring data (Fig. 4), likely being associated with various factors substantially altering local environmental conditions, such as peatland drying, including drainage (Linderholm and Leine, 2004; Freléchoux et al., 2000, 2003, 2004; Edvardsson et al., 2012a, b, 2014, 2015a), clear cutting (Freléchoux et al., 2003, 2004), peat mining (Freléchoux et al., 2000) or fire (Filicetti and Nielsen, 2020). Based on the tree ring data on the early Scots pine growth in the same habitat conditions in the Białowieża Forest, north-eastern Poland, which proved seven years as the time needed to reach breast height (E. Zin, K. Pilch, M. Klisz, unpubl. data) and on the relatively high growth rate of our sample trees in the young age (Fig. S6), we propose that seven years may be a reliable value for determining the real tree recruitment dates. Hence, the pine cohort recorded in our study site, most likely originated from 1816–1820, during a period of unfavourable tree growth conditions evidenced by a growth depression recorded in older pines as revealed by both site chronology (Fig. 3) and the individual tree growth series (Fig. S6). This growth depression followed a positive pointer year 1813 (recorded by all sample trees) and an interesting signature year 1812, the latter characterised by both positive and negative growth reactions (Figs. 4 and S6) recorded by three (33.33 %) and six (66.67 %) sample trees, respectively, suggesting fire disturbance rather than climate as the possible main driver of tree growth (Zin et al., 2015).

We acknowledge that our dendrochronological fire history record was substantially constrained by our sampling design. The sampling procedure we used was not designed for a tree ring fire history reconstruction (Arno and Sneck, 1977; McBride, 1983; Van Horne and Fulé, 2006), so it definitely could not provide a complete inventory of fire years, especially considering the complex process of fire scar formation in trees (McBride, 1983; Farris et al., 2010; Piha et al., 2013). However, fires in the Solska Forest during this period of our study site's history were mentioned in the historical data (AS6-7; Kubrak, 2010). Further, fire disturbances have been documented as frequent and probably crucial for the development and dynamics of peatland ecosystems in temperate latitudes (Marcisz et al., 2015; Sutheimer et al., 2021). They have also been shown to both limit and enhance Scots pine growth, not only in mineral soils (Blanck et al., 2013; Zin et al., 2015), but also in peatlands (González de Andrés et al., 2022). Therefore, we consider fire to be a very likely disturbance that affected our study site in 1812. Yet, since our wood samples showed no fire scar (cf. Fig. 4), it is also possible that the growth response observed in our sample trees in 1812 was a reaction to a disturbance in the previous year, 1811, as the effects of fire on tree growth can also be documented with a one-year delay by tree rings (González de Andrés et al., 2022). Remarkably, both the historical and climate data for the years 1811-1812 support our conclusion that a fire disturbance was very likely at our study site in 1811 or 1812. The daily activity protocols for the Zamoyski Family Estate frequently mention the severe drought in the summer of 1811, which led to crop failures and numerous forest fires. This is also confirmed by the records of the municipality of Tereszpol village, which is located near our study site, and which contain complaints about drought and crop failures at the turn of July and August 1811. Crop failures were also reported for the year 1812 in the daily activity protocols (AS6-11). This is consistent with the climate data for the region documenting very dry and very warm summers during 1811–1812 (Fig. 3).

Since peatland fires are well documented as effective peat consumers regardless of the combustion type (smouldering or flaming) (Lavoie et al., 2005; Benscoter and Vitt, 2008; Turetsky et al., 2015), the fire in 1811/1812 is also a very likely cause of the hiatus in our peat archive (cf. Marcisz et al., 2015). Another fire that could be responsible





for this is a fire in 1830, which marks the end of this period of our reconstruction and which all our sample trees survived (Fig. 4). This fire was recorded by almost all of them, namely 93.33%, as a narrow or wide ring (cf. Fig. S6) or as a fire scar, by one of our sample trees (Fig. 4). As for 1812, we interpret this different growth response in 1830 as a fire effect, relying on existing data showing both positive and negative post-fire growth responses in Scots pine trees (Blanck et al., 2013; Zin et al., 2015; González de Andrés et al., 2022). Interestingly, a negative growth response was found in both 1830 and the following year 1831 (Figs. 4 and S6), with both years classified as negative pointer years (data not shown), confirming the previously discussed delay in the effects of fire on tree growth (González de Andrés et al., 2022). Further arguments in favour of fire as the cause of the hiatus in our peat sediment chronology are a pronounced horizon rich in macroscopic charcoal that we observed in the peat core in the transition between the two lithological segments and the climate data from Kraków documenting the first decades of the 19th century (period: 1812–1828) as a clearly dry and warm period (Figs. 3 and S3), which could result in the possibly increased fire occurrence (González de Andrés et al., 2022). Nevertheless, drought alone cannot be completely ruled out as another possible reason for the hiatus in our sedimentary record (Van Geel et al., 1981), as a drop in the water table leads to peat oxidation and mineralisation and thus to peat decomposition and loss (Päivänen and Hånell, 2012; Joosten, 2016).

Our climate data (Figs. 3 and S3) also support the interpretation of the relationship between climate and tree growth that we found in the first decades of the 19th century. We were able to demonstrate a positive correlation between the radial increment of peatland pines and hydrological parameters: precipitation, SPEI3, and SPEI6 in spring and summer of this period (Figs. 6 and S5), which is consistent with data from south-west Siberia, the north-eastern Italian Alps, Sweden, Lithuania, Belarus and northern Poland (Linderholm et al., 2002; Vitas and Erlickytė, 2007; Cedro and Lamentowicz, 2011; Edvardsson and Hansson, 2015; Dinella et al., 2021; González de Andrés et al., 2022; Ignatiev and Yermokhin, 2022). This effect could be related to the water stress to which peatland trees are exposed during dry periods when the water table is low, that may result in reduced physiological processes such as stomatal conductance or photosynthesis (Dang et al., 1991; Pepin et al., 2002) as well as reduced plant growth, including limited root development (Pearson et al., 2013). Remarkably, a positive influence of precipitation during the growing season on the radial growth of Scots pine has been broadly reported at mineral soil sites across Eurasia, including Poland (Linderholm et al., 2002; Opała, 2015; Misi et al., 2019; Harvey et al., 2020; Waszak et al., 2021; González de Andrés et al., 2022; Janecka et al., 2025).

However, the latter part of this period in the history of our study site was not completely homogeneous in terms of climatic conditions, which is reflected in our climate record (Figs. 3 and S3) and historical accounts, especially the daily activity protocols of the Zamoyski Family Estate (AS4–13). In addition to droughts and crop failures, hailstorms were also reported in the years 1811–1812 (AS6–11). Interestingly, in the dry first half of the 19th century (Fig. S3), flooding events were recorded in the Solska Forest, including areas close to our study site. In August 1813, the bridges on the road to Biłgoraj (on the Łada River) were destroyed, the lock in Ciosmy was broken, and the Branwia, Bukowa, and San rivers overflowed their banks (AS11–12). Very wet conditions and floods (e.g., on the Tanew River) were also reported for the years 1814–1815 (AS14). This information is confirmed by the climate data we analysed, which show wet conditions in 1813 and 1815 (Figs. 3 and S3) and could explain the positive correlation between pine growth and hydrological parameters we found during this period (Figs. 6 and S5). Further, the very high tree growth in 1813 displayed by all trees in our sample (Figs. 4 and S6) may reflect not only the positive growth response to a previous fire disturbance in 1811/1812, as mentioned above, but also high precipitation in summer 1813 (Fig. 3; AS11–12), or both. Yet, the lack of other environmental proxies (testate amoebae, sedimentary charcoal or fire scar data) definitely limits the possibilities to disentangle these effects.





4.1.3 Sphagnum & Pinus expansion – transformation into Scots pine bog forest (ca. 1830–2022 CE)

The next phase in the development of the Wielkie Bagno peatland was characterised by the gradual increase in the dominance of *Sphagnum* and *Pinus* in the peat profile. Noteworthy, already the end of the earlier phase in the peat archive was marked by a slight increase of *Sphagnum* and the highest proportion of *Eriophorum* macrofossils (approx. 20%), suggesting the beginning of a gradual development towards more acidic, ombrotrophic conditions (Fig. 9). For the last period of our environmental reconstruction, we were initially able to distinguish three sub-periods based on the macrofossil data, which were later confirmed by the other peat sediment proxies and are reflected in the climate, tree ring and historical data.

ca. 1830-1947 CE

The period 1830–1947 CE was characterised by a gradual decline of deciduous trees in the landscape such as *Quercus*, *Carpinus*, *Carylus*, *Fagus*, *Betula*, and *Alnus*, and a continuous increase in the *Pinus* occurrence. Share of the non-arboreal pollen (NAP) was high, including *Poaceae*, cereals, and several other anthropogenic indicators such as *Plantago lanceolata*-type, *Rumex*, and *Cannabis sativa* indicating the increasing human impact on the study site and its surrounding (Behre, 1981; Poska et al., 2004) (Fig. 8). The changing share of *Eriophorum* macrofossils, with high values in the beginning and in the end of this period, proved unstable moisture conditions of the peatland (Shaver et al., 1986; Rydin and Jeglum, 2013; Marcisz et al., 2015; Słowiński et al., 2016) (Fig. 9), which is also supported by our reconstruction of depth to the water table (DWT) based on testate amoebae. This period is marked by the presence of *Galeripora discoides*, which may indicate hydrological instability of the Wielkie Bagno peatland during that time (Lamentowicz et al., 2009; Sullivan and Booth, 2011; Łuców et al., 2021, 2022). However, during this period, the testate amoeba community was dominated by *Cryptodifflugia oviformis*, a species typically associated with dry habitats (Mazei and Tsyganov, 2006; Łuców et al., 2020), suggesting prevailing dry conditions despite signs of hydrological instability. The overall trend of declining water levels observed on Wielkie Bagno (Fig. 11) aligns with the broader understanding that most European peatlands were drier than in the past during this period (Swindles et al., 2019).

Numerous European studies (also from northern Poland) have shown that peatland hydrology is driven by both climate and human impacts, often interacting (e.g., Lamentowicz et al., 2009; Van der Knaap et al., 2011; Gałka et al., 2014; Łuców et al., 2021). We cannot exclude a possible climate forcing upon fluctuations of the water levels we found (Fig. 11), since several exceptionally cold and dry years fell in the periods characterised by the strongest water level declines in our record (notably 1856, 1858, and 1869 in the 1850s/60s; 1894 in the 1890s; and 1942, 1944, and 1948 in the 1940s), as shown by the climate data we analysed (Fig. 3). Nevertheless, we consider the connection between the lowering of the water table in the Wielkie Bagno peatland and the drainage activities to be very probable. The historical data we examined revealed that drainage measures were carried out in our study site and its immediate vicinity from the late 19th to the first half of the 20th century (Fig. 1f-i). As a very wet and swampy area (Janeczek et al., 2015), the Wielkie Bagno peatland and its surroundings posed significant management challenges. Estate maps from the second half of the 19th century showed that attempts to utilise the wetlands and floodplains around our study site were successfully implemented. The Rakowe Bagno peatland, located directly south of the Wielkie Bagno peatland, was drained between around 1850 and 1939 to create land for cattle grazing (AS15; Fig. 1g). Further drainage activities were undertaken after the end of the partition period (i.e., after World War I), when the new Polish authorities continued the earlier drainage plans. This is confirmed by the historical data stored in the Archives of the Zamoyski Family Estate (APL, AOZ), which include not only plans but also records of actual measures taken to modernise the estate and increase its economic efficiency. Two maps from the first half of the 20th century show a considerable increase in the drainage system of our study area, especially in the number of ditches located directly in the Wielkie Bagno and the Rakowe Bagno peatlands





(Fig. 1h–i). Remarkably, the ditch located in the central part of the Wielkie Bagno peatland, along its west-east axis, remains visible in the terrain topography, as evidenced by the digital terrain model (Fig. 1c).

The hydrological instability of our study site as proven by the DWT fluctuations we found (Fig. 11), coupled with the climatic conditions during this period (Figs. 3 and S3), were important for shaping the temporal variability in climate sensitivity of peatland trees during this phase of peatland history (Figs. 6 and S5). The climate data documented the first phase of this period (1829–1855) as humid (Figs. 3 and S3). The entire period (1830–1947) proved to be generally cold, with a slight warming in the last phase, in the 1930s-1940s (Fig. 3), which is consistent with existing climate reconstructions (Büntgen et al., 2021b; Björklund et al., 2023). Under the overall wet and cold conditions in the first part of this period, until the late 19th century, our tree ring archive showed a growth-limiting effect of high temperatures during the growing season (spring-summer) (Fig. 6), which is consistent with data from drained peatlands in northern Poland (Cedro and Lamentowicz, 2008, 2011; Cedro and Sotek, 2016), suggesting that drainage measures in our study area had the predominant effect on pine growth at this time. In the second half of the 19th century, this effect was combined with the negative correlation between mean air temperature in autumn of the current year (October-November) and tree growth (Fig. 6), which agrees with data from southwest Sweden, where a comparable relationship was found for September-October. However, as this study (Janecka et al., 2025) did not discuss the eventual impacts of drainage (especially in the area surrounding the study site), it is not readily possible to judge whether the recorded pattern is a direct analogue for our results. By contrast, the relationship between tree growth and climate that we found in the last phase of this period, from the late 19th to the first half of the 20th century, demonstrating the positive correlation with precipitation and SPEI in early summer (May-July) (Figs. 6 and S5), can be associated with aforementioned drainage activities in our study area (Fig. 1f-i), lowering of the DWT (Fig. 11), and the generally dry conditions (Figs. 3 and S3). Interestingly, it aligns with our results for the first decades of the 19th century (1812-1828) (Figs. 6 and S5) and is consistent with numerous studies across Eurasia (see earlier discussion, Section 4.1.2).

The gradual decline in microcharcoal particles and *Calluna* pollen (Fig. 8) suggests a progressive decrease in landscape-level fire activity during this phase of peatland history, which agrees well with data demonstrating a continuous reduction in the forest fire frequency over the last centuries as a consequence of land use change and fire suppression both regionally (Rolstad et al., 2017; Ryzhkova et al., 2020; Zin et al., 2022) and globally (Nowacki and Abrams, 2008; Wallenius, 2011). Nevertheless, the sediment charcoal data (both microcharcoal and macrocharcoal) confirm that fire disturbance still occurred in our study area and its surroundings during this period, especially in the 1830s–1860s, in the late 19th century (1880s–1890s), and around 1940–1945, as shown by the peaks in charcoal distribution we recorded (Figs. 8–9). The highest distribution of the macrocharcoal particles in the profile (both in terms of influx and concentration) documented around 1940–1945 (Fig. 9) was probably related to various wartime events, including resistance movements or other military operations that took place in the vicinity of the Wielkie Bagno peatland during World War II (Klukowski, 1945–1947). As already mentioned, our tree ring data confirmed fire disturbance at our study site in the first half of the 19th century (Fig. 4; Section 4.1.2).

It is noteworthy that in addition to the information on the drainage of the Wielkie Bagno peatland and its surroundings in this period of our reconstruction (Fig. 1f–i), the human archives also provided valuable data on the forest structure and logging campaigns. The forest inventory of 1924 (AS16) shows that the stands around the peatland were dominated by pine populations of various age classes from 70 to 160 years, which is consistent with forestry documents from the late 18th century that demonstrate a high proportion of pine forests in the area even earlier (AS2; Section 4.1.2). As the leaving of seed trees was used in forest management in the early 20th century (AS16), some individuals may have been older. Thus, the 1924 forest inventory data reflect effective pine recruitment in the 1760s–1850s, probably even earlier. This clearly agrees with our tree ring data (Fig. 4) and confirms the conditions for successful tree establishment





in our study site both in this and the earlier period of its history. However, there were also periods of increased tree felling during this phase. In 1844, the decision of the then landowner to reduce the number of professional forest managers and transfer responsibility for the forests to the peasants resulted in considerable deforestation and devastation, which in turn led to the reintroduction of the old rules from the 1850s onwards (Rajca, 1972). The abolition of serfdom in the 1860s was followed by increasing, often unregulated or illegal logging by peasants who saw tree felling as a way of realising their new land rights (Mazurek, 1957). In the early 20th century, the forests surrounding our study site became part of the Tereszpol Forest District and were divided into concessions and forest sub-districts (AS20). After World War I, some of the estate's forests were sold to support its rebuilding. The increasing demand for timber in the 1920s triggered further intensive logging (greater than the growth of wood biomass) that levelled off after the introduction of rational forest management in the 1930s (Kozaczka, 2002).

ca. 1947-2004 CE

The second half of the 20th century brought further changes in the development of the Wielkie Bagno peatland. A high proportion of Sphagnum was accompanied by the disappearance of Eriophurum macroremains and a further increase in Pinus pollen (Figs. 8-9), documenting the gradual acidification of the site (Clymo, 1984; Koks et al., 2025), which was possibly a consequence of the increasing share of pine-dominated forests in the region, including our study area (Lamentowicz et al., 2007; Bak et al., 2024, 2025; see also the following discussion). This process is probably also reflected in the strong decrease in the proportion of *Populus*, *Picea* and *Abies* pollen during this period, as well as in a further decline in deciduous tree taxa (such as Quercus, Carpinus, Corylus, Fagus and Alnus). The presence of anthropogenic pollen indicators proves the human impact on the landscape surrounding our study site. Interestingly, this phase of peatland history is characterised by a very sharp reduction in Calluna pollen (Fig. 8). This could be related to the general decline in fire occurrence during this period, as shown by the decrease in micro- and macrocharcoal distribution, with only sporadic fire activity (Figs. 8-9), apparently indicating further land use changes and fire suppression measures in the region (cf. Ryzhkova et al., 2020; Zin et al., 2022; see earlier discussion) that would likely eliminate frequent surface fires, which in turn would lead to decreasing forest openness (Niklasson et al., 2010; Zin et al., 2015), being definitely unfavourable for the light-demanding heather Calluna vulgaris (Ellenberg et al., 2001; Zarzycki et al., 2002; cf. Skre et al., 1998). Around 1980 (depth: 11 cm), a decrease in Pinus pollen was observed with a simultaneous increase in non-arboreal pollen (such as Poa) (Fig. 8), indicating an increase in the landscape openness (Sugita et al., 1999). This could be the result of clear-cutting in the vicinity of our study site. Indeed, about 450-500 m southwest, there is a group of pine-dominated stands currently 37-46 years old (total area: 10.25 ha) and several other patches of younger pine stands (aged 30-50 years) surrounding our peat sampling site (Forest Data Bank, https://www.bdl.lasy.gov.pl/portal/mapy, accessed: 2025-01-15), which are a legacy of logging operations in the 1970s-1990s.

The testate amoebae data showed an increase in water level as demonstrated by the DWT reconstruction. In addition, the strong increase in the proportion of *Galeripora discoides* (an indicator of wet conditions) combined with a decrease in *Cryptodifflugia oviformis* (an indicator of dry conditions) (Fig. 11) is further evidence of water level fluctuations in this phase of our study site's history (Mazei and Tsyganov, 2006; Lamentowicz et al., 2009; Sullivan and Booth, 2011; Łuców et al., 2020, 2021). These changes in peatland hydrology could be related to both hydroclimatic conditions and nationwide land use transformations during this period, including shifts in population density due to migration associated with new state boundaries, fluctuations in arable land, and large afforestation campaigns (Broda, 2000; Gorzelak, 2004). The climate data show that this period was relatively dry and has warmed since the 1980s (Figs. 3 and S2), which is consistent with regional and global trends (Degirmendžić et al., 2004; Büntgen et al., 2021a; Björklund





et al., 2023). In conjunction with the above-mentioned dynamics of the DWT (Fig. 11), this corresponds well with the tree growth response we have documented. During this period, a clear negative correlation of tree growth with summer (August) temperatures was observed in combination with a positive correlation with precipitation in late winter/early spring (February). Our results are comparable with data from northern Poland, where a negative impact of high temperatures in summer (June, August) (Cedro and Sotek, 2016) and a positive (although not always significant) relationship between tree growth and precipitation in February and March (Cedro and Lamentowicz, 2008, 2011) were found in some Scots pine populations growing in peatlands. Likewise, a growth-promoting impact of precipitation in February or March has been documented for *Pinus sylvestris* in peat soils in southern Sweden (Linderhom et al., 2002; Edvardsson and Hansson, 2015). These results may be related especially to snow cover dynamics. The advanced biological spring and the general decrease in the frequency and duration of snow cover occurrence in recent decades reduces snowmelt water availability and potentially leads to early spring drought (Degirmendžić et al., 2004; Kreyling, 2010), which would explain the positive response of tree growth to precipitation. On the other hand, the growthaccelerating effect of warm winters, indicating an earlier onset of secondary meristem activity or photosynthetic activity in winter, can lead to higher storage of non-structural carbohydrates which can facilitate tree growth in spring irrespective of precipitation. Interestingly, we also recorded a negative effect of wet conditions (precipitation and SPEI3) in spring, summer and autumn (Figs. 6 and S5). Besides the complex relation between tree growth and the hydroclimatic conditions, this could reflect a possible recovery of the Wielkie Bagno peatland after previous disturbances, such as drainage activities that took place in the former period (Fig. 1f-i). Our data are consistent with results from Sweden, Lithuania and western Siberia, where a negative correlation of Pinus sylvestris radial growth with spring (March) and summer (August) precipitation has been documented in undisturbed peatland sites (Linderholm, 1999; Edvardsson et al., 2015b; Blanchet et al., 2017; Janecka et al., 2025).

ca. 2004–2022 CE

The most recent period in the history of the Wielkie Bagno peatland (2004–2022 CE) was characterised by a decreasing share of non-arboreal pollen (NAP) as well as a decrease in the proportion of anthropogenic indicators, including cereals and taxa such as *Plantago* and *Rumex* (Fig. 8). This may reflect the decline in agriculture in the region, which led to the land abandonment and the resulting increase in forest cover (Gorzelak, 2004). In general, the regional vegetation and landscape features documented for the previous phase, such as the increasing proportion of *Pinus* and the limited fire occurrence (Figs. 8–9), were still present. The observed fluctuations in the DWT and the high proportion of *Galeripora discoides* (Fig. 11) also demonstrate the hydrological instability of our study site (Lamentowicz et al., 2009; Sullivan and Booth, 2011; Łuców et al., 2021) as in the preceding period. In this phase, macrofossils of *Polytrichum commune* and *Aulacomnium palustre* suddenly appeared at the expense of *Sphagnum* Secc. Cuspidata (Fig. 9), indicating a disturbance in the peatland hydrology and nutrient content (Toet et al., 2006; Purre and Ilomets, 2018) around 2005–2020 CE. The dominance of idiosomic testate amoebae, including dry indicators such as *Alabasta militaris* and *Nebela tincta* (Koening et al., 2018), suggests drying of the Wielkie Bagno peatland during this period. This is consistent with data from other studies in northern Poland (Gałka et al., 2022) and Europe (Swindles et al., 2019), which document peatland drying in recent decades as a result of climate change, particularly warming (Swindles et al., 2019).

As elsewhere (Ustrnul et al., 2021; Marosz et al., 2023), the climate data in our study area also show a substantial increase in temperature since the beginning of the 21st century (Figs. 3 and S2). We associate this with the negative correlation of pine growth with temperature and the growth-accelerating effect of the positive water balance (precipitation, SPEI3) in autumn (September–November) of the current season, which we have documented (Fig. 5). Remarkably, the positive correlation of Scots pine growth with precipitation and the negative correlation with temperature in the growing





season (spring-summer) was reported from both mineral and peat soil sites, albeit with highly variable and not always statistically significant results (Linderholm et al., 2002; Cedro and Lamentowicz, 2011; Edvardsson and Hansson, 2015; Edvardsson et al., 2015b; Blanchet et al., 2017; Janecka et al., 2025). A possible explanation for our results (Fig. 5) could be that the trees extend their growing season beyond summer due to climate change (R. Puchałka and M. Klisz, unpublished data) and thus also respond to hydroclimatic conditions in the autumn months. Photoperiod and air temperature were proven to have interactive effects on the growth cessation of both conifers and deciduous trees. Although data are remarkably scarcer than for growth onset, it has been demonstrated that global warming can either accelerate or delay the growth cessation of temperate trees, depending on the species or ecotype (Hänninen and Tanino, 2011). For three conifers, including Scots pine, it has been demonstrated that under a temperate climate, xylogenesis in latewood (both cell enlargement and cell wall thickening), lasted until September-November in the early 21st century (Cuny and Rathgeber, 2016). Further, there is also evidence that growth cessation of *Pinus sylvestris* in peat soils can occur as late as September, even if data on the wood phenology of peatland pines are extremely limited so far and cover very short periods (no longer than two years) (Smiljanić and Wilmking, 2018; Francon et al., 2024). However, the last two decades of peatland history also showed a growth-limiting (albeit not significant) influence of wet conditions (positive water balance, high precipitation) in spring-summer (Fig. 5), which was already observed in the previous phase. As such a relationship has also been found in undisturbed peatlands (Linderholm, 1999; Edvardsson et al., 2015b; Blanchet et al., 2017; Janecka et al., 2025), we see this as a possible indication of ecosystem recovery (see earlier discussion). Interestingly, this finding does not align with the aforementioned demonstration of drying documented during this period (Figs. 8-9 and 11), which shows the complexity of the peatland tree growth response that has been discussed in numerous studies (e.g., Linderhom et al., 2002; Edvardsson and Hansson, 2015; Dinella et al., 2019), and suggests that tree ring width alone may not be a sufficient proxy for assessing the climate-growth relationship of peatland trees (Dinella et al., 2021; Janecka et al., 2025).

4.2 The turning point – ecosystem change: its reasons and effects

The change we have documented from an *Alnus*- to a *Pinus*- and *Sphagnum*-dominated ecosystem (Fig. 10; Section 4.1), which, as we have shown, took place during the transition period of our environmental reconstruction (1400–1830 CE), probably had complex and interacting origins. Therefore, it may be difficult, if not impossible, to identify a single main cause, especially since it dates back to a period that is not fully recorded in the archives we have analysed (Fig. 2). However, as reflected in the ecosystem and landscape dynamics we have discussed (Section 4.1), we propose that this habitat transformation was initiated in the 16th to 18th centuries, and it is impossible to deny the role of humans in this ecosystem change, with several factors at play that we would like to review in more detail. In addition to human influence at the local and landscape level, other interrelated environmental phenomena and processes must also be listed.

Our study proves the crucial importance of human impact in shaping the long-term dynamics of the Wielkie Bagno peatland and its surroundings, as has been demonstrated for the entire terrestrial biosphere (Ellis et al., 2021). Although the Solska Forest was not densely populated until relatively late – the end of the 16th century (Szczygieł, 1985; Buraczyński, 2008) – the area was definitely not completely free of human pressure, which is confirmed by the occurrence of anthropogenic pollen indicators in the oldest part of our reconstruction period (Fig. 8). Nevertheless, the relatively low level of human activity recorded at that time was clearly not conducive to significant landscape changes, including deforestation (Samojlik et al., 2013a), similar to other locations in north-eastern Poland, where continuous forest cover was never fully disturbed (Zimny et al., 2017; Jaroszewicz et al., 2019) or where forest decline occurred much later (16th–17th centuries) compared to sites in the north-western and north-central part of the region (7th–9th centuries) (Marcisz et al., 2020; Czerwiński et al., 2022).



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Our study site, the Wielkie Bagno peatland, known in the late 18th century as Rakowe Bagno or Rakówka Bagno (Eng. Rakowe Swamp / Rakówka Swamp), and its surroundings were possibly used by the inhabitants of the neighbouring villages and forest settlements from the mid-17th century (AS17). Local settlement development followed the expansion of traditional forest industry in the area (Kubrak, 2010; Róg, 2021). Clusters of forest settlements were located along the nearby Ratwica and Rakówka streams, among others. Already at the beginning of the 18th century, some tar workers lived in the nearby village of Tereszpol and the surrounding forests (AS18). The inhabitants of the villages of Tereszpol and Hedwiżyn established enclaves of forest meadows near our study site (AS19). Our results on dynamic settlement development in the second half of the 18th century (Tables S3–S4) correspond well with the data for the region. In Europe, a steady increase in human population has been documented since 1700 CE together with an increase in anthropogenic ecosystem changes (Ellis et al., 2021), including substantial deforestation of large parts of the continent (Kaplan et al., 2009). For northern Poland, several studies confirmed the growing human impact on forest and peatland ecosystems with comparable timing of its onset: 1720s CE (Marcisz et al., 2020), ~1750 CE (Słowiński et al., 2019), 1790s/1800 CE (Czerwiński et al., 2021), 1830s (Bak et al., 2024). At sites in the vicinity of the Wielkie Bagno peatland, an increase in human activity was recorded in the uppermost sections of the peat profiles, as shown by pollen of anthropogenic indicators such as Artemisia, Asteraceae, Plantago lanceolata, Rumex, Urtica, Chenopodiaceae, cereals, etc. These profile sections have all been dated to the Subatlantic chronozone, although different dates in the Common Era have been attributed to them due to the varying temporal resolution of radiocarbon dating of the samples and the resulting time span covered by the peat archives (Bałaga, 1998; Korzeń et al., 2015; Margielewski et al., 2015, 2022). The most comparable time frame was reported from the Kobyle Jezioro peatland, where the beginning of the youngest period in its history was dated to 60 ±70 BP (i.e., 1890 ±70 CE) (Korzeń et al., 2015). Similarly, in the Obary and the Imielty Ług peatlands, located west of our study site (approx. 18 km and 47 km, respectively), the highest proportion of anthropogenic plants was documented in the most recent phase of vegetation development. However, radiocarbon dating of the samples is missing in this study, which precludes precise dating of the material (Mamakowa, 1962).

Interestingly, in all of the above palaeoecological datasets, the increase in human impact indicators is associated with a decrease in the proportion of deciduous tree taxa as well as an increase in the share of *Pinus* pollen, often coupled with a rise in non-arboreal pollen of terrestrial plants indicating landscape openness (e.g., Korzeń et al., 2015; Margielewski et al., 2015, 2022; Słowiński et al., 2019; Bak et al., 2024), which is fully consistent with our results (Fig. 8) and the environmental changes in the 16th-18th centuries in the Solska Forest, which we discussed earlier (Section 4.1.2). Deciduous trees such as hornbeam (Carpinus), birch (Betula), beech (Fagus) or oak (Quercus) were used extensively: for firewood, charcoal, ash, potash (especially white potash) and wood tar, construction timber (including material for shipbuilding), shoemaking and tanning, everyday objects, etc. (Kubrak, 2010; Samojlik et al. 2013b; Cywa, 2018), which resulted in the decline of deciduous forests in the landscape. The increasing human presence also leads to an increasing landscape openness caused by deforestation related to timber harvesting (Broda, 2000; Kubrak, 2010; Czerwiński et al., 2021), agricultural development (Kaplan et al., 2009; Ellis et al., 2021), or anthropogenic fire (Marcisz et al., 2015; Dietze et al., 2019; Bonk et al., 2022), which favours the spread of light-demanding pioneer tree species (Svenning, 2002; Dyer, 2010; Kubrak, 2010) such as Scots pine, especially on poor and dry soils, where it can outcompete other tree taxa due to its broad edaphic amplitude (Przybylski, 1993) or its high tolerance to frequent fire disturbances of both low and high intensity (Kubrak, 2010; Niklasson et al., 2010; Keeley, 2012; Zin et al., 2015). However, the increase in Pinus presence in the landscape may also directly result from human activities. Pinus sylvestris has been widely introduced into forests of Central Europe over the last 200 years (Broda, 1993; Schabel, 2001; Timbal et al., 2005; McGrath et al., 2015), leading to its large-scale dominance in the region, including Poland (Timbal et al., 2005; Leuschner and Ellenberg, 2017c; Zajączkowski et al., 2023). This was closely linked to the idea of sustainability (Ger.





Nachhaltigkeit) and sustainable forest use, which, initiated by von Carlowitz (1713), was further developed in Germanspeaking Central Europe in the late 18th and 19th centuries. Its basis was rationalisation, measurements, and calculations, while its main focus was on the production of wood biomass and its economic value. Consequently, rules for forest inventory (including cartography) and management were established, including the division of forest areas into management units, the formulation of rotation ages, the creation of tables allowing for effortless estimation of wood mass, etc. Besides sustained yield, minimum diversity was one of the key principles of quantitative forest management, as it enabled easy assessment, control and prediction of timber biomass. Therefore, even-aged monocultures were strongly favoured as a counterpoint to diverse and often unpredictable nature (Lowood, 1990). The German school of forest management spread to neighbouring areas, including the Zamojski Family Estate, whose owners were known to value highly qualified managers from abroad (Germany, Czech Republic, England) and who gradually introduced the principles of quantitative forest management into their estate from the 1770s onwards, including the main rule of continuity of wood mass production, rotation ages, parcelling into management units, certain measures to protect the forest from insect outbreaks and fires (Rajca, 1972), and, most probably, monocultures.

Land use changes, such as deforestation, can lead to hydrological shifts that promote the formation of new peatland types (Warner et al., 1989). Studies north of our study area (northern Poland) have shown that the introduction of pine monocultures into forest management has played a significant role in the dynamics of peatland ecosystems (Słowiński et al., 2019; Łuców et al., 2021: Bąk et al., 2024, 2025). A high proportion of *Pinus* plantations in the catchment area can lead to peatland acidification, which in turn can stimulate the expansion of *Sphagnum* (Lamentowicz et al., 2007; Bąk et al., 2024, 2025; Marcisz et al., 2025). In addition, colonisation by *Sphagnum* can exacerbate acidification (Gorham et al., 1987) through cation exchange between the cell walls of the moss plants and the peatland water (Clymo, 1964, 1987; Wheeler, 1992). Conifer monocultures are generally known to cause environmental acidification by altering soil properties (Biały, 1999) and modifying the chemistry of both surface waters and groundwater, including a reduction in pH (Allen and Chapman, 2001; Neal et al., 2010; Drinan et al., 2013). The second process is influenced by several factors (Larssen and Holme, 2006), such as the acidic litterfall from coniferous trees (Alexander and Cresser, 1995; Burges-Conforti et al., 2019), as well as the fact that conifer forests uptake more ions, such as compounds of atmospheric pollutants (nowadays mainly nitrogen, N) and marine ions (e.g., sodium, Na), than nonforested areas (Reynolds et al., 1994, 1997; Harriman et al., 2003). The cation exchange of sodium ions to hydrogen and aluminium ions in the soil can further amplify the acidification of surface waters (Larssen and Holme, 2006).

As our results show and as already mentioned (Section 4.1), drainage was undoubtedly another factor of anthropogenic origin that was of great importance for the dynamics of our study area. Drainage of peatlands has an enormous impact on their structure and functioning, including hydrology, vegetation, decomposition, thermal conditions, and nutrient budget along with carbon balance. Furthermore, it also has an immense effect on the catchment hydrology (Holden et al., 2004; Ramchunder et al., 2009; Päivänen and Hånell, 2012; Kruczkowska et al., 2021). Following the lowering of the water table as a result of drainage, a number of processes are initiated in the peat that alter its physical and chemical properties under the interacting influence of environmental and substrate factors (Holden et al., 2004). In general, the water level drawdown enables oxic decomposition in a thicker surface peat layer (Päivänen and Hånell, 2012). Increased oxygen levels promote the mineralisation of nutrients such as carbon-bound sulphur and nitrogen and organically bound phosphorus, which can lead to their loss and reduce peat fertility (Holden et al., 2004). However, the amount of nutrients such as nitrogen and phosphorus in the surface peat layers may also increase as a result of drainage, mainly related to increased bulk density (Holden et al., 2004; Päivänen and Hånell, 2012). Another ecological consequence of lowering the water table is strong vegetation dynamics, including secondary vegetation succession of the ground layer from peatland taxa towards forest vegetation (Laine et al., 1995; Päivänen and Hånell, 2012) and the





development of the tree layer through increased tree encroachment and tree growth (Laine et al., 1995; Linderholm and Leine, 2004; Freléchoux et al., 2000; Päivänen and Hånell, 2012), which was the main rationale behind large-scale peatland drainage for forestry worldwide (Päivänen and Hånell, 2012; Joosten, 2016). Interestingly, forest drainage operations can both increase and decrease environmental acidification (Kazda, 1995; Minkkinen et al., 2008; Päivänen and Hånell, 2012; Nisbet and Evans, 2014; Kļaviņa et al., 2025). The transition from alderwoods to *Sphagnum*-dominated acidic peatlands (i.e., bogs) or Scots pine bog forests (*Vaccinio uliginosi-Pinetum*) has been documented (McVean, 1956; Solińska-Górnicka, 1987), which is probably related to the spread of *Sphagnum* and *Eriophorum*, especially considering that the proximity of *Sphagnum* can cause very high mortality of alder seedlings (McVean, 1956). Therefore, we hypothesise that land use changes, together with the landscape-wide increase in *Pinus* occurrence and the resulting acidification of catchment waters, followed by *Sphagnum* encroachment (and further acidification), combined with concurrent drainage activities, contributed to the ecosystem changes observed at our study site.

However, we assume that the human-driven landscape change and the resulting environmental consequences occurred prior to the intensive drainage measures in our study area, i.e. in the 16th to 18th centuries (Section 4.1). The absence of ditches on the map of the Wielkie Bagno peatland and its surroundings from the 1840s (Fig. 1f) is not necessarily due to the lack of drainage activities in the area at that time, but may simply result from the cartographic principles and accuracy of the map. On another map from a slightly later period, the second half of the 19th century, a ditch network in the Rakowe Bagno peatland immediately south of our study site is shown in great detail (Fig. 1g), which in turn is not depicted on a map from a later period, the 1910s (Fig. 1h), confirming that the degree of map accuracy can sometimes be decisive for the landscape features recorded. Nevertheless, in the daily activity protocols of the Zamoyski Family Estate from 1810 to 1814, there is no evidence of drainage operations in the vicinity of our study site. Furthermore, severe floods were reported from this period (AS4–13), which would probably have been less possible with the drainage systems in place to facilitate landscape-level water runoff. Additionally, we documented successful pine recruitment in our study site much earlier, in the 1700s (and as early as the 1720s–1730s) (Fig. 4), which is not common in a black alder bog forest *Carici elongatae-Alnetum* (Solińska-Górnicka, 1987; Leuschner and Ellenberg, 2017a), suggesting that an ecosystem transition must have been initiated earlier.

Still, an influence of the climate on the ecosystem shift documented in our study cannot be ruled out. The period of transition, from around 1400 CE until 1830 CE, overlaps with the cool period of the Little Ice Age (1450–1850 CE, Björklund et al., 2023) that was characterised by low values of the warm-season temperatures in the region (Büntgen et al., 2011; Björklund et al., 2023). A colder climate would definitely favour Scots pine as a tree species with a very wide thermal amplitude, including a high tolerance to low temperatures and frost (Przybylski, 1993; Leuschner and Ellenberg, 2017b), which is currently predicted to substantially reduce its future range in Europe as a result of climate change, not because of dispersal limitations, but due to limited areas for colonisation in northern Europe (Dyderski et al., 2018, 2025). The relatively short period of dry and warm conditions recorded in our climate data from Kraków in the first decades of the 19th century (Figs. 3 and S3) also had no negative impact on the population dynamics of *Pinus sylvestris* in the Wielkie Bagno peatland, as shown by our tree ring data (Fig. 4). Given the evidence that climate warming can exacerbate acidification (Murdoch et al., 2000; Evans et al., 2008; Whitehead et al., 2009), we consider a positive influence of cool thermal conditions rather unlikely.

As already mentioned (Section 4.1), another factor promoting the spread of pine in the landscape could be fire. *Pinus sylvestris* is one of the most fire-adapted European tree taxa, as confirmed by data at broad temporal (centennial to millennial) and spatial (local and regional) scales across its geographic range in Eurasia (Niklasson and Drakenberg, 2001; McRae et al., 2006; Olsson et al., 2010; Blanck et al., 2013; Novenko et al., 2018), including temperate Europe (Niklasson et al., 2010; Novák et al., 2012; Adámek et al., 2015, 2016; Spînu et al., 2020). Besides increasing landscape



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or forest openness, which favours the establishment of the light-demanding Scots pine (Lindbladh et al., 2003), fire has also been proven to facilitate pine regeneration on mineral soils by improving seedbed conditions (Kuuluvainen and Rouvinen, 2000; Hille and den Ouden, 2004; cf. Kubrak, 2010) or removing other, more fire-sensitive tree species that could be potential competitors (Niklasson et al., 2010; Spînu et al., 2020). Interestingly, fire activity can affect peatland hydrology and functioning in several ways (e.g., Väliranta et al., 2007; Benscoter et al., 2015; Lukenbach et al., 2016; Filicetti and Nielsen, 2020; Davies et al., 2023). At the landscape scale, fire can reduce tree cover, which affects both local evapotranspiration and runoff regimes (as reduction in vegetation decreases evapotranspiration and increases runoff, e.g., Piao et al., 2007; Sterling et al., 2013; Hrachowitz et al., 2021), causing an increase in peatland water levels (Sillasoo et al., 2007; Väliranta et al., 2007; Marcisz et al., 2015). However, fire activity can also be associated with periods of peatland drying (Väliranta et al., 2007; Marcisz et al., 2015). In our study, fire record from the peat archive showed that the highest fire activity, documented at depths of ca. 33 cm, 26 cm, and 16 cm (Figs. 8–9), coincided with low water table levels (Fig. 10). During dry periods, more peatland fuels are available for burning, the likelihood of fire spread from neighbouring sites on mineral soils increases, and the probability of substantial acrotelm consumption rises. As a result, hollows may be locally formed (Benscoter et al., 2005, 2015; Sillasoo et al., 2007; Väliranta et al., 2007), which in turn have a positive effect on peatland surface wetness, demonstrating that the relationship between fire disturbance and peatland moisture is complex and difficult to interpret unambiguously (Sillasoo et al., 2007; Väliranta et al., 2007). Moreover, the link between fire and subsequent vegetation succession, including tree regeneration, is also intricate, as it involves – in addition to peatland hydrology – environmental variables such as burn severity, pre-fire species composition and cover, availability of microsites for recruitment, inter- and intra-species competition, etc. (Ohlson et al., 2001; Brümelis et al., 2009; Lukenbach et al., 2016; Davies et al., 2023). In Europe, fires have been shown to trigger successional changes in peatland vegetation and influence the regeneration of Scots pine (Durno and McVean, 1959; Bellamy, 1962; Ågren et al., 1983; Brūmelis et al., 2009). In addition, the importance of interactions between Pinus sylvestris and Sphagnum mosses has been demonstrated (Ohlsson et al., 2001). Sphagnum has been shown to make up important recruitment sites for pine (Ohlsson et al., 2001; Brūmelis et al., 2009), with an average germination success of up to 75% (Gunnarsson and Rydin, 1998; Ohlson, 1999). However, severe mortality of Scots pine seedlings (especially with a stem diameter of less than 10 mm) resulting from being bogged down by Sphagnum (Gunnarsson and Rydin, 1998; Ohlson, 1999; Ohlsson et al., 2001) due to its higher growth rate is very common, which proves that reduced growth of Sphagnum is a prerequisite for successful pine regeneration in peatlands. At the same time, the establishment and growth of Pinus sylvestris has been demonstrated to be able to terminate the Sphagnum dominance by impeding its growth and peat accumulation rate (once pine trees have reached a stem diameter of about 20 mm) (Ohlson et al., 2001). As fire has been proven to reduce water availability for Sphagnum mosses (Lukenbach et al., 2016), this disturbance could be a factor facilitating pine recruitment. Yet, post-fire water availability for mosses, tightly linked to the hydrophysical properties of peat (water repellency and moisture retention), is shaped by both, the pre-disturbance vegetation species composition and structure (microtopography), and the burn severity, leading to variable post-fire recovery pathways of the ground layer community (Benscoter and Vitt, 2008; Lukenbach et al., 2016).

Notably, the general pattern of peatland pine climate—growth relationship we documented is typical for mineral soils—the positive influence of moist conditions (SPEI, precipitation) and the negative impact of high temperatures during the warm season months, coupled with the growth-promoting effect of warmer conditions in early spring (February—March) (Fig. 5) (e.g., Linderholm, 1999; Edvardsson et al., 2015b; Misi et al., 2019; Waszak et al., 2021; Bak et al., 2024). This growth-climate relation, typical for mineral soils, could indicate that the trees have established during a dry period, e.g., following peatland drainage (Linderholm and Leine, 2004; Freléchoux et al., 2000, 2003, 2004; Edvardsson et al., 2012a, b, 2014, 2015a). However, we consider this unlikely for several reasons. As discussed earlier, large-scale





drainage measures in our study area probably took place later than the oldest pines in the population we studied (Figs. 1e-h and 3). Of course, the lack of historical evidence is not proof of the absence of an environmental factor (here: drainage). Nevertheless, the data demonstrating continuous recruitment of *Pinus sylvestris* in pristine peatlands without drainage activities during the last 200-400+ years (Ågren et al., 1983; Ågren and Zackrisson, 1990; Brūmelis et al., 2009; González de Andrés et al., 2022) show that this tree species is able to successfully establish in peatland ecosystems even without their draining. A possible explanation for our findings could be the fact that our sampling site was located at the edge of the Wielkie Bagno peatland (Fig. 1), where the peat depth was not particularly high, i.e., 0.5 m. This is consistent with the results of a recent study in southern Sweden, which documented certain similarities (although not always significant and not for all hydroclimate variables analysed) in the tree growth–climate relationship in Scots pines at the peatland edge and on the neighbouring mineral soil site, which differed from the relationship in trees in the peatland's centre (Janecka et al., 2025). Considering that studies comparing the climate sensitivity of trees in peatlands and on adjacent mineral soils usually use one sampling site per substrate (Linderholm et al., 2002; Cedro and Lamentowicz, 2011; Edvardsson et al., 2015b; Blanchet et al., 2017), without distinguishing between the edge and the centre of the peatland, it is difficult to find further empirical evidence.

4.3 Temporal perspective in conservation

The ecological importance of peatlands and peatland forests is widely recognised in Europe, making them one of the most significant targets in nature conservation, ecosystem restoration and climate change mitigation efforts (Rydin and Jeglum, 2013; Joosten, 2016; Grzybowski and Glińska-Lewczuk, 2020; Jurasinski et al., 2020; Tannenberger et al., 2021). In addition, the importance of the temporal perspective in their conservation and restoration has already been emphasised by demonstrating how difficult it can be to define ecosystem reference conditions that should be targeted in these activities (Marcisz et al., 2022). Although there is palaeoecological evidence for millennia-long ecosystem stability in temperate Europe (Novák et al., 2012), including peatlands (Marcisz et al., 2020), our results, similar to studies from northern Poland or Estonia (Lamentowicz et al., 2020; Czerwiński et al., 2021; Łuców et al., 2022), clearly show that ecosystem transition (Fig. 10) is not uncommon in the long-term peatland dynamics. When they are caused by humans, novel anthroecosystems are created which are now being protected or restored (Marcisz et al., 2022). This is in line with the increasing amount of data challenging the static approach in vegetation ecology (Chiarucci et al., 2010) by documenting significant changes in ecosystems over longer time periods (Willis and Birks, 2006; Nowacki and Abrams, 2008, 2015; Spînu et al., 2020), as well as with the theory of alternative stable states/alternative equilibria (Scheffer et al., 1993; Beisner et al., 2003; Scheffer and van Nes, 2007) and the general understanding that disturbance and ecosystem change are inevitable features of nature and the environment and are therefore key mechanisms of vegetation dynamics (Pickett et al., 2009; Kuuluvainen, 2016; Graham et al., 2021). In fact, alternative stable states have been already recognised and are being implemented in peatland restoration (e.g., Temmink et al., 2021).

One of the key issues in nature conservation (and ecosystem management) is defining the conservation targets by answering the basic question about what is to be conserved: a species, community, ecosystem, landscape, processes (Groves et al., 2002) and how, with active or passive approach being the most frequent choices (e.g., Hartup et al., 2022). Often it couples with further points to consider such as degree of naturalness, level of variability, etc. (Willis and Birks, 2006), which may prove a given ecosystem to represent a certain successional stage, not necessarily pristine (Marcisz et al., 2022). Our findings demonstrate how landscape-scale environmental changes can impact local ecosystems in a time-scale longer than human memory (Fig. 2) and are another proof for the importance of long-term data in science-based resource management, conservation, and restoration (Heyerdahl and Card, 2000; Willis and Birks, 2006; Froyd and Willis, 2008; Marcisz et al., 2022), especially in such complex ecosystems as peatlands (Päivänen and Hånell, 2012; Waddington





et al., 2015; Joosten, 2016). As ecosystem change in peatlands can occur in both directions, either through a switch to degradation or regeneration, and through a tipping point either from a non-degraded to a degraded state or vice versa (Milner et al., 2021), the need for further interdisciplinary multi-proxy studies that include both reconstructions of past dynamics and monitoring of current changes remains very high.

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4.4 Challenges and opportunities in palaeoecological research: an interdisciplinary approach

Working on this demanding study has encountered numerous challenges, ranging from incomplete archives, through gaps in peat deposits (hiatuses), to discontinuity in written sources and integrating quantitative and qualitative data (Fig. 2). Despite these difficulties, this study has opened new opportunities for palaeoecological research, encompassing a broad perspective that extends beyond classical palaeoecology. Rather than solely focusing on expanding existing datasets, its primary goal has been a critical reassessment of analytical approaches and methodologies, which is essential for refining our understanding of past landscape dynamics (Ellis et al., 2021; Słowiński et al. 2021, 2024; Związek et al., 2024). While working on this study, authors from various disciplines - climatology, dendroecology, dendroeclimatology, history, cartography, and palaeoecology - set themselves the goal not only of processing and publishing results but, above all, of gaining a deeper understanding and added value from combining different approaches. This approach has facilitated a rigorous re-evaluation of prior assumptions, at times revealing inconsistencies in previous interpretations and highlighting the need for methodological refinements. Additionally, integrating quantitative and qualitative data of different resolutions (Fig. 2) enabled a broader perspective on the possibilities and scope of result interpretation, both in terms of analysis accuracy and the evaluation of reconstructed uncertainties, such as those concerning changes in water levels or air temperature across different archives and sources. The issue of integrating data with different temporal and spatial resolutions is becoming a key challenge in contemporary palaeoecology (Seddon et al., 2014). Researchers emphasize the need to develop methods that allow the combination of palaeoenvironmental records that differ in precision and origin (e.g., lake and peat sediments, dendrochronological records, historical sources, or cartographic materials). In this context, our study serves as an example of such synthesis, allowing the comparison of data across various temporal and spatial scales, thus enabling the identification of long-term trends and a more nuanced understanding of environmental dynamics. Furthermore, the diversity of temporal scales - from daily data (climatic, demographic) (e.g., Słowińska et al., 2022; Sobechowicz et al., 2025), through annual or even seasonal (dendrochronological) (e.g., Zin et al., 2022; Klisz et al., 2023), multi-annual, and decadal, to non-uniform data sets shaped by peat decomposition rates and accumulation processes (e.g., Łuców et al., 2020), and the temporal limitations of historical records (e.g., Róg, 2021) - has allowed for an interdisciplinary reconstruction of landscape change. As highlighted by Seddon et al. (2014), advancing methodologies for assessing synchrony and relationships between different sources of palaeoecological data remains a crucial research priority. In our case, the integration of multi-scale analyses has enabled the detection of patterns and processes that would have remained hidden if individual archives had been examined in isolation. In summary, such studies present inherent challenges due to the complexity of the analyses and the necessity of collaboration among experts from various scientific disciplines. However, it is precisely this interdisciplinary approach that enables the expansion of interpretative frameworks and the formulation of novel research questions. Recent literature underscores the importance of reducing uncertainty in palaeoenvironmental reconstructions through robust chronological frameworks and a critical evaluation of methodological biases (Seddon et al., 2014). Our work contributes to these ongoing efforts of analyzing and interpreting complex environmental systems. Moreover, it offers a fresh perspective on palaeoecological questions, allowing us to critically engage with established interpretations rather than simply reproducing them, which is essential for advancing scientific discourse.

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5 Conclusions

This study documented a transition of a peatland ecosystem from black alder bog forest to Scots pine bog forest (Fig. 10), most likely triggered by several factors, mainly land use changes and in particular the landscape-scale increase in the proportion of pine forests and the resulting environmental acidification that triggered the encroachment of *Sphagnum*. Interestingly, this ecosystem shift and the current ecosystem type represent a much shorter period in its history (>300–400 years) than the earlier, substantially different ecosystem type (>1,700 years). In addition, our reconstruction using various nature and human archives covering the last >2,300 years revealed considerable hydrological instability of the peatland and highlighted certain advantages and challenges of multi-proxy studies of landscape history and ecosystem dynamics, such as the different temporal resolution and coverage of the archives studied (including the problem of incomplete data) or the different information, which quantitative and qualitative data provide, especially considering that human archives may be biased towards exceptional, catastrophic environmental events (e.g., McClain et al., 2021). In line with existing studies, we confirmed the importance of long-term environmental records for conservation ecology and land management (e.g., Willis and Birks, 2006; Froyd and Willis, 2008; Marcisz et al., 2022) and emphasised the still existing demand for further research on peatland ecology, including past and current changes.

Author contributions. EZ, TZ, MK and MS designed the study. EZ, TZ, MK, DR and MS selected the study site. EZ, TZ, MK, DR, JPo, KPil and MS carried out fieldwork. SS and KPio conducted the analysis of climatic data, EZ, MK and KPil conducted the analysis of tree ring data, MO conducted the pollen and microcharcoal analysis, MS and JPi conducted the plant macrofossil analysis, MS and KS conducted the macrocharcoal analysis, AH conducted the non-metric multidimensional scaling (NMDS) and k-means clustering, DŁ conducted the testate amoebae analysis and depth to water table reconstruction (DWT), TZ, DR and JPo conducted the analysis of historical data. EZ, TZ, MK, SS, DR, MO, AH, DŁ, KPio, KPil and MS designed and prepared figures and tables. EZ wrote the initial draft (with input from co-authors in the description of methods and results). EZ, TZ, MK, MS, SS, DR, JPo, DŁ, KPio, and KPil reviewed and edited the manuscript. All authors contributed to the discussion of the manuscript and approved the submitted version.

Competing interests. The contact author has declared that none of the authors has any competing interests.

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