



# 1 Integrating palaeoecology and dendrochronology to explore the 2 impact of climate and forest management on a peatland in Scots pine 3 monoculture

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5 Mariusz Bąk<sup>1</sup>, Mariusz Lamentowicz<sup>1</sup>, Piotr Kołaczek<sup>1</sup>, Daria Wochal<sup>1</sup>, Paweł Matulewski<sup>2</sup>, Dominik  
6 Kopec<sup>3,4</sup>, Martyna Wietecha<sup>3,4</sup>, Dominika Jaster<sup>2</sup>, Katarzyna Marcisz<sup>1</sup>

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8 <sup>1</sup>Climate Change Ecology Research Unit, Faculty of Geographical and Geological Sciences, Adam  
9 Mickiewicz University, Poznań, Poland

10 <sup>2</sup>Anthropocene Research Unit, Faculty of Geographical and Geological Sciences, Adam Mickiewicz  
11 University, Poznań, Poland

12 <sup>3</sup>Department of Biogeography, Paleoecology and Nature Conservation, University of Lodz, Łódź, Poland

13 <sup>4</sup>MGGP Aero Sp. z o. o., Tarnów, Poland

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15 *Correspondence to:* Mariusz Bąk, [mariusz.bak@amu.edu.pl](mailto:mariusz.bak@amu.edu.pl)

16

17 **Abstract:** Assessing the scale, rate and consequences of climate change, manifested primarily by rising  
18 average air temperatures and altered precipitation regimes, is a critical challenge in contemporary scientific  
19 research. These changes are accompanied by various anomalies and extreme events that negatively impact  
20 ecosystems worldwide. Monoculture forests, including Scots pine (*Pinus sylvestris* L.) monocultures, are  
21 particularly vulnerable to these changes due to their homogeneous structure and simplified ecosystem  
22 linkages compared to mixed forests, making them more sensitive to extreme events such as insect outbreaks,  
23 droughts, fires and strong winds. In the context of global warming, forest fires are becoming extremely  
24 dangerous, and the risk of their occurrence increases as average temperatures rise. The situation becomes  
25 even more dramatic when fire enters areas of peatlands, as these ecosystems effectively withdraw carbon  
26 from the rapid carbon cycle and store it for up to thousands of years. Consequently, peatlands become  
27 emitters of carbon dioxide into the atmosphere.

28 In this study, we aim to trace the last 300 years of historical development of a peatland situated in a Scots  
29 pine monoculture. Our focus is on the Okoniny peatland located within the Tuchola Pinewoods in northern  
30 Poland, one of the country's largest forest complexes. We delved into the phase when the peatland's  
31 surroundings transitioned from a mixed forest to a pine monoculture and investigated the impact of changes  
32 in forest management on the peatland vegetation and hydrology. Our reconstructions are based on a multi-  
33 proxy approach using: pollen, plant macrofossils, micro- and macrocharcoal and testate amoebae. We  
34 combine the peatland palaeoecological record with the dendrochronology of *Pinus sylvestris* to compare the  
35 response of these two archives. Our results show that a change in forest management and progressive climate  
36 warming affected the development of the peatland. We note an increase in acidity over the analyzed period



37 and a decrease in the water table over the last few decades that led to the lake-peatland transition. These  
38 changes progressed with the strongest agricultural activity in the area in the 19<sup>th</sup> century. However, the 20<sup>th</sup>  
39 century was a period of continuous decline in agriculture and an increase in the dominance of Scots pine in  
40 the landscape as the effect of afforestation. Dendroclimatic data indicate a negative effect of temperature on  
41 Scots pine and pressure from summer rainfall deficiency. Additional remote sensing analysis, using  
42 hyperspectral, LiDAR and thermal airborne data, provided information about the current condition of the  
43 peatland vegetation. With the application of spectral indices and the analysis of land surface temperature,  
44 spatial variations in peatland drying have been identified. Considering the context of forest management  
45 and the protection of valuable ecosystems in monocultural forests, the conclusions are relevant for peatland  
46 and forest ecology, palaeoecology and forestry.

47

48 **Keywords:** palaeoecological data, dendroclimatic data, climate change, monoculture forests, plantation,  
49 remote sensing, historical maps, historical data, multi-proxy, high-resolution, airborne data, thermal data,  
50 vegetation indices

51

## 52 1. Introduction

53 ~~Recognizing how different ecosystems function under a changing climate and increasing human impact is~~  
54 ~~crucial for their conservation and management.~~ Peatlands are vulnerable to various types of change, which  
55 play an important role in the global carbon cycle and whose destabilization can create catastrophic positive  
56 feedback for climate warming (Gallego-Sala et al., 2018; Wilson et al., 2016). Peatlands, although they only  
57 cover about 3% of the Earth's total land area (Parish et al., 2008; Rydin and Jeglum, 2013), store more than  
58 30% of the organic carbon (C) (Freeman et al., 2004; Gorham, 1991; Harenda et al., 2018), which is far  
59 more carbon than the entire biomass of the world's forests (Beaulne et al., 2021b). Their advantage over  
60 forests is not only due to their ability to accumulate C but also to the fact that they do not emit decomposed  
61 carbon from the so-called rapid C cycle for up to thousands of years (Blodau, 2002; Gorham, 1991). The  
62 estimation of C content accumulated in peatlands is challenging (Sanderson et al., 2023), although some  
63 studies indicate ca. 600 Gt of C in the Northern Hemisphere alone (Yu et al., 2010). It has recently been  
64 shown that even the smallest kettle-hole peatlands effectively accumulate of C and serve as important C hot  
65 spots (Karpińska-Kończak et al., 2024).

66 Insufficient awareness of the ecological importance of peatlands has led to them being treated as  
67 wastelands and drained for hundreds of years to obtain land for agriculture, and forestry or exploited  
68 commercially as an energy resource (Joosten et al., 2012; Łuców et al., 2022; Paavilainen and Päivänen,  
69 1995). Many of these areas have also had to adapt to a changing environment resulting from the use of  
70 various forest management techniques, e.g., the replacement of mixed forests with more easily managed



71 monoculture forests (plantations) (Lee et al., 2023; Łuców et al., 2021; Słowiński et al., 2019). Mixed  
72 forests, through greater biodiversity, are more resilient and better able to adapt to environmental change  
73 (Bauhus et al., 2017; Messier et al., 2022), providing a more comprehensive range of ecosystem services  
74 (Felton et al., 2016; Huuskonen et al., 2021).

75         Despite being more straightforward to manage, forest monocultures are characterized by simplified  
76 ecosystem linkages (Chapin et al., 2012). As a result, they are more susceptible to various extreme events  
77 and disturbances, both natural and anthropogenic, including droughts, fires, strong winds, and pest  
78 gradations (Grondin et al., 2014). This is particularly important as disturbances of these types of forests are  
79 becoming more common (Seidl et al., 2014; Westerling, 2016). Natural disturbance regimes in forests are  
80 mainly a response to climate change (Hanson and Weltzin, 2000; Pureswaran et al., 2015; Seidl et al., 2017;  
81 Trumbore et al., 2015), therefore they are expected to increase in frequency and severity in the coming years  
82 (Gregow et al., 2017; Moritz et al., 2012; Wotton et al., 2010). Moreover, the problem applies to all kinds  
83 of monoculture forests regardless of the dominant species and climate zones (Booth, 2013; Guariguata et  
84 al., 2008; McNulty et al., 2013; Spiecker, 2000), including pine plantations in the temperate climate zone of  
85 Central and Eastern Europe (Łuców et al., 2021; Schüle et al., 2023). Thus, peatlands, which are so crucial  
86 in terms of their impact on global climate change, located in the area of forest monocultures are even more  
87 vulnerable to extreme phenomena and disturbance, despite the already high climatic and anthropogenic  
88 pressure.

89         The history of peatlands' development can be traced using palaeoecological analyses, which allow  
90 numerous reconstructions of past environmental conditions, including climate change (Lamentowicz et al.,  
91 2015; Mauquoy and Yeloff, 2008). These include reconstructions of vegetation changes in the peatland and  
92 its surroundings, changes in the water table, and reconstructions of past fire activity (Gałka et al., 2022;  
93 Kołaczek et al., 2018; Marcisz et al., 2020b, 2017; Mroczkowska et al., 2021). This is because peat  
94 preserves, plant remains, pollen, spores, microbial remains, and charcoal are deposited in situ and brought  
95 in by wind or water, collectively called peat archives (Godwin, 1981). While paleoenvironmental  
96 reconstructions based on peat records have become common, few studies still integrate palaeoecological  
97 data with other methods. For example, studies that combine palaeoecological and dendrochronological  
98 records, including dendroclimatic reconstructions based on analysis of the annual growth of tree rings, are  
99 still relatively rare (Ballesteros-Cánovas et al., 2022; Beaulne et al., 2021a; Dinella et al., 2021; Edvardsson  
100 et al., 2022, 2019, 2016; González de Andrés et al., 2022; Kuosmanen et al., 2020; Lamentowicz et al.,  
101 2009b). Yet, combining peat records with dendrochronological data can benefit interpretations of trees and  
102 forest resilience and resistance to disturbances compared to local environmental changes recorded in peat.  
103 Such a view of past environmental changes through several proxies and other archive types is fundamental  
104 and will be helpful for forest management and nature conservation in the future. To assess the current state



105 of the peatland, we also included remote sensing data in the analysis. Remote sensing methods have been  
106 applied to study wetland conditions for over 50 years and are currently regarded as one of the most useful  
107 methods in this research area (FAO, 2020; Guo et al., 2017). Remote sensing technologies enable the remote  
108 and non-invasive acquisition of information about the research object using specialized sensors, typically  
109 mounted aboard satellites or aircraft. In this study, data obtained from a multisensor aerial platform were  
110 used to assess the extent of peatland, the identification of drainage ditches and the current vegetation  
111 condition.

112 Our study aims to assess the impact of the introduction of pine monoculture on the development of  
113 *Sphagnum* peatlands in central and eastern Europe. We reconstructed hydrological conditions caused by  
114 changing climate and forest management, identified peat layers corresponding to the occurrence of extreme  
115 phenomena known from historical sources, and integrated palaeoecological and dendrochronological  
116 (dendroclimatic) data developed from annual growths of Scots pine (*Pinus sylvestris*). We also explored  
117 how peatland responded to extreme phenomena, such as outbreaks or fires, in situ and in the immediate  
118 environment.

119 We have assumed that the introduction of pine monoculture has led to significant changes in peatland  
120 species composition in favour of peat mosses and a stabilization of the groundwater table. We also undertook  
121 to confirm that peatlands record and respond to extreme phenomena, both occurring in situ and in the  
122 immediate environment. We assumed that disturbance events that happened in the monoculture forest  
123 throughout the years would be recorded in the pine tree ring record and would validate and complete  
124 peatland reconstruction.

125

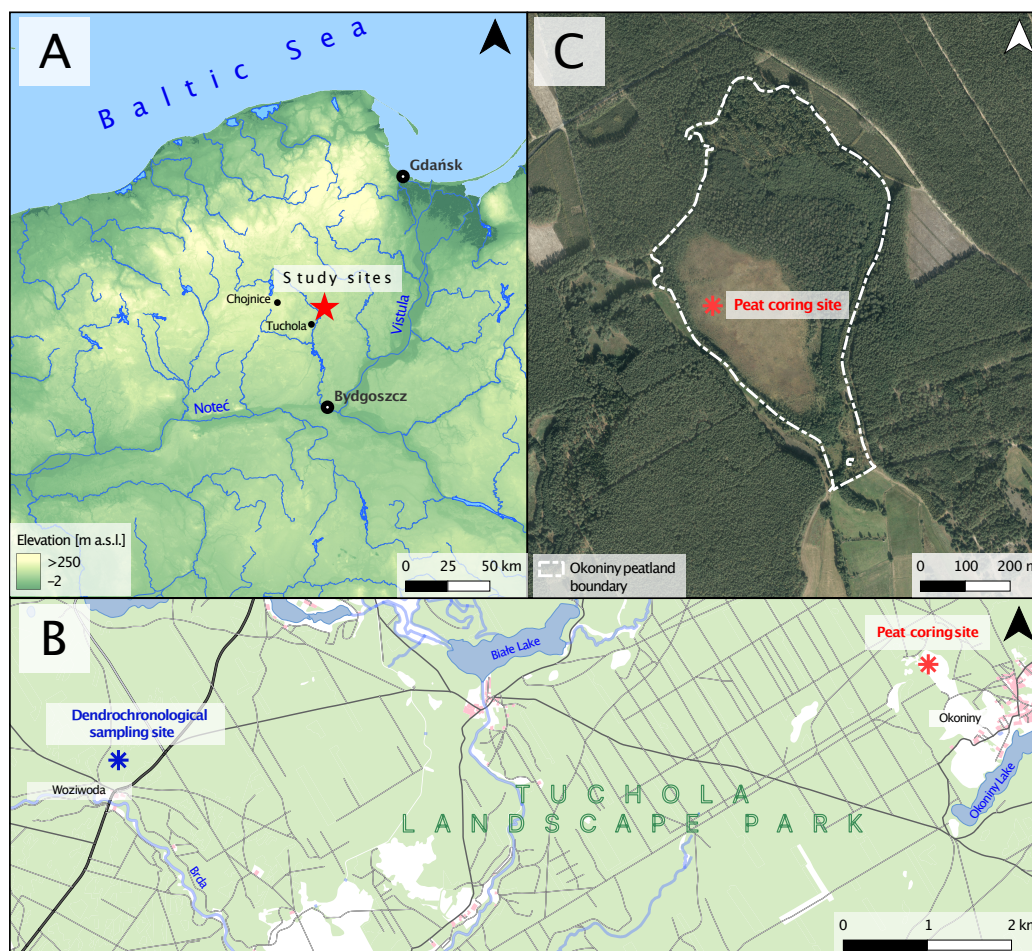
## 126 2. Materials and methods

### 127 2.1. Study site

128 The Okoniny peatland (53°40'52"–53°41'21"N 18°03'09"–18°03'40"E according to standard WGS  
129 84) is located in northern Poland, about 60 km north of Bydgoszcz and about 20 km northeast of Tuchola  
130 (Fig. 1). The study area is located within the Tuchola Pinewoods mesoregion (Kondracki, 2001), close to  
131 the Pomeranian ice margin of the Vistulian Glaciation dated to ca. 17,000–16,000 cal. BP (Marks, 2012).  
132 The entire area of the Tuchola Pinewoods is a young glacial landscape covered by glacial till, sand, and  
133 numerous depressions and other forms originating from melting dead ice (Błaszkiwicz et al., 2015). Based  
134 on the analysis of remote sensing data, it was determined that the surface area of the peatland is 27.08  
135 hectares, with approximately 7.00 hectares designated as non-forested area. The direct catchment area of  
136 the peatland covers a surface of 33.23 hectares. The current elevation of the peatland is around 119 m asl,  
137 with the highest elevated area within the direct catchment reaching around 128 m asl. It is part of a protected  
138 area (Regulation No. 64/97, 1997), included within the boundaries of the Tuchola Landscape Park (created



139 in 1985). Moreover, since 2008 the entire complex of the Tuchola Pinewoods has been included on the  
140 Natura 2000 list as a Special Protection Area. Since 2010, it has been listed as a UNESCO Biosphere  
141 Reserve (UNESCO, 2024).



142  
143 Figure 1. Location of the study area. (A) Location on a map of north-western Poland. (B) Location of the  
144 two study sites – dendrochronological sampling site and peat coring site. (C) Okoniny peatland sampling  
145 site with current peatland boundaries.

146  
147 The Okoniny peatland is located in a temperate latitude zone, with a transitional climate influenced  
148 by continental air masses from eastern Europe and oceanic air masses from the Atlantic Ocean (Beck et al.,  
149 2018). According to climate data obtained from the Institute of Meteorology and Water Management for the  
150 meteorological station in Chojnice (35 km west of the study area) for the thirty years 1991-2020, the coldest



151 month is January with an average temperature of  $-1.5\text{ }^{\circ}\text{C}$ , the warmest month is July with an average  
152 temperature of  $18.0\text{ }^{\circ}\text{C}$ . In the thirty years 1961-1990, both January and July were cooler by  $1.6\text{ }^{\circ}\text{C}$  compared  
153 to 1991-2020. The average annual temperature increased from  $6.9\text{ }^{\circ}\text{C}$  in 1951-1990 to  $8.1\text{ }^{\circ}\text{C}$  in 1991-2020.  
154 In terms of precipitation, February has the least amount with an average of  $31.1\text{ mm}$  for the period 1991-  
155 2020, and July has the most with an average of  $80.7\text{ mm}$  for the period 1991-2020. Compared to 1951-1990,  
156 the average precipitation for February increased by  $7.7\text{ mm}$  and for July decreased by  $4.1\text{ mm}$ . Mean annual  
157 rainfall increased from  $558.1\text{ mm}$  for 1951-1990 to  $612.4\text{ mm}$  for 1991-2020.

158 Samples for dendroclimatic analysis were taken from forest division no. 91 in the Woziwoda  
159 Forestry, Woziwoda Forest District, about  $9.5\text{ km}$  west of the study site (Fig. 1). The oldest pine trees in the  
160 forest district were selected for the study according to the indications of the forest survey and taxonomic  
161 descriptions.

162

## 163 2.2. Peat and tree core sampling

164 A peat core was taken from the north-western part of the peatland in February 2022 using a Wardenaar corer  
165 (chamber dimension:  $10\text{ cm} \times 10\text{ cm} \times 100\text{ cm}$ ) (Wardenaar, 1987). The entire length of the sampled peat  
166 core –  $96\text{ cm}$ -long monolith – was analyzed. The core was sampled continuously every  $1\text{ cm}$ , except for the  
167 top  $10\text{ cm}$ , which contained a living *Sphagnum* layer. The first sample covered  $4\text{ cm}$  of the surface layer ( $0$ -  
168  $4\text{ cm}$ ), and the following three samples were taken every  $2\text{ cm}$  ( $4$ - $6$ ,  $6$ - $8$  and  $8$ - $10\text{ cm}$ ).  $90$  samples were  
169 obtained and analyzed for bulk density, ash content, peat and carbon accumulation rates, plant macrofossils,  
170 testate amoebae, macroscopic and microscopic charcoal, and pollen.

171 The research tree stem material was taken in April 2023 from  $23$  living and healthy trees at the Woziwoda  
172 site, ca.  $9.5\text{ km}$  west of the Okoniny peatland. From each tree, a minimum of two cores were taken (from  
173 the east and west sides) at a breast height ( $1.3\text{ m}$ ) with a Pressler increment corer. In total,  $50$  cores were  
174 acquired from the Scots pine tree stems.

175

## 176 2.3. Radiocarbon dating and chronology

177 Ten samples containing *Sphagnum* stems and leaves were used for accelerator mass spectroscopy (AMS)  
178  $^{14}\text{C}$  dating of the entire length of the profile. The survey was conducted at the Poznan Radiocarbon  
179 Laboratory in Poland (laboratory code marked Poz; Tab. 1). The IntCal20 (Reimer et al., 2020) and  
180 Bomb21NH1 (Hua et al., 2021) atmospheric curves were used to calibrate the dates.

181

182 Table 1. The list of radiocarbon dates from Okoniny peatland with calibration in the OxCal v4.4.4 software  
183 using IntCal20 calibration curve for the atmospheric data and Bomb21NH1 curve for bomb series.



No	Laboratory code – number sample	Depth (cm)	<sup>14</sup> C date ( <sup>14</sup> C BP)	Calibrated dates [cal. CE (2σ – 95.4%)	Dated material
1	Poz-150386	10.5	100.86 ± 0.33 pMC	1952-1958 (33.9%) 2013-... (61.5%)	<i>Sphagnum</i> stems
2	Poz-150387	20.5	107.92 ± 0.34 pMC	1952-1958 (11.1%) 1996-2009 (84.4%)	<i>Sphagnum</i> stems
3	Poz-150388	30.5	132.8 ± 0.36 pMC	1958-1962 (20.8%) 1972-1984 (74.6%)	<i>Sphagnum</i> stems
4	Poz-150445	40.5	165 ± 30	1661-1706 (17.2%) 1720-1818 (44.0%) 1832-1892 (14.9%) 1906-... (19.5%)	<i>Sphagnum</i> stems
5	Poz-150446	50.5	85 ± 30	1688-1730 (26.1%) 1806-1924 (69.3%)	<i>Sphagnum</i> stems
6	Poz-150447	60.5	105 ± 30	1682-1736 (25.9%) 1802-1936 (69.5%)	<i>Sphagnum</i> stems
7	Poz-150449	70.5	135 ± 30	1674-1766 (32.8%) 1774-1776 (0.6%) 1798-1942 (62.0%)	<i>Sphagnum</i> stems
8	Poz-150450	80.5	165 ± 30	1661-1706 (17.2%) 1720-1818 (44.0%) 1832-1892 (14.9%) 1906-... (19.5%)	<i>Sphagnum</i> stems
9	Poz-150631	90.5	280 ± 30	1505-1596 (55.0%) 1616-1665 (37.8%) 1784-1794 (2.6%)	<i>Sphagnum</i> stems
10	Poz-150633	95.5	100 ± 30	1683-1735 (26.1%) 1802-1930 (69.3%)	<i>Sphagnum</i> stems

184

185 The absolute chronology of the entire core was based on a Bayesian age-depth model using OxCal v4.4.4  
 186 (Bronk Ramsey, 2021). The *P\_Sequence* command with a parameter *k* of 0.1 cm<sup>-1</sup> was used to calculate the  
 187 model, assuming  $\log_{10}(k/k_0) = 2$ , and interpolation = 1 cm. The most pronounced change in peat composition,  
 188 as manifested by changes in pollen concentration, testate amoeba species composition and species  
 189 composition of plant macrofossils, which may signal changes in peat accumulation rates, was input using



190 the *Boundary* command at a depth of 66 cm. For better readability of the age-depth model, mean values ( $\mu$ )  
191 were introduced and used to illustrate the modeled age.

192

#### 193 **2.4. Peat properties and carbon accumulation rate**

194 Analyses of bulk density, loss on ignition, and peat carbon accumulation rate (PCAR) were carried out for  
195 each of the ninety samples. Each sample's volume [ $\text{cm}^3$ ] was carefully and cautiously measured beforehand  
196 using calipers to avoid compressing the material. Each sample was then placed in a separate crucible and  
197 dried to determine the percentage of water content. The weighed and dried samples were incinerated at 550  
198 °C for 12 hours and reweighed according to the protocol of Heiri et al. (2001) to determine the ash mass  
199 [g]. Bulk density [ $\text{g}/\text{cm}^3$ ] was obtained by dividing the dry sample mass by the volume of the fresh sample  
200 according to Chambers et al. (2010). Loss on ignition [g] was obtained by subtracting the ash mass from the  
201 dry sample mass. Accumulation rates obtained from the peat core chronologies were multiplied by  
202 measuring the bulk density without ash and by 50% to obtain the PCAR, following the protocol of Loisel et  
203 al. (2014). The top eleven centimeters of the core (0-11 cm) were discarded for PCAR assessment due to  
204 the unrepresentative nature of the results obtained, as increased values of carbon accumulation in near-  
205 surface peat cannot be used for inference (Young et al., 2019).

206

#### 207 **2.5. Plant macrofossils analysis**

208 The analysis of plant macrofossils was carried out using the modified protocol of Mauquoy et al., 2010.  
209 Each sample of approximately  $5\text{cm}^3$  was wet sieved (mesh diameter: 200  $\mu\text{m}$ ). The generalized content of  
210 the sample was estimated in percentage using a binocular microscope. Fruits, seeds, caryopses, achenes,  
211 perigynia, bud scales, catkin scales, whole preserved leaves, whole preserved needles, cones, anthers,  
212 sporangia, opercula, fungi sclerotia, and wood pieces were counted as total numbers in each sample. The  
213 tissues of monocotyledon species and moss leaves (brown and *Sphagnum* mosses) were identified on slides  
214 using a magnification of  $\times 200$  and  $\times 400$ . The material was compared with the guides (Anderberg, 1994;  
215 Berggren, 1969; Bojnanský and Fargašová, 2007; Mauquoy and van Geel, 2007).

216

#### 217 **2.6. Testate amoebae analysis**

218 Samples for testate amoeba analysis (volume: ca.  $5\text{cm}^3$ ) were washed under 300  $\mu\text{m}$  sieves following the  
219 method described by Booth et al. (2010). Testate amoebae were analyzed under a light microscope with  
220  $\times 200$  and  $\times 400$  magnifications until the sum of 100 tests per sample was reached (Payne and Mitchell,  
221 2009). Several keys and taxonomic monographs (Clarke, 2003; Mazei and Tsyganov, 2006; Meisterfeld,  
222 2001; Ogden and Hedley, 1980) as well as online resources (Siemensma, 2023) were used to achieve the  
223 highest possible taxonomic resolution. The results of a testate amoebae analysis were used for the





224 quantitative depth-to-water table (DWT) and pH reconstructions. Both reconstructions were performed in  
225 C2 software (Juggins, 2007) using the European training set (Amesbury et al., 2016).

226

### 227 **2.7. Pollen and non-pollen palynomorphs (NPPs)**

228 Samples for palynological analysis (volume: 2 cm<sup>3</sup>) were prepared using standard laboratory procedures  
229 (Berglund and Ralska-Jasiewiczowa, 1986). To remove the carbonates, samples were treated with 10%  
230 hydrochloric acid. This step was followed by digestion in hot 10% potassium hydroxide (to remove humic  
231 compounds) and soaking in 40% hydrofluoric acid for 24 h (to remove the mineral fraction). Next, acetolysis  
232 was carried out. Three *Lycopodium* tablets (Batch 280521291, containing 18407 spores per tablet; produced  
233 by Lund University) were added to each sample during the laboratory procedures for the calculation of  
234 microfossil concentration (Stockmarr, 1971). Pollen, spores, and selected non-pollen palynomorphs (NPPs)  
235 were counted under an upright microscope (Zeiss Axio SCOPE A1) until the number of total pollen sum  
236 (TPS) grains in each sample reached at least 500, apart from 23 samples in which pollen concentrations  
237 were very low. Sporomorphs were identified with the assistance of atlases, keys (Beug, 2004; Moore et al.,  
238 1991), various publications, and the image database in the case of NPPs, for which there are no atlases  
239 (Miola, 2012; Shumilovskikh et al., 2022; Shumilovskikh and van Geel, 2020). The results of the  
240 palynological analysis were expressed as percentages, calculations are based on the ratio of an individual  
241 taxon to the TPS, i.e., the sum of AP (arboreal pollen) and NAP (non-arboreal pollen), excluding aquatic  
242 and wetland plants (together with Cyperaceae and Ericaceae), cryptogams, and fungi.

243

### 244 **2.8. Macro- and microcharcoal analysis**

245 Microscopic charcoal particles (size: > 10 µm) were counted from the same slides as pollen until the number  
246 of charcoal particles and *Lycopodium* spores counted together, exceeded 200 (Finsinger and Tinner, 2005;  
247 Tinner and Hu, 2003). Microscopic charcoal influx or accumulation rates (MIC) were calculated by  
248 multiplying charcoal concentrations by peat accumulation rates (PAR) (Davis and Deevey, 1964; Tinner and  
249 Hu, 2003).

250 For macroscopic charcoal analysis, samples (volume: 2 cm<sup>3</sup>) were prepared by bleaching to create a more  
251 visible contrast between the charcoal and the remaining organic matter following the method described by  
252 Whitlock and Larsen (2001). Samples were sieved through a 500-µm mesh and only large charcoal  
253 fragments > 600 µm were analyzed to obtain a local fire signal (Adolf et al., 2018). Samples were analyzed  
254 with a binocular under 60× magnification. Macroscopic charcoal influx or accumulation rates (MAC,  
255 particles/cm<sup>2</sup>/year) were calculated using the charcoal concentrations and PAR.

256

### 257 **2.9. Visualization of the palaeoecological results**



258 Palaeoecological diagrams for the analyzed proxies were plotted using Tilia/Tilia graph software (pollen)  
259 (Grimm, 1992, 1991), C2 software (testate amoebae) (Juggins, 2007) and riojaPlot package for R (plant  
260 macrofossils) (Juggins, 2023). Quantitative reconstructions of testate amoebae-based depth to water table  
261 (DWT) and pH changes were done in C2 software (Juggins, 2007), using the European training set  
262 (Amesbury et al., 2016).

263

#### 264 **2.10. Tree core chronology construction**

265 Tree cores underwent a standardized dendrochronological procedure (Zielski and Krapiec, 2004). Polished  
266 cores were scanned between 1200 - 2400 DPI using an Epson Perfection V700 Photo scanner. Annual  
267 growth rings were measured on digital images with an accuracy of 0.01mm using CooRecorder. This  
268 facilitated the selection of individual growth sequences, which were utilized to form a chronology for each  
269 plot. Visual comparisons were made between individual sequences, and the significance of correlations was  
270 assessed using Student's t-test (Baillie and Pilcher, 1973). Subsequently, cross-dating was conducted using  
271 COFECHA software (Grissino-Mayer, 2001), which evaluates each data series concerning the reference  
272 chronology created and compares the correlation coefficients obtained. Raw chronologies were derived by  
273 employing an arithmetic mean. For climate-growth analysis standardized chronologies were used, obtained  
274 by fitting a spline function (i.e., the "n-year spline" was set at 2/3 of the wavelength of n years of single  
275 growth series) using the 'dplr' package (Bunn, 2008) package version 1.7.6 (2023) in the software R version  
276 4.3.0 (R Core Team, 2022). By using this standardization method, random variation in the radial growth was  
277 removed (Cook et al., 1990). For the obtained chronologies i.e., raw (TRW) and standardized (RWI), values  
278 for the following descriptive statistics were computed: the mean correlation between series (inter-series  
279 correlation or Rbar), the GLK index (Gleichläufigkeit; Eckstein and Bauch, 1969), and EPS (express  
280 population signal) (McCarroll and Loader, 2004).

281

#### 282 **2.11. Dendroclimatological and pointer years analysis**

283 The 'chron' function from 'dplr' package allowed for the making of a residual chronology, which was used  
284 for climate-growth analysis. The 'dcc' function and its moving response (25-yrs window) function method  
285 were used to determine the effects of climate conditions on the growth of Scots pine using the 'treeclim'  
286 package (Zang and Biondi, 2015) version 2.0.6.0 in R (R Core Team, 2022). This package allows the use  
287 of the bootstrap procedure to test the significance and stability of the coefficients of determination ( $r^2$ ) over  
288 a set period (Guiot, 1991). Monthly mean air temperature (TEMP) and total monthly precipitation (PREC)  
289 were used to analyze climate-growth for the period 1920-2022 (Klein Tank et al., 2002). Climate data were  
290 acquired via Climate Explorer (Trouet and van Oldenborgh, 2013) and calculated from the monthly gridded



291 observational dataset E OBS v. 25.0e (Haylock et al., 2008) obtained for the 17.75-18.00°E and 53.50-  
292 53.75°N grid.

293 The Becker algorithm (Becker et al., 1994) was used to determine the pointer years in the Woziwoda  
294 chronology. Calculations were made using the 'dplR' package in R and the 'pointer' function (Bunn, 2008).  
295 Pointer years were calculated using adjustable thresholds of relative variation in radial growth set to a 10-  
296 year time window and the number of series exhibiting a similar incremental growth pattern. The main  
297 criterion for determining pointer years was the occurrence of unidirectional changes (i.e., a decrease or  
298 increase in the number of annual rings) in a minimum of 85% of the tested sequences of annual increments  
299 observed in a group of trees at the Woziwoda site.

300

#### 301 **2.12. Acquisition and post-processing of remote sensing data**

302 The analysis of the current state of Okoniny peatland was conducted using airborne remote sensing data.  
303 The data were acquired through a multisensor aerial platform by the MGGP Aero company on March 25,  
304 2022 (leaf-off collection) and July 20, 2022, one of the warmest days of the year, which was particularly  
305 important for acquiring thermal data (leaf-on collection). Multispectral images (acquired with the IXM-100  
306 camera) and Airborne Laser Scanning data (ALS; acquired with the Riegl VQ780-II scanner) were obtained  
307 in the leaf-off season. Subsequently, during the vegetation season, the dataset was enhanced by acquiring  
308 hyperspectral data (collected using the HySpex VS-725 scanner) and thermal data (obtained with the  
309 InfraTEC 9400 camera). Based on the multispectral images, an orthophotomap was generated with a Ground  
310 Sampling Distance (GSD) of 10 cm. Hyperspectral data were used to create a mosaic consisting of 430  
311 bands (in the range from 400 to 2500 nm), ALS data were applied for the development of a Digital Terrain  
312 Model (DTM), and thermal data were used to produce a land surface temperature (LST) mosaic. Thermal  
313 and hyperspectral mosaics and DTM were prepared with GSD = 1 m.

314 Photo interpretation was carried out to assess the extent of peatlands and the course of drainage ditches  
315 using orthophotos and DTM as a base map. DTM was also used to delineate the catchment area of the  
316 peatland. Hydrological modelling methods based on watershed analyses were employed for this purpose. A  
317 hyperspectral mosaic was used to calculate spectral indices such as the Normalized Difference Vegetation  
318 Index (NDVI; Rouse et al., 1974) and Moisture Stress Index (MSI; Hunt and Rock, 1989). Spectral indices  
319 are mathematical formulas that enable the simultaneous analysis of reflectance across multiple spectral  
320 ranges. The NDVI is a measure of healthy, green vegetation ranging from -1 to 1. Vegetation values  
321 typically range from 0.2 to 0.8, with higher values indicating healthier and denser vegetation. The MSI index  
322 is sensitive to increasing leaf water content. Its values range from 0 to more than 3, but the common values  
323 for vegetation are from 0.4 to 2. Higher values indicate greater water stress and less water content in this  
324 case. Thermal data was used for calculating Land Surface Temperature (LST), measured in degrees Celsius.



325

### 326 **2.13. Historical maps and cartographic information**

327 Several historical cartographic studies were used to assess changes to the peatland and its surroundings. The  
328 oldest of the materials used is the Schrötter-Engelhardt map of 1803. Work on creating the map began in  
329 1796 under the leadership of the Prussian government minister Friedrich Leopold von Schrötter (1743-1815)  
330 and topographer Friedrich Bernhard Engelhardt (1768-1854). The manuscript was produced at a scale of  
331 1:50,000. Still, due to the concerns of the Prussian army command about the map being too detailed and  
332 capable of being used by enemy armies, a generalized version was eventually published at a scale of  
333 1:150,000. A larger-scale version of the map was not available until the 1920s (Jäger, 1982, 1981). In this  
334 article, the generalized version of the map is interpreted.

335 The Prussian topographic map Messtischblatt of 1874 on a scale of 1:25 000, sheet No. 982, Zalesie section,  
336 was also analyzed. and the Detailed Map of Poland issued by the Military Geographical Institute in 1933 at  
337 a scale of 1:25,000, PAN map sheet 34 - SLUP 26 - B (Linsk). In addition, a geological-agricultural map  
338 compiled between 1899 and 1900 on the topographic Messtischblatt of 1874 was considered. The Prussian  
339 Geological Survey produced the map (Königlich-Preußische Geologische Landesanstalt) and provides  
340 information on alluvial and diluvial deposits covering the area under study. The maps show the changes in  
341 the peat bog and its surroundings from the early 19th century to the 1930s. Aerial images from 1964, 1984,  
342 and 1997 obtained from the Central Office of Geodesy and Cartography were also used for the same purpose  
343 (license no. DIO.7211.457.2023\_PL\_N).

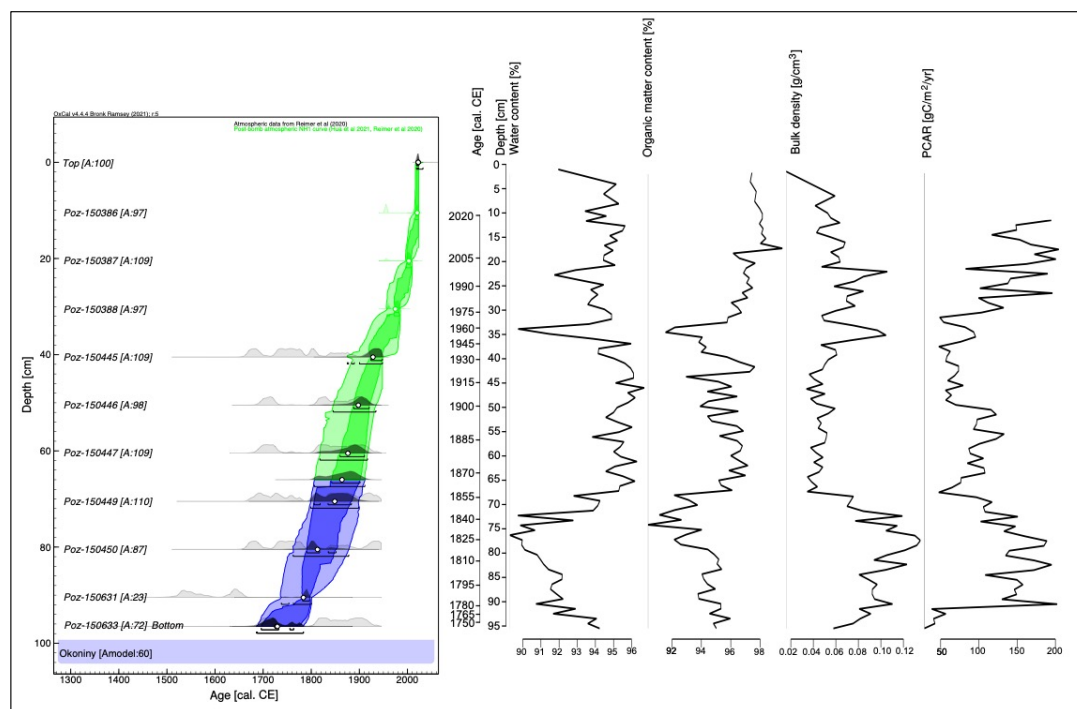
344

## 345 **3. Results and interpretation**

### 346 **3.1. Age-depth model and peat accumulation rate**

347 The age-depth model showed a model agreement index ( $A_{\text{model}}$ ) of 60% (Fig. 2), precisely at the limit of the  
348 recommended minimum for its reliability (60% according to Bronk Ramsey, 2008). The model spanned the  
349 period of ca. 282 years, with a maximum uncertainty ca. 30 years (mostly in the section of ca. 1883-1783  
350 cal. CE). Most of the core consisted of well-preserved *Sphagnum* peat, while the lower part consisted of  
351 sedge peat. The peat accumulation rate averaged 3.6 mm/yr, with the highest values associated with the  
352 undecomposed acrotelm zone. The upper layers located between 0 and 11 cm were excluded from the  
353 analysis of peat accumulation rates. The fastest rate was 0.71 cm/yr (at 11.5 cm), and the slowest was 0.1  
354 cm/yr (at 91.5 cm). The mean BD value across the core was 0.07 g/cm<sup>3</sup>. It was highest in the lower part of  
355 the core with 0.10 g/cm<sup>3</sup> between 96 and 70 cm, and lowest in the middle part - 0.05 g/cm<sup>3</sup>, between 69 and  
356 30 cm. In the upper part between 29 and 0 cm, it was 0.06 g/cm<sup>3</sup>.

357



358

359 Figure 2. Age-depth model of the peat profile in Okoniny based on  $^{14}\text{C}$  dating. Water content, organic matter  
 360 content, bulk density, and PCAR are also marked.

361

### 362 3.2. Palaeoecological analyses

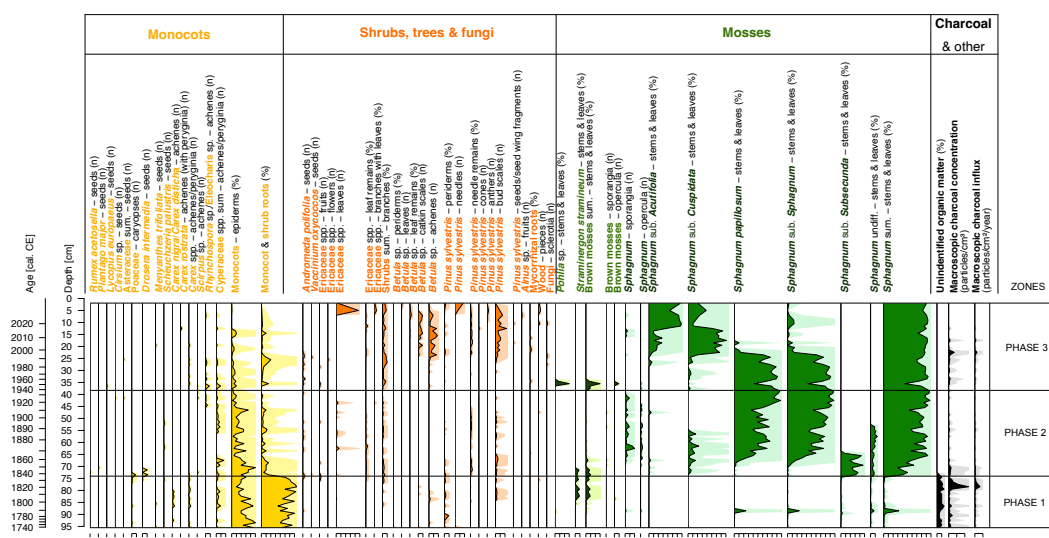
#### 363 3.2.1. Phase 1 (~1726–1838, 96–74 cm): wet conditions and low human impact

364 The high concentration of non-pollen palynomorphs (NPPs) such as cyanobacteria and the algae *Tetraëdron*  
 365 *minimum*, *Scenedesmus*, *Botryococcus*, and *Pediastrum* point to the presence of a shallow water body in  
 366 this time (Fig. 5). This was also confirmed by the plant macrofossils and pollen analyses. Plant macrofossil  
 367 analysis (Fig. 3) showed that the peatland vegetation in this phase was strongly dominated by vascular  
 368 vegetation, mainly monocotyledons with *Carex* spp. Shallow waters and edges of the water body were  
 369 overgrown by sedge communities (Cyperaceae pollen) (2.8-14.5%) (Fig. 5). Additionally, this was indicated  
 370 by the presence of macrophytes represented by pollen of *Potamogeton* subgen. *Eupotamogeton* (0-0.9%),  
 371 *Nymphaea* (0-0.4%), and *Utricularia* (0-0.3%) (Fig. 5).

372 This phase was also characterized by the brown moss *Straminergon stramineum* (max. 9% of the subsample  
 373 content) (Fig. 3). This species occurs in a wide range of habitats (Hedenäs, 1993) but is most common in  
 374 wet, moderately acidic habitats (Blockeel, 2010). *Straminergon stramineum* is usually found as scattered  
 375 stems or small patches among other mosses but occasionally forms scattered mats, sometimes partially



376 submerged in water, next to lakes, on the edges of peat bogs or in lakeside marshes (Hill and Blockeel,  
 377 2014).  
 378 This phase of peatland development was characterized by a very low concentration of testate amoebae in  
 379 the samples. *Centropyxis aculeata* was the most abundant species (Fig. 4). The dominance of plagiostomic  
 380 species from the genus *Centropyxis* may point to the presence of mineral input into the peatland  
 381 (Lamentowicz et al., 2009a; Marcisz et al., 2020a). The water level in the peatland was quite unstable and  
 382 fluctuated between 4.3 and 16.5 cm below the ground and the pH value ranged between 4.5 and 5.2, but due  
 383 to the low number of identified tests, these reconstructions should be taken suggestively (Fig. 4).  
 384 The surrounding vegetation was characterized by the dominance of forests, as evidenced by the high  
 385 proportion of arboreal pollen (AP) (83.6-91.1%) in total pollen content (TP) (Fig. 5). Main species was  
 386 *Pinus sylvestris* (62.6-81.3% AP) and *Betula* (6.8-16.0% AP), with admixtures of *Alnus* (2.5-7.7% AP),  
 387 *Quercus* (1.8-8.1% AP), *Corylus avellana* (0.6-3.8% AP), *Carpinus betulus* (0-3.4% AP) and *Fagus*  
 388 *sylvatica* (0.4-3.3% AP). Values of Cerealia pollen sum (0-7.8% TP) with *Centaurea cyanus*, a crop weed,  
 389 indicated a stable presence of cultivated fields.  
 390

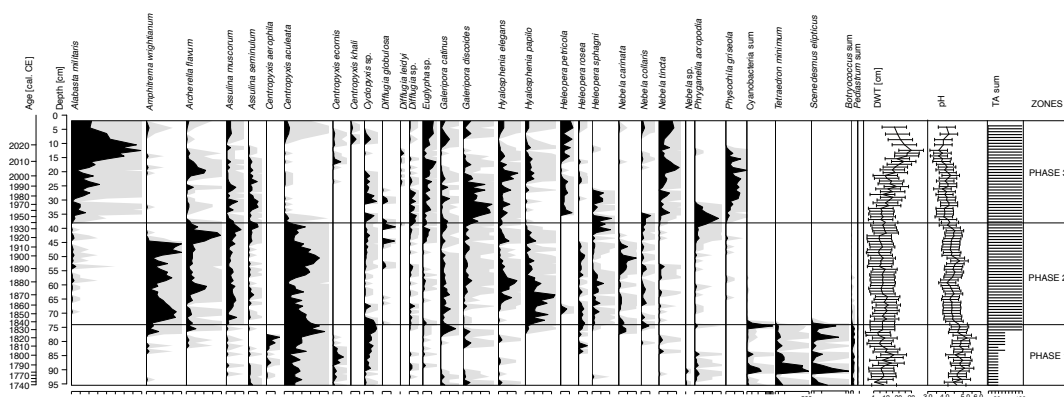


391  
 392 Figure 3. Diagram showing macrofossil percentages, macroscopic charcoal concentrations, and influx as a  
 393 local fires proxy. 10 times exaggeration is marked.  
 394

395 This phase also had the highest influx of macroscopic charcoal (MAC) of all three distinguished  
 396 phases (Fig. 3). Towards the end of the phase, at depths of 79.5 and 78.5 cm (1st half of the 1820s according  
 397 to calibrated dates), influx reached the highest values throughout the core and equaled 24.5 and 11.5

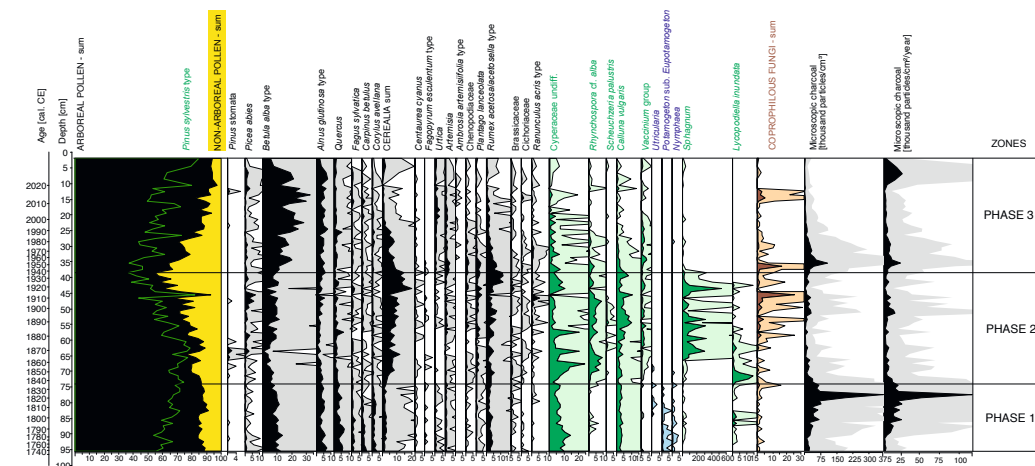


398 particles/cm<sup>2</sup>/year, respectively. The highest influx of MAC in both subsamples corresponded with the influx  
 399 of microscopic charcoal (MIC), reaching over 53,200 particles/cm<sup>2</sup>/year for the 79.5 cm subsample and over  
 400 125,000 particles/cm<sup>2</sup>/year for the 78.5 cm subsample (Fig. 5). This distinct fire event was followed by a  
 401 slight decrease in pH, an appearance of wet indicator mixotrophic testate amoeba species (*Amphitrema*  
 402 *wrightianum*, *Archerella flavum*, *Hyalosphenia papilio*), and the disappearance of cyanobacteria and algae  
 403 (Fig. 4).



404  
 405 Figure 4. Testate amoebae and non-pollen palynomorphs (Cyanobacteria, *Tetraëdron minimum*,  
 406 *Scenedesmus*, *Botryococcus*, and *Pediastrum*) diagram. Percentages are shown in black and 10 times  
 407 exaggeration is marked. Testate amoeba-based depth-to-water table (DWT) and pH reconstructions as well  
 408 as the sum of testate amoeba shells counted in each sample (TA sum) are presented.

409





410 Figure 5. Pollen diagram with selected taxa presented (list of taxa presented in the associated open dataset).  
411 Pollen percentages are shown in black, and 5 times exaggeration is marked. Microscopic charcoal  
412 concentrations and influx as an extra-local fires proxy are also presented.

413

414 **3.2.2. Phase 2: (~1838–1945, 74–37 cm): stabilization of water table and increase in acidity, a**  
415 **transition from mixed forest to pine monoculture and agricultural development**

416

417 The local vegetation (Fig. 3) in this phase was dominated by *Sphagnum*, first by the subgenus *Subsecunda*,  
418 then for most of this period by *Sphagnum papillosum*. *S. papillosum* occupies the more oligotrophic lawns  
419 with a preference for open space (Clymo and Hayward, 1982; Laine et al., 2018). Along with the appearance  
420 of *Sphagnum* from the subgenus *Subsecunda*, *Drosera intermedia* was also recorded. Currently, in Poland,  
421 it is a very rare species, found in dispersed peatlands (Mirek et al., 2006). Individuals often stand in the  
422 water even throughout the season. *Andromeda polifolia* also appeared in this phase. Initially, the presence  
423 of *Sphagnum* was accompanied by *Straminergon stramineum* (max. 10%), but later it disappeared  
424 completely. By the beginning of the twentieth century, a relatively high proportion of monocotyledonous  
425 plants was also observed, represented in the samples by their epidermis, averaging about 20% in a sample,  
426 with a much higher proportion in the early stages. All these taxa indicate an intermediate environment  
427 between a shallow lake and a moss peatland.

428 After an initial decline (from 9.2 cm at 73.5 cm, 1838 cal. CE, to 13.0 cm at 66.5 cm, 1862 cal. CE), the  
429 water table level increased and stabilized at a high level, reaching a maximum of 6.8 cm at 47.5 cm, 1907  
430 cal. CE (Fig. 4). The abundance of individual testate amoeba species also increased. Initially, *C. aculeata*  
431 dominated, but later *Amphitrema wrightianum* and *Hyalosphenia papilo*, mixotrophic taxa that contain  
432 endosymbiotic photosynthetic algae, begin to prevail (Lamentowicz and Mitchell, 2005a; Marcisz et al.,  
433 2020a) (Fig. 4). Subsequently, the proportion of *A. wrightianum* and *H. papilo* began to decline in favour  
434 of *Archerella flavum* and *Hyalosphenia elegans* (Fig. 4). All four species are associated with the presence  
435 of *Sphagnum*, with *A. flavum* and *A. wrightianum* tolerating very wet or even submerged *Sphagnum* habitats,  
436 which corresponds to a stably high-water table. Then, from the mid-1880s for another ca. 20 years, *C.*  
437 *aculeata* again became dominant. After this period, species associated with *Sphagnum*– *A. wrightianum*, *A.*  
438 *flavum* and *Heleopera sphagni* – began to dominate again. During this phase, further acidification of the site  
439 was noted through a drop in the pH value from the initial 4.8 to 4.1 (Fig. 4).

440 The forests surrounding the peatland (55.1-92.7% TP) were still dominated by pine (64.5-92.8% AP),  
441 although their percentage has decreased in comparison to phase 1, especially during the 1920s and 1930s  
442 (Fig. 5). Deciduous taxa such as *Quercus*, *Corylus avellana*, *Carpinus betulus* and *Fagus sylvatica* retreated.  
443 The percentage of Cerealia in the TP increased significantly, from 0-7.8% TP in the first phase to 2.8-19.8%





444 in the second phase, with a peak in the late 1910s and early 1920s, indicating the development of agriculture  
445 in the vicinity of the peatland (Fig. 5). Around the same time, the proportion of *Rumex* also increases  
446 significantly (0-11.5%). The low values of MAC (Fig. 3) and MIC (Fig. 5) indicate a low fire activity in the  
447 studied area.

448

449 **3.2.3. Phase 3: (~1945–present, 37–0 cm): Lowering of the groundwater table as a result of climate**  
450 **change, further afforestation with *Pinus sylvestris*, a succession of *Betula***

451

452 The local vegetation (Fig. 3) underwent several changes during this phase. Although *Sphagnum* dominated  
453 for the entire time, the subgenus *Sphagnum* receded in favour of first the subgenus *Cuspidata* and then the  
454 subgenus *Acutifolia*. The beginning of the phase was marked by *Pohlia nutans*, which can win the  
455 competition in unstable habitat conditions, such as during the dry season (Boulc'h et al., 2020). Its  
456 occurrence correlated with the presence of Phryganella acropodia among testate amoebae (Fig. 4), which is  
457 an indicator of low water levels in Sphagnum peatland (Diaconu et al., 2017; Lamentowicz and Mitchell,  
458 2005b).

459 This was followed by *Alabasta militaris* ( $\bar{x} = 25.5\%$ ), *Galeripora discoides* ( $\bar{x} = 10.5\%$ ) and *Nebela tincta*  
460 ( $\bar{x} = 8.2\%$ ) beginning to dominate (Fig. 4). *G. discoides* is typically present in acidic sites with unstable  
461 hydrological conditions (Lamentowicz and Mitchell, 2005b; Sullivan and Booth, 2011). *N. tincta* tolerates  
462 dry, highly acidic conditions with mineral matter supply (Booth, 2002; Koenig et al., 2018; Lamentowicz et  
463 al., 2011). *A. militaris*, dominant in recent years, is indicative of dry and markedly acidic conditions  
464 (Amesbury et al., 2016; Booth, 2002; Lamentowicz et al., 2011; Marcisz et al., 2020a; Sullivan and Booth,  
465 2011). Based on testate amoebae, this phase was distinguished by a significant drop in the groundwater  
466 table, from an average level of 9.6 cm below the ground surface in the second phase to 15.7 cm. In the last  
467 decade, the most significant decline was observed, with an average level of 21.9 cm, with a maximum of  
468 27.5 cm, 1983 cal. CE. The pH continued to decrease – from 4.4 to 4.0 (Fig. 4).

469 On a regional scale, there is an increase in the relative abundance of *Pinus* pollen in the TP, from about 46%  
470 at the beginning of the phase to about 85% today as an effect of afforestation (Fig. 5). *Betula* pollen  
471 concentration has an apparent increase, from 0,7-11,3% in the second phase to 5,6-32,5%. The increased  
472 concentration of *Betula* pollen, combined with macroscopic remains in the form of achenes and catkin scale,  
473 indicates the intensive succession of this species on the peatland surface. The ruderal species *Urtica* and  
474 *Artemisia* were also more strongly manifested. The average proportion of *Urtica* pollen in the TP increased  
475 almost 8 times (from 0-0.7% to 0-2.9%). The percentage of Cerealia in TP has decreased significantly, from  
476 nearly 20% in the early 1920s to just over 1% today.



477 Local (Fig. 3) and regional (Fig. 5) fire activity continued to be low, although two slightly more intensive  
 478 periods of regional fires were marked – ca. 1945-1963 and the early 2020s.

479

480 **3.3. Dendrochronological and pointer years analysis**

481 A total of 50 tree-ring series of 23 *Pinus sylvestris* L. trees from the Woziwoda site were successfully cross-  
 482 dated. Based on the well-synchronized tree-ring series TRW (Fig. 6) and RWI site chronologies spanning  
 483 222 years (1801-2022) were developed. The statistical characteristics of the ring-width series and the  
 484 statistical parameters indicating the signal strength of the regional RWI chronology are shown in Tab. 2.  
 485 The mean EPS was 0.93, which is well above the threshold value (EPS = 0.85) required to produce a  
 486 statistically robust RWI chronology. Mean series inter-correlation, MS, SNR, and other statistical  
 487 parameters indicating the strength of chronology signals were also high, indicating the suitability of  
 488 chronology for climate-growth analysis.

489 Tab. 2 Descriptive statistics of standardized *Pinus sylvestris* L. (RWI) chronology for Woziwoda site

Chronology length	1801-2022
Mean tree age [yrs]	197
Number of tree/cores	23/50
Mean ring width (mm) ± SD	1.256 ± 0.702
Series intercorrelation	0.623
Average mean sensitivity	0.265
Expressed Population Signal (EPS)	0.93
Signal-to-noise ratio (SNR)	12.97
Rbar.eff (effective chronology signal)	0.361

490

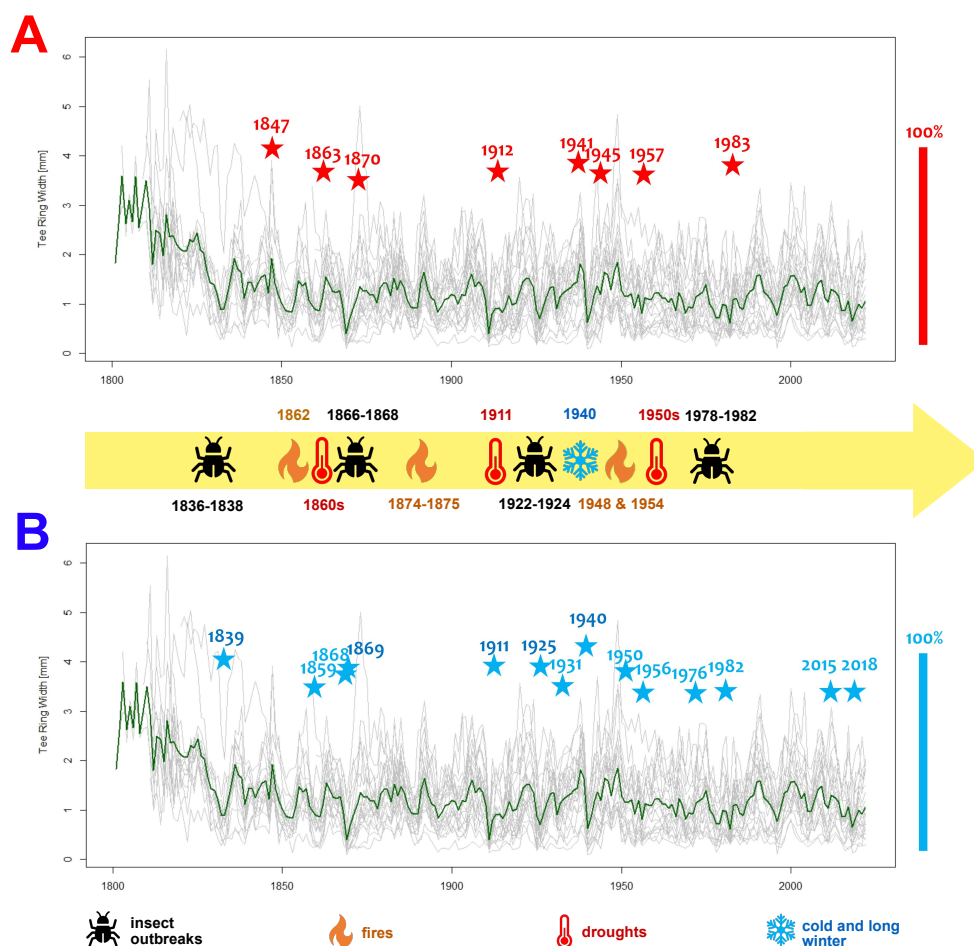
491 Across the study period (1920-2022) significant positive relationship between growth and February mean  
 492 temperature was identified (Fig. 7). The moving correlation analysis showed an increasing trend in the  
 493 sensitivity of tree growth to climatic factors (Fig. 8). The positive response of tree growth to February mean  
 494 temperature remained constant throughout the study period (1920-2022) (Fig. 8). However, the sensitivity  
 495 of tree growth to summer temperature increased. The relationship between annual growth and summer  
 496 temperature was not stable during the period 1920-2022. Nevertheless, in the last 30 years, a significant  
 497 negative relationship between annual growth and June mean temperature was observed.

498 Climate-growth analysis for monthly data did not show a statistically significant relationship between  
 499 growth and precipitation (Fig. 7). However, moving response analysis revealed significant short-term  
 500 relationships between tree growth and precipitation. Furthermore, it was demonstrated that the influence of  
 501 precipitation in the current year's months on tree growth calculated for the years 1960-2022 was more



502 significant than the relationships calculated for the years 1921-1959. In recent years, a particularly positive  
 503 relationship between tree growth and early-year (February-April) precipitation as well as June precipitation  
 504 has become apparent.

505 For Woziwoda site 8 positive and 13 negative pointer years were identified for the period 1814-2022 (with  
 506 a minimum sample depth 10 trees) (Fig. 6). The most pronounced positive pointer years with more than  
 507 90% tree response were as follows: 1847, 1863, 1870, 1912, 1941, 1945, 1957, and 1983. The most pronounced  
 508 negative pointer years were: 1839, 1868, 1869, 1911, 1925, 1940, and 1950. Figure 6 provides marks of  
 509 pointer years together with meteorological and ecological characteristics.

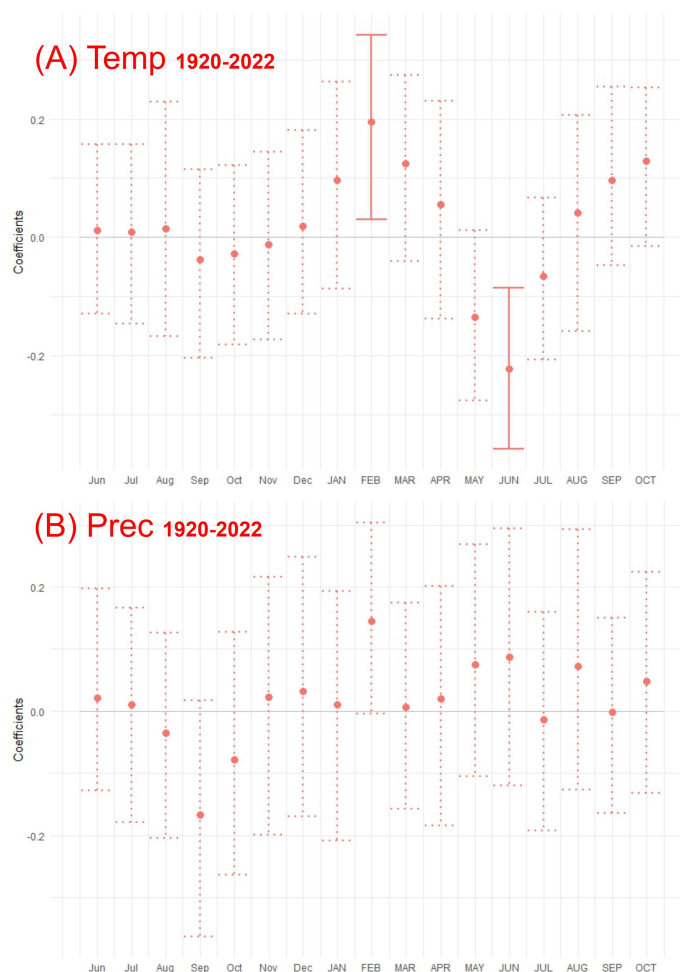


510

511 **Figure 6.** The grey lines depict the individual tree ring series of each tree, while the green line represents  
 512 the average raw chronology of *Pinus sylvestris* L. at the Woziwoda site. Identified within the Scots pine



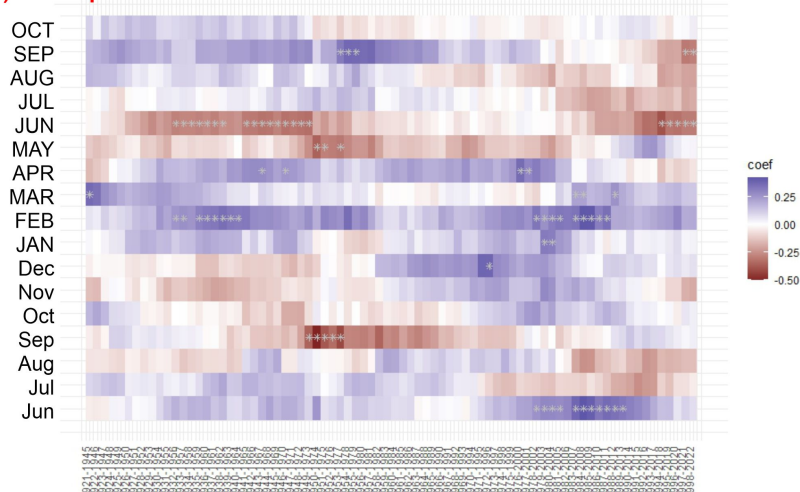
513 chronology from Woziwoda are pointer years, categorized as negative (NEG) (A) and positive (POS) (B).  
514 These pointer years are highlighted with colored asterisks: red for positive pointer years and blue for  
515 negative pointer years. The position of the asterisks refers to a scale of 0-100%.



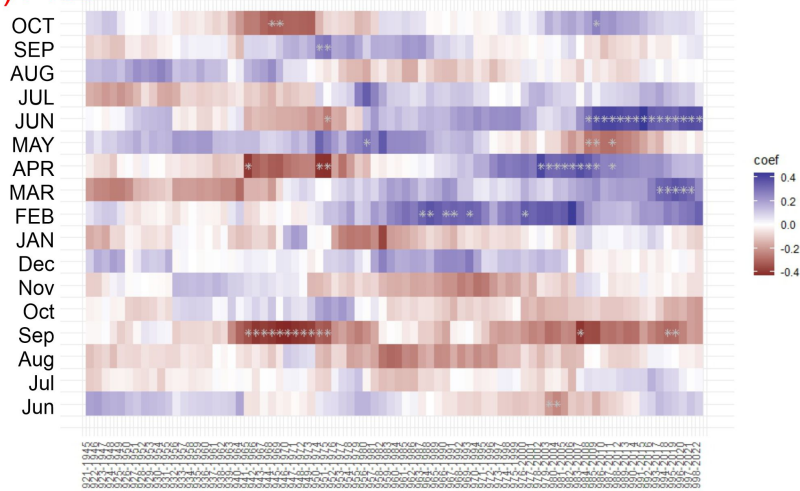
516  
517 Figure 7. Response function coefficients between residual *Pinus sylvestris* L. chronology residual *Pinus*  
518 *sylvestris* L. chronology and climate variables: (A) mean air temperature (TEMP), and (B) precipitation for  
519 the period 1920–2022. Names of the previous year’s months start with a lowercase letter. Solid lines  
520 represent significant coefficients at  $p < 0.05$ .



(A) Temp



(B) Prec



521

522 Figure 8. Moving response correlations (25-year window) between residual *Pinus sylvestris* L. chronology  
 523 and climate variables: (A) mean air temperature (TEMP), and (B) precipitation for the period 1920–2022.  
 524 The color code represents the correlation coefficient. Significant correlations are indicated by white  
 525 asterisks.

526

527 **3.4. The current state of the peatland based on remote sensing data analysis**

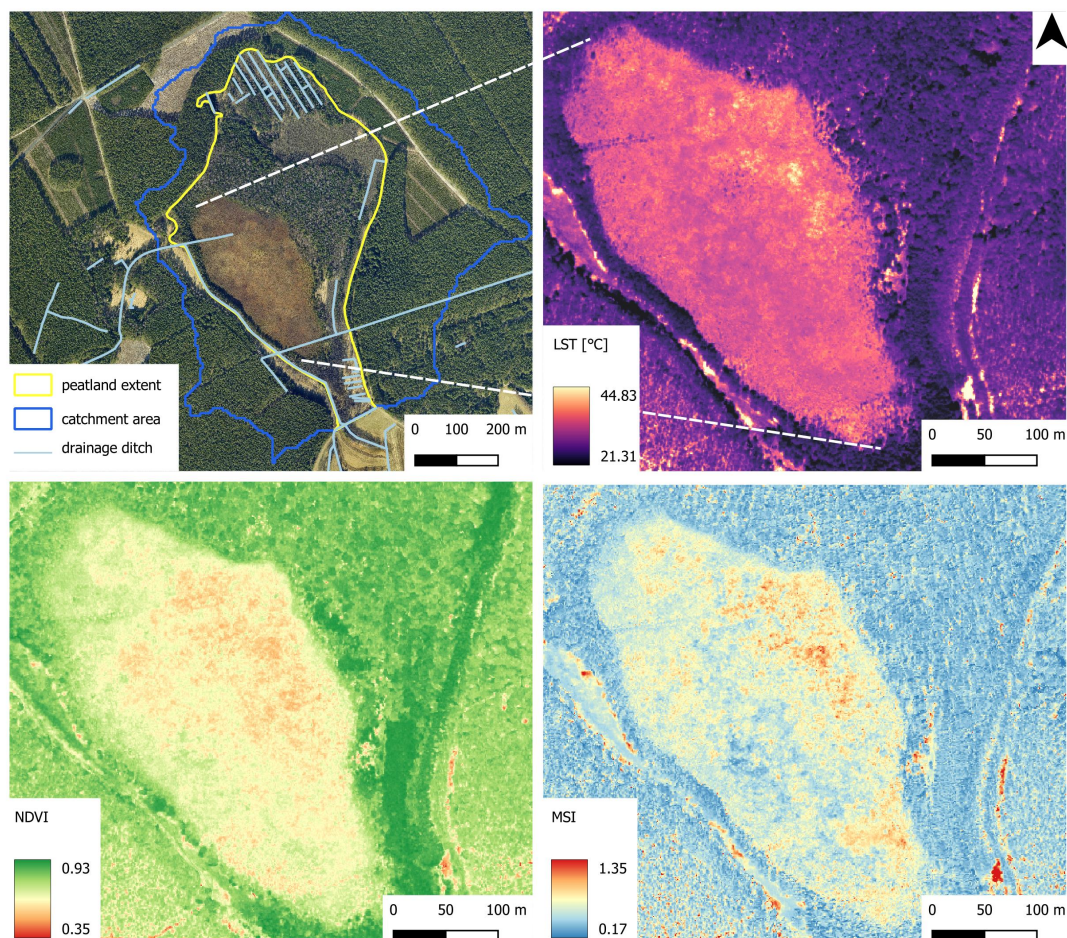
528

529

Presently, the non-forest part of the peatland is drained by two parallel ditches. One is located in the northern, and the other is in the southern non-forested part of the peatland. The analysis of thermal data



530 obtained on a torrid midsummer day indicates that the average LST for the non-forested part of the peatland  
531 is approximately 34.29 °C, with a temperature range extending from 19.22 °C to 46.37 °C. There is a distinct  
532 internal variability in LST values within the studied area. Higher values, indicative of more significant  
533 dehydration, were identified in the eastern part of the peatland, while lower values were observed in the  
534 western part. A repeating spatial pattern of their values was observed in the analysis of vegetation indices  
535 (NDVI and MSI). High NDVI values and low MSI values, indicative of good vegetation condition and low  
536 water stress, were observed in the western and southwestern parts of the peatland (Fig. 9). The average  
537 NDVI value in these areas is 0.71, and MSI is 0.6. Conversely, low NDVI values and high MSI values,  
538 indicative of significant dehydration of the peatland and low vegetation vigor, were observed in the eastern  
539 part of the object (Fig. 9), where NDVI averages 0.63, and MSI is around 0.69. The overall average NDVI  
540 for the object was 0.65, and for MSI, it was 0.68.



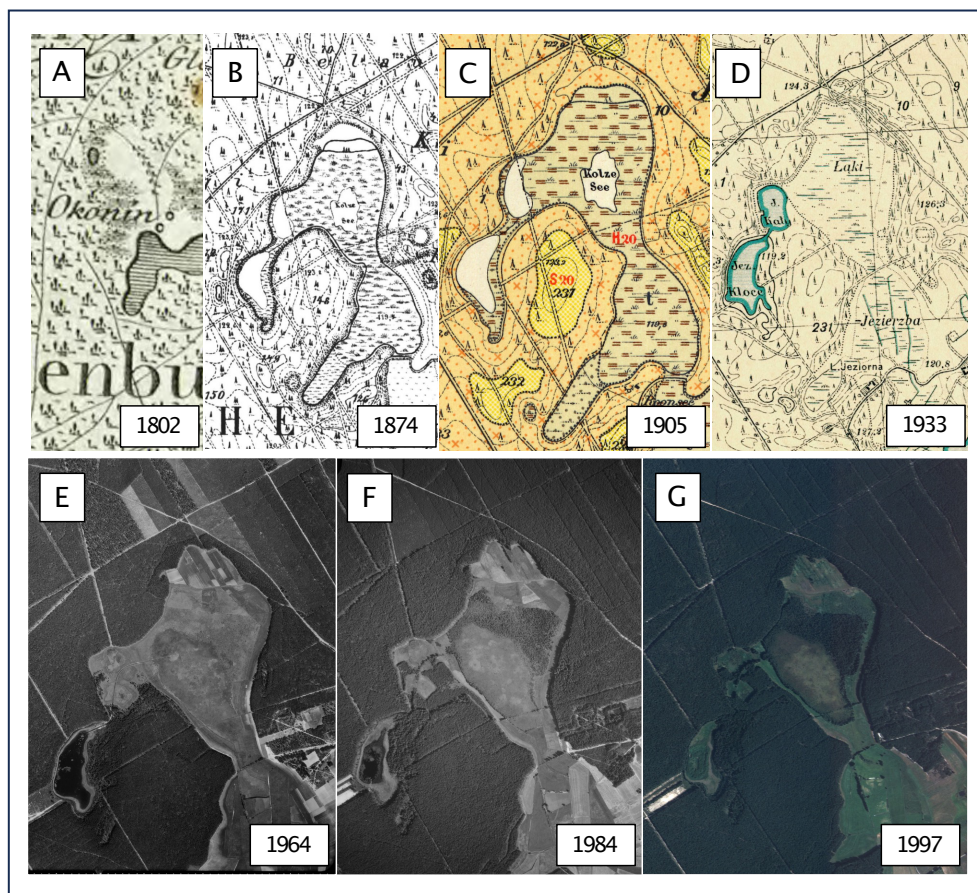
541



542 Figure 9. Remote sensing characteristics of Okoniny peatland based on multisensorial airborne data acquired  
543 in 2022.

544

545 **3.5. Historical maps and airborne images as confirmation of changes shown in palaeoecological data**



546

547 Figure 10. Changes in the peatland and its surroundings since the beginning of the 19th century based on  
548 historical maps and aerial images. (A) Schrötter-Engelhardt map 1:150 000 (1802), (B) Messtischblatt map  
549 no. 982 1:25 000 (1874), (C) Prussian geological and agricultural map no. 2374 1:25 000 (1905), (D)  
550 Detailed Map of Poland 1:25 000 (1933), (E) Aerial photograph from 1964, (F) Aerial photograph from  
551 1984, (G) Aerial photograph from 1997. Maps no. A, B, C, and D are in the public domain. Aerial  
552 photographs were obtained from © Central Office of Geodesy and Cartography in Poland, license no.  
553 DIO.7211.457.2023\_PL\_N.

554



555 Analysis of historical materials (Fig. 10), including maps and airborne images, confirms the results of the  
556 palaeoecological analysis. Both the Schrötter-Engelhardt map of 1802 and the Messtischblatt of 1874  
557 indicate the existence of a small lake in the coring area. Again, however, it should be noted that the Schrötter-  
558 Engelhardt map is a highly generalized study and does not give much information about the surroundings  
559 of today's peatland, other than that we are dealing with an area with the character of a dense forest complex  
560 with wetlands in isolated places. Messtischblatt allows us to better interpret the surroundings of the analyzed  
561 modern peatland at the time in which the map was prepared. A small lake named "Kolze See" is observed  
562 in an advanced stage of development, i.e., progressive overgrowth. This lake is located in the surroundings  
563 of wetlands (Bruch in German) somewhat distant heathland (Heide in German) and wasteland (Ödland in  
564 German) (the original nomenclature of the map legend was adopted). This lake and two other lakes close  
565 by are enclosed within a single catchment area. To the south, the area of the current peatland was adjacent  
566 to an open, extensive meadow.

567 Even more information is provided by a 1905 geological-agricultural map prepared on the topographic base  
568 Messtischblatt map of 1874. In addition to land use, it shows the type and thickness of alluvial and diluvial  
569 deposits. According to this map, the area around the lake was covered by alluvial sediments – humus with  
570 peat subsoil and shallow groundwater (org. in German: Humus (Peat) mit Torf-Untergrund und nahem  
571 Grundwasser). The thickness of the peat was marked at two meters. However, it should be noted that drilling  
572 surveys at that time only covered a maximum depth of two meters, so the maps do not provide information  
573 on the total thickness of the sediments (Jasnowski, 1962). Places that were used as heathland and wasteland  
574 on the topographic map are covered by sandy humus on a sandy substrate with shallow groundwater (org.  
575 in German: Sandiger Humus mit Sand-Untergrund und nahem Grundwasser) and by humic sands on a  
576 substrate of permeable sands with shallow groundwater (org. in German: Humoser Sand mit durchlässigen  
577 Sand-Untergrund und nahem Grundwasser).

578 A Detailed Map of Poland from 1933 documents the change in an ecosystem from lake to land. The area,  
579 which on Prussian topographic maps was a lake with a surrounding bog, is described as a meadow on this  
580 map. Moreover, the meadows adjacent to the south were marked with drainage ditches, which were not on  
581 the Prussian maps. The area's surroundings, as before, were dominated by coniferous forests.

582 Aerial photos document subsequent changes in the ecosystem. The 1964 photo shows the northern part of  
583 today's peatland's agricultural use (regular surface layout). Lake Kały, located nearby, became completely  
584 overgrown, and its area was later dug by a drainage ditch, brought to the studied peat bog. The surrounding  
585 area of the peatland is dominated by dense forest with occasional open clear-cutting areas. A photo from  
586 1984 documents the succession of trees in the north-central part of the peatland. In the surrounding area,  
587 open forest areas have entirely disappeared. A photo from 1997 clearly shows the development of trees on  
588 the peatland, which have formed a dense block in its north-central part. A distinct area of *Sphagnum-*





589 dominated peatland with a well-marked edge has also emerged. Currently, the northernmost part of the  
590 peatland is overgrown by pine; it is almost impossible to identify the maximum extent of the peatland surface  
591 in the field (Fig. 1).

592

#### 593 **4. Discussion**

##### 594 **4.1. Exceptionally high peat accumulation rate**

595 ~~Peat accumulates when vegetation production exceeds organic losses under high water levels and anaerobic~~  
596 ~~conditions (Tobolski, 2000).~~ In the Okoniny peatland, a rapid rate of peat accumulation is observed,  
597 averaging 3.56 mm/yr, with a maximum value of 7.1 mm/yr at a depth between 11 and 12 cm. There are  
598 several peatlands in Poland for which higher accumulation rates were reported. In the Tuchola Pinewoods,  
599 the faster average rate of peat accumulation was recorded at Dury – 10 mm/yr (Pawlyta and Lamentowicz,  
600 2010) and Mukrza – 4.6 mm (Lamentowicz and Obremska, 2010). At Jelenia Wyspa mire the accumulation  
601 rates reached 0.4 mm/yr for the first 3000 years but accelerated to 3 mm/yr in the last 150 years  
602 (Lamentowicz et al., 2007). A much slower rate was on the Tuchola kettle-hole bog – 1.2 mm and after ca.  
603 1320 cal. yr BP the accumulation rate dropped to 0.4 mm/yr (Lamentowicz et al., 2008b). In other pine  
604 monocultures, such as the Noteć Forest, the Rzecin peatland stands out for its high accumulation rate – an  
605 average of 6.8 mm/yr in one profile and 7.5 mm/yr in the other one (Milecka et al., 2017). Peatlands in  
606 Tuchola Pinewoods, including Okoniny peatland, generally have a faster accumulation rate than peatlands  
607 located in other parts of Pomerania. The small kettle-hole peatland characteristic of Tuchola Pinewoods  
608 accumulates carbon the fastest of all peatland types (Karpńska-Kołaczek et al., 2024). For the Stążki mire,  
609 the highest accumulation rates were reported for the period between ca. 150-1230 AD and reached 2.2  
610 mm/yr (unfortunately, the more recent, topmost material was not analysed) (Lamentowicz et al., 2008a).  
611 Peat accumulation was even slower on Słowińskie Błota raised bog – 1.38 mm between 1830 and 2006,  
612 although the highest accumulation rate was 5 mm/yr (during AD 840-860) (Lamentowicz et al., 2009b). At  
613 the Gołębiewo sites the maximum accumulation rate was 1.85 mm/yr for the first site and 0.36 mm/yr for  
614 the second site (Pędziszewska and Latałowa, 2016). The average 2 mm/yr accumulation rate for the  
615 Kusowskie Bagno bog was in its 4000-year history (Lamentowicz et al., 2015). At Gązwa bog, the  
616 accumulation rate was estimated at 1.46 mm/yr, more than twice as slow as at Okoniny peatland (Gałka et  
617 al., 2015). In other regions of Poland, Jaczno bog (Suwałki Lakeland) stands out where peat accumulation  
618 rate in this peatland was very rapid, averaging 2.76 mm/yr, with the highest values recorded in  
619 undecomposed and uncompacted acrotelm – up to 12.7 mm/yr (Marcisz et al., 2020b). At the Pawski Ług  
620 bog PAR was similar – 2.6 mm/yr (Lamentowicz et al., 2020). Such high accumulation rate values are also  
621 rare in other parts of the temperate climate zone of Europe. Teici bog (Latvia) showed similar accumulation  
622 rates - 3.5 mm/yr - from 1835 to 1965 AD and 10 mm/yr after 2000 (Stivrins et al., 2018). Okoniny peatland



623 after 2000 (between 21.5 and 11.5 cm) recorded an accumulation of 5.7 mm/yr. Saxnäs mosse in Sweden  
624 showed an almost linear peat accumulation rate of 2-2.5 mm/yr (van der Linden et al., 2014). The maximum  
625 accumulation was recorded at around 2310-2250 cal on the Estonian Hara bog, BP (31-15 cm) reaching 2.4  
626 mm/yr (Łuców et al., 2022).

627

## 628 **4.2. Relationships between forest management and pollen analysis**

### 629 **4.2.1. The complex history of the Tuchola Pinewoods and its influence on the forest**

630 The results of pollen analysis of the collected core enabled us to illustrate how the forest was managed over  
631 the past 300 years. Due to political changes and several administrative decisions, the management strategies  
632 of the Tuchola Pinewoods underwent vital changes. The consequences of the implementation of forest  
633 management techniques were visible in the palaeoecological record.

634 In 1772, the area of Gdansk Pomerania with the Tuchola Pinewoods was included in the borders of the  
635 Kingdom of Prussia as a result of the First Partition of Poland (Wilson, 2012). At that time, some of the first  
636 legal regulations for planned forest management in the area appeared (Jaszczak, 2008a). Nevertheless, in  
637 1775, Frederick II the Great (1740-1786) issued a decree regarding government forests in Prussia, and later  
638 state forests in Poland. It proposed the division of the forest into districts consisting of 50 man-made  
639 clearings. However, this method of forest management worked well in the area of small forests in western  
640 Prussia, but not for large forest complexes like the Tuchola Pinewoods. In 1782 Frederick II the Great issued  
641 a special decree "On the development of the Tuchola Forest," in which it was written that the area of the  
642 Tuchola Pinewoods was to be divided into eight districts of about 6000 hectares and 60 cutting areas in each  
643 district. Only one man-made clearing in each district was provided for economic use, so no more than 100  
644 hectares of forest per district (Jaszczak, 2008b). However, despite the introduction of many regulations  
645 relating to forest management, the first decades of the 19th century brought devastating and predatory  
646 deforestation on a large scale. For most of the 19th century, progressive deforestation was a problem in the  
647 region, making the already poor conditions for agricultural development much worse (Wilson, 2012). With  
648 each successive partition of Poland (1772, 1793, 1795), the Prussian government took over the state forests,  
649 first the royal table estates (in Polish: dobra stołowe), and then also royal land (in Polish: królewszczyzny).  
650 After the second partition, state forests were separated from agricultural land and transferred to separate  
651 administrations (Nienartowicz, 2012). In 1810, the Prussian government issued the so-called Secularization  
652 Act, under which forests were removed from churches and monasteries and attached to state forests. A law  
653 had been in effect in Prussia since 1713, which prohibited the selling of state-owned property, but the  
654 approach was different in Prussia.

655 To carry out the fastest possible Germanization of these lands, the local state property was sold off to the  
656 Prussian nobilities, inviting them to settle in the area. Prussia's defeat of Napoleon's forces at the Battle of



657 Jena-Auerstedt in 1806 and the contribution Napoleon imposed in 1808 also contributed to the selling off  
658 of the state forests. In December 1808, the government in Berlin passed an edict (published in November  
659 1809) allowing the sale of state land, including forests, to cover the national debt (Broda, 2000; Kozikowski,  
660 1911). Only large, compact forest complexes of a protective nature and economic importance were excluded  
661 from this regulation (Broda, 2000). An additional reason for the loss of state forest area was the need to  
662 redeem the servitude rights vested in peasants when selling property. The government compensated the  
663 peasants for their rights to use the forest by transferring other forests without looking at area losses. The  
664 peasants most often cut down all the forest given to them and turned the land into agricultural land. The  
665 cause for such action was provided by the 1807 edict that removed state supervision of private forests, which  
666 was later extended in 1811 (Broda, 2000; Kozikowski, 1911). Private forests could be freely managed from  
667 then on, including dividing into smaller parcels, converting to agricultural land and selling.

668 This period was also a time of intense social and economic change, marked by the collapse of feudalism in  
669 favour of a capitalist economy. The end of these transformations in Prussia was the enfranchisement of  
670 peasants in 1811-1823. Economic development entailed a considerable demand for timber, and this, in turn,  
671 became the basis for the robbery economy in forests. The selling off of state forests slowed down only in  
672 the 1830s largely due to the efforts of G.L. Hartig, the general director of state forests in Prussia, and stopped  
673 entirely in 1860.

674 Exploited forest areas were restored mainly with pine and spruce, either artificially or naturally. Because of  
675 this, deciduous admixture species with entirely different life requirements began to disappear over time  
676 (Broda, 2000). The introduction of easier-to-maintain coniferous species was driven by the growing demand  
677 for wood in industry. The trend toward introducing pine monocultures intensified from the 1830s onward.  
678 Since forest management in Prussia's state forests served mainly fiscal purposes, the concept of monoculture  
679 plantations did well for several more decades. This situation persisted until the 1860s when a devastating  
680 pest gradation occurred (Broda, 2000). At that time, the first steps were taken regarding the introduction of  
681 admixtures into restoration.

682 Our data confirm an increase in the proportion of pine pollen in the forest composition and a decrease in the  
683 proportion of pollen of other species. From the 1730s to the mid-1860s, the share of pine pollen in the pollen  
684 of all trees increased from about 60% to about 90%. Our pollen diagram shows the rapid increase in *Pinus*  
685 *sylvestris* pollen concentration after 1850. It can, therefore, be assumed that this resulted from *Pinus*  
686 *sylvestris* introduced by mass monoculture plantings in the early 1830s reaching reproductive capacity. Pine  
687 usually reaches sexual maturity between 10 and 15 years (Sullivan, 1993), although the threshold age has  
688 been set at 25 years (Matthias and Giesecke, 2014). The decline in the share of deciduous species and the  
689 increase in the share of Scots pine in the landscape began in Poland with the formation of the state. However,  
690 at that time, it was associated with the expansion of agriculture and the harvesting of preferred species such



691 as *Carpinus betulus* (Czerwiński et al., 2021) Nevertheless, in the Prussian partition, planned forest  
692 management permanently changed the composition of Poland's largest forest complexes, which were  
693 dominated by easy-to-grow pine (Broda, 1993). A dynamic increase in the share of pine pollen until the  
694 1860s in the Tuchola Pinewoods was also recorded at the Czechowskie Lake (Słowiński et al., 2019). An  
695 increase in pine pollen concentration since the 19th century was also shown in pollen diagrams of other sites  
696 from Pomerania – Stążki (Lamentowicz et al., 2008a), Słowińskie Błota (Lamentowicz et al., 2009b) – and  
697 in other monoculture plantation complexes from Prussian partitioning area – Rzecin peatland in the Noteć  
698 Forest (Milecka et al., 2017).

699 Although attempts were undertaken to correct earlier mistakes, this did not stop the massive deforestation.  
700 Until the 1870s, the feudal system was still mixed with capitalist components, but from the 1870s onward,  
701 under monopoly capitalism, timber trade and processing began to reach a significant size (Broda, 2000).  
702 However, it has been noted that forests regulate air temperature, store water in the soil more efficiently, and  
703 reduce wind speed, preventing soil erosion, which can help local agriculture face difficult environmental  
704 conditions (Wilson, 2012). For this reason, as early as the 1870s, the state administration encouraged  
705 landowners to protect forest stands on their lands and establish forestry cooperatives. The government also  
706 guaranteed funds for the reforestation of private and municipal lands. In the mid-1870s, the Landtag set  
707 aside a budget for the purchase and reforestation of wasteland by the state. However, these funds were used  
708 to a small extent, although this somewhat reduced the share of forested private property (Broda, 2000;  
709 Wilson, 2012). In 1886, the Royal Settlement Commission (in German: Königliche  
710 Ansiedlungskommission) was established to buy up the estates of impoverished Polish nobility to acquire  
711 agricultural land for German settlers (Wilson, 2012).

712 At the end of the 19th century, Tuchola Pinewoods became the largest timber production hub in the Prussian  
713 partition. The Bydgoszcz timber industry region also played a major role in wood processing. The first steam  
714 sawmill in the Bydgoszcz region was built in 1873, and by 1913, there were 20 of them, processing some  
715 500,000 m<sup>3</sup> of wood and employing more than 1,600 people (Broda, 2000). All this resulted in a significant  
716 decline in the concentration of tree pollen in the total pollen concentration in our diagram, to less than 60%  
717 by the late 1920s and early 1930s. At the same time, we have seen intensive agricultural development. At  
718 Okoniny, the proportion of Cerealia pollen doubled between ca. 1900-1920. This trend is also confirmed by  
719 pollen data from the site in Okoniny Nadjeziorne, on the other side of Okonińskie Lake (Tipton, 2023), as  
720 well as from Czechowskie Lake, about 25 km northeast of our site (Słowiński et al., 2019). Despite intensive  
721 deforestation in general, further afforestation with pine was also progressing. In 1893, pine forests accounted  
722 for 99% of all forests in Tuchola County (Szwankowski, 2005). Intense changes in forest management (pine  
723 dominance) and agricultural development (high concentration of Cerealia pollen) in the 19<sup>th</sup> century are also



724 evident in records of profiles outside large, dense forest complexes – Kusowskie Bagno (Gałka et al., 2014),  
725 Linje mire (Marcisz et al., 2015).

726

#### 727 **4.2.2. Impact of forest management on peatland vegetation**

728 As a result of changes related to forest management, lake to peatland transition occurred rapidly. We assume  
729 that this was primarily the result of drainage, which was undertaken in the area at the end of the 19<sup>th</sup> century  
730 (see drainage ditches on the southern side and a dike in the middle part of the site on maps in Figure 6), and  
731 secondly, to a lesser extent, the transition from mixed forests to pine monoculture. These activities  
732 contributed to an increase in the acidity of the peatland. Forest drainage is often associated with the  
733 acidification of surface waters (Miller et al., 1990). The introduction of forest drainage, on or near peatlands,  
734 to improve tree growth has been quite common in northern and northeastern Europe (Westman and Laiho,  
735 2003). The oxidation of organic sediments and the detachment of hydrogen ions H<sup>+</sup> increase acidity (Ulrich,  
736 1980). In addition, the supply of alkaline cations to the peat is impeded by drainage ditches (Minkinen et  
737 al., 2008). However, the long-term consequences of drainage are devastating to peatlands, as they initiate  
738 vegetation succession, in which species typical of peatlands are replaced by forest vegetation (Laine et al.,  
739 1995). In the example of our palaeoecological data, the dynamic succession of pine and birch in the Okoniny  
740 peatland is evident, which is also supported by aerial imaging. As already mentioned, the successive decline  
741 in pH is also the result of the impact of pine plantations growing in catchments. A drop in pH in Okoniny  
742 has likely enabled the rapid growth and expansion of *Sphagnum* and the peatland initiation. The crowns of  
743 forests, especially the needles, can increase the uptake of atmospheric pollutants such as sulfur and nitrogen  
744 components, contributing to the acidification of surface waters (Nisbet, 2001; Reynolds et al., 1994).  
745 Conifers also can capture ions of marine origin - Na and Mg cations. These, in turn, displace hydrogen and  
746 aluminium cations from the soil, leading to acid runoff from the forests along with surface runoff, which is  
747 known as the "sea-salt effect" (Drinan et al., 2013; Harriman et al., 2003; Reynolds et al., 1994). We  
748 observed the presence of *Pinus* needles at the beginning of phase 2 (from 1838 cal. CE), at the transition  
749 from pond to peatland ecosystem. Moreover, *Pinus* stomata were also present in palynological samples at  
750 that time, pointing to more frequent needle falls. More pine trees in the Tuchola Pinewoods resulted in much  
751 higher amounts of needles and other pine fragments accumulating on the forest ground, leading to soil  
752 acidification. This, together with drier conditions, could quickly lead to acidification around the pond,  
753 forming perfect conditions for *Sphagnum* to encroach – first as a floating mat that successively overgrows  
754 the pond. We sampled the peat core close to the edge of the peatland, thus in the place where moss  
755 encroachment on the open water body began; therefore, we were able to track this succession in our record.  
756 This succession and disappearance of Lake Kolze are also clearly visible in historical maps (Figure 10).  
757 Other examples of quick encroachment of floating mats on the surface of the lake have been observed and



758 mapped in other open water bodies in the Tuchola Pinewoods (Kowalewski, 2003; Kowalewski and  
759 Milecka, 2003) and other regions (Warner, 1993).

760

#### 761 **4.3. Anomalies and extreme events**

##### 762 **4.3.1. The impact of droughts and fires on the forest and peatland**

763 Historical sources indicate that in the 18<sup>th</sup> and 19<sup>th</sup> centuries, the Tuchola Pinewoods were relatively often  
764 affected by droughts resulting in fires (Wilson, 2012). In 1781, there was a fire in Tuchola (ca. 16 km SW),  
765 during which a large part of the city with the church and town hall burned down, and in 1792, Starogard  
766 Gdański (ca. 42 km NE) burned almost to the ground (Orłowicz, 1924). Major fires also occurred in 1794,  
767 and 1807, when more than 34,000 hectares of forest burned (Orłowicz, 1924; Schütte, 1893). Fires in 1809,  
768 1810, 1812, 1813 and 1828 in the Świt forest district about 15 km from the study site were also recorded  
769 (Cyzman, 2008). Palaeoecological data, especially MIC, confirm high fire activity in the first decades of the  
770 19<sup>th</sup> century (a rapid increase). Słowiński et al. (2019) emphasized that data on fires before the 1830s,  
771 especially regarding their area, should be treated with caution due to the lack of accurate measurement  
772 techniques. In the Woziwoda Forest District, within which the Okoniny peatland is located, the forests of  
773 the Biała and Barłogi forest districts also burned in 1842 (Cyzman, 2008). Intense fires also appeared in the  
774 Tuchola Pinewoods between 1846 and 1848 (Orłowicz, 1924; Schütte, 1893).

775 Later, numerous fires were also reported in the Woziwoda Forest District. Between 1860 and 1889, 310 fires  
776 were observed, destroying 4206 hectares of the forest (Orłowicz, 1924; Schütte, 1893). The highest number  
777 of fires in this period was registered in 1862-1864 and 1874-1875 when 3565 hectares of forest burned;  
778 altogether, nearly 85% of the area burned in 1860-1889 (Schütte, 1893). The largest area burned in 1863  
779 equaled 2333 hectares, including more than 1250 hectares in the Woziwoda forest district; altogether, 25%  
780 of all the forest burned in 1860-1889 (Orłowicz, 1924; Schütte, 1893). Meteorological data confirm dry  
781 years in the period from 1862 to 1865. In 1862 and 1863, the annual precipitation in Bydgoszcz was only a  
782 little over 450 mm (Kirschenstein, 2005), and it was then that the largest number of hectares of forest in the  
783 known history of the Tuchola Forest burned (Dietze et al., 2019).

784 However, contemporary linked the number of fires with political events and nationalist sentiment among  
785 the Polish population (Orłowicz, 1924; Schütte, 1893; Wilson, 2012). In 1901, in the nearby Trzebciny and  
786 Gołąbek Forest Districts, a fire consumed 663 hectares of forest (there was a parallel children's strike in  
787 Września Province) (Orłowicz, 1924; Wilson, 2012). Fires could also be caused by agricultural activities  
788 and land preparation for crops (Poraj-Górska et al., 2017). By the 1830s, charcoal production was  
789 widespread (McGrath et al., 2015), and forest burning was used to create heathlands for beekeeping  
790 (Bienias, 2009).



791 Fires of the 1860s provide a regional signal at another site in the Tuchola Pinewoods – Czechowskie Lake  
792 (Dietze et al., 2019). Increased fire activity in the mid-19<sup>th</sup> century was also observed at the Lake Jaczno  
793 site (Poraj-Górska et al., 2017). At the Okoniny peatland, MIC and MAC values decreased after 1850, but  
794 at the same time, the water level stabilized and remained high. Fire activity remained low in areas where  
795 wet conditions prevailed, such as southern Finland (Väliranta et al., 2007) and eastern Estonia (Sillasoo et  
796 al., 2011).

797 In 1948, about 450 hectares of forest were burned near Osieczna, and in 1954, 80 hectares were burned near  
798 Ocypel (Cherek, 2007). Palaeoecological data record an increased MIC supply during this period. The first  
799 of these fires was also recorded in the sediments of Czechowskie Lake (Słowiński et al., 2019). The summer  
800 drought of 1921 occurred over a larger area of Europe, from Poland and the Czech Republic to the UK (van  
801 der Schrier et al., 2021). Summer droughts also affected the Tuchola Pinewoods in 1951 and 1959. In 1959  
802 Bydgoszcz received only 37 mm of precipitation from August to October (Mitosek, 1960), and from 1950  
803 to 1958 Bydgoszcz received less than 500 mm of rain per year (Kirschenstein, 2005). Our palaeoecological  
804 data confirm droughts in the 1950s. There is a sharp increase in the proportion of *Phryganella acropodia*  
805 among the testate amoebae, an indicator of dry conditions (Diaconu et al., 2017), and a high concentration  
806 of coprophilous fungi and an expansion of brown mosses in the form of *Pohlia nutans* (up to 30% of the  
807 peat sample composition) are also marked. Dendroclimatic data recorded the negative impact of climatic  
808 conditions on pine, especially strongly in 1950 and 1956.

809 Studies show that particle size illustrates the distance of the fire from the site, the heavier the particles, the  
810 shorter distances they travel (Clark, 1988; Peters and Higuera, 2007). However, many factors determine the  
811 particles' transport—the fire's intensity, the burning areas and the wind direction. Adolf et al. (2018) point out  
812 that the charcoal source area of occurrence of both MIC and MAC can reach a radius of 40 km. However,  
813 it is often assumed that MAC indicates fires that occurred up to 1-3 km (Clark, 1990; Higuera et al., 2007;  
814 Oris et al., 2014). The distances to which particles move are also determined by terrain and vegetation. They  
815 move longer distances on flat terrain covered with grasses (Woodward and Haines, 2020), while they move  
816 shorter distances in dense forests (Kelly et al., 2013; Oris et al., 2014). In this context, it should be assessed  
817 that the local fire activity in the studied peatland was low, with an average of 0.36 particles/cm<sup>3</sup>/year,  
818 although from historical sources, fires are known to have occurred nearby.

819

#### 820 **4.3.2. Insect outbreaks and their impact on pine monoculture**

821 The earliest information on insect outbreaks from the forests of the Tuchola Pinewoods under planned forest  
822 management dates back to 1836-1838. A gradation of the *Panolis flammea* occurred at that time (Schütte,  
823 1893). The insects also attacked between 1866 and 1868. As a result of this gradation, 1380 hectares of  
824 forest were destroyed in the Woziwoda forest district alone (Schütte, 1893). The pollen diagram from the



825 Okoniny peatland documents the phenomenon in the 1860s with a decrease in *Pinus sylvestris* pollen and  
826 an increased presence of *Pinus stomata* that may indicate the event of the insect outbreak (Barabach, 2015).  
827 The needles that fell were partially decomposed and carried downwind to the peatland, where they were  
828 preserved (Słowiński et al., 2019). The same effect was noted in another closely located peatland in Okoniny  
829 Nadjeziorne, where the 1866-1868 gradation also corresponds with increased numbers of *Pinus stomata*  
830 (Tipton, 2023). In 1855, *Lymantria monachal* appeared in large numbers but damaged only some of the  
831 younger stands (Schütte, 1893).  
832 A serious incidence of *Panolis flammea* gradation also occurred in 1922-1924 (Kielczewski, 1947;  
833 Mokrzejcki, 1928). Between 1978 and 1985, with a peak in 1982, the forests of the northern part of the  
834 country were overrun by *Lymantria monacha*, and this was the largest gradation since the establishment of  
835 the National Forests in 1924, with salvage treatments covering more than 6.3 million hectares of forest over  
836 seven years (Broda, 2000; Jabłoński, 2015; Śliwa, 1989, 1987). Both major gradations are reflected in  
837 palynological data, manifested by declines in pollen percentage of trees, primarily *Pinus* and *Picea*. A  
838 decrease in conifer pollen during the gradation period has also been shown by studies of other sites in the  
839 Tuchola Pinewoods (Łuców et al., 2021; Tipton, 2023). Other pine monoculture in Poland, the Noteć Forest  
840 was also affected by gradation in 1922-1924, and this event manifested itself in palaeoecological data  
841 (Barabach, 2015; Lamentowicz et al., 2015; Milecka et al., 2017). Among other things, Barabach (2015)  
842 noted an increase in *Glomeromycota* fungal spores, which according to this author may indicate intense soil  
843 erosion caused by the felling of dead trees and a marked increase in *Calluna* and Poaceae indicating an  
844 increase in the openness of the landscape. Lamentowicz et al. (2015) noted an increase in mineral content  
845 in the sediment as indicated by *Centropxyxis platystoma*, which was confirmed by XMT analysis of the peat.  
846 Milecka et al. (2017) described higher ash content and higher charcoal content in the sediments. Although  
847 the Tuchola Pinewoods and the Noteć Forest are in the region of highest risk of outbreaks, other areas of  
848 Poland were also affected, such as the Kampinos Forest in 1972 (Śliwa, 1974), or over the last decade, the  
849 Białowieża Primeval Forest (Grodzki, 2016; Kamińska et al., 2021).  
850 Palaeoecological studies based on the presence of insect head capsules and/or feces, as well as other insect  
851 remains could be helpful, but these methods are rarely used (Bhiry and Filion, 1996; Lavoie et al., 2009;  
852 Simard et al., 2006; Waller, 2013). Often the main obstacle to performing this method is bad preservation  
853 of insect remains in peat. In the Okoniny peatland, we did not find any insect remains, even though quite a  
854 large sample volume has been analyzed for the plant macrofossil analysis. Therefore, we can interpret the  
855 effect of insect outbreaks using other sources of evidence.  
856 It's difficult to assess unequivocally whether the gradations affected the immediate vicinity of the peatland,  
857 or whether this is a regional signal. Historical maps could be helpful, but these usually do not show the  
858 difference between old and new plantings (Barabach, 2012). However, dendrochronological data obtained





859 from pine trees could help to reconstruct the extent of the outbreak. The main problem in monoculture  
860 forests though is that the forest is successively cut and new trees are planted regularly. However, for our  
861 dendrochronological record, we were able to obtain samples from the oldest pine trees in the area. The oldest  
862 trees in the region analyzed in this study were planted over 200 years ago in the close vicinity of the  
863 Woziwoda Forest District, after the introduction of the Prussian forest management strategies, and have  
864 been kept there by foresters for obtaining tree saplings and for monitoring. The influence of insect outbreaks  
865 has been recorded in these pine trees and we were able to track all the outbreak events in the wood. The first  
866 years after the gradations - 1839, 1869, 1925 and 1982 - manifested very strongly in the dendrochronological  
867 data as negative indicator years.

868

#### 869 **4.4. Current condition of the peatland vs. remote sensing and dendroclimatic data**

870 The assessed growth reactions of pine trees to climate factors at the Woziwoda site may be considered  
871 typical. The effect of February air temperatures on Scots pine growth in northern Poland was previously  
872 noted (Cedro, 2001; Cedro and Lamentowicz, 2011; Feliksik and Wilczyński, 2009; Koprowski et al., 2012,  
873 2011; Matulewski et al., 2019; Zielski, 1996; Zielski et al., 2010; Zielski and Sygit, 1998). Although the  
874 studied pines from Woziwoda showed a similar growth response to climate as other pines from northern  
875 Poland, their climate sensitivity was greater. The highest negative correlation for pine radial growth from  
876 the Woziwoda site was found with July's mean air temperature.

877 Another factor commonly affecting the radial growth of Scots pine, according to the literature, is pluvial  
878 conditions in February. This linkage was identified by Cedro (2001), Feliksik and Wilczyński (2009),  
879 Koprowski et al. (2011) in the Pomeranian region (Northern Poland). The present study confirmed a short-  
880 term relationship between pine radial growth and precipitation sums in February (Fig. 7). Late February and  
881 early March are when additional water is required due to the initiation of biochemical processes in trees  
882 (Przybylski, 1993). Additionally, in our study, a stronger dependence of pine radial growth on precipitation  
883 was demonstrated in June. A similar result for pine from northern Poland was obtained by Matulewski et al.  
884 (2019), Zielski and Barankiewicz (2000), where pine growth was threatened by a water deficit in the summer  
885 season. Increased pine demand for water occurs in June and July, which are the months of the most intense  
886 growth (Obmiński, 1970). At the same time, these are the months when droughts have become more frequent  
887 in recent years (Łabędzki, 2004; Spinoni et al., 2018). Our results confirm that within the temperature and  
888 monthly precipitation values typically observed in Central Europe, the primary environmental factor  
889 influencing the diversity of species growth in the near future will be the availability of water (Boczoń et al.,  
890 2017; Taeger et al., 2013). This availability is determined by both the level of precipitation and losses caused  
891 by evapotranspiration (Boczoń and Wróbel, 2015; Zajączkowski et al., 2013).



892 The higher climatic sensitivity of pines at the Woziwoda site was manifested also by a higher number of  
893 pointer years. The pointer years identified in this study are confirmed by earlier studies performed on pine  
894 trees in northern Poland for the period 1910-2014 (Matulewski et al., 2019; Zielski et al., 1998; Zielski and  
895 Barankiewicz, 2000). The years 1911, 1940, 1950 and 1982 attract particular attention. These are years in  
896 which dry and hot summers were recorded (Matulewski et al., 2019; Zielski, 1996). Moreover, the years  
897 1925 and 1982 are marked by insect outbreaks.

898 Our data show that *Pinus sylvestris* has been under critical climatic pressure and is responding negatively  
899 to a warming climate and changing precipitation regime. Models predict a severe decline in coniferous  
900 species in the next 50 years, including *Pinus sylvestris* in the temperate zone of Europe (Dyderski et al.,  
901 2018; Hanewinkel et al., 2013; Schueler et al., 2014). The disappearance of species currently dominant in  
902 the forests of Central and Eastern Europe will result in the profound disruption or disappearance of  
903 ecosystems functionally related to them, such as peatlands (Dyderski et al., 2018).

904 Peatlands are also affected by accelerating climate change and on top of that they are at risk of losing their  
905 favourable environment, especially in *Pinus sylvestris* monoculture forests particularly vulnerable to  
906 increasing extreme events. Studies conducted by various researchers confirm that remote sensing data,  
907 provide a valuable source of information about peatlands and help in monitoring their condition (Czapiewski  
908 and Szumińska, 2021; Kaplan et al., 2019; Lees et al., 2021; Rapinel et al., 2023). The analyses conducted  
909 in this study have demonstrated that multisensor airborne data can be successfully utilized to assess the  
910 current state of peatlands vegetation. The application of simple remote sensing indices enabled the detection  
911 of spatial differences in the condition and water stress of vegetation in the Okoniny peatland. According to  
912 Rastogi et al. (2019), NDVI values for peatland vegetation may decrease in areas affected by stress factors  
913 such as warming and reduced precipitation. Moreover, NDVI values for healthy Sphagnum moss in peatland  
914 usually range from 0.8 to 0.9 during the summer, but they are also species-dependent (Harris, 2008; Letendre  
915 et al., 2008; Péli et al., 2015). Consequently, the values of NDVI observed in this study (averaging 0.65)  
916 may indicate a prevailing drought situation in certain areas of the Okoniny peatland. Comparable findings  
917 can be drawn from the spatial variation of MSI values presented in this study. Harris et al. (2006, 2005)  
918 demonstrated that MSI is significantly correlated with near-surface moisture condition of Sphagnum moss.  
919 Despite the wide application of optical data and spectral indices in assessing peatland conditions, Gerhards  
920 (2018) found that spectral indices may only be useful under conditions of severe or prolonged water stress.  
921 For the pre-visual detection of initial vegetation water stress symptoms, temperature-based indices are most  
922 suitable, exemplified by the LST index used in this study. Although aerial thermal data has been previously  
923 applied in peatland research (Kopeć et al., 2016), further research into the potential use of airborne thermal  
924 data in assessing peatland vegetation conditions is recommended. To date, there have been few works in



925 Poland using spectral data in peatland monitoring (Bandopadhyay et al., 2021, 2019). However, none has  
926 attempted to collate palaeoecological, dendrochronological, and remote sensing data.

927

## 928 **5. Conclusions**

929 Our data show that peatlands are highly sensitive to the progressive rise in Earth's temperatures and changing  
930 precipitation regimes. Groundwater levels have dropped dramatically in recent years, causing intense  
931 heating of the peatland surface in summer and stressing peat-forming vegetation to water scarcity. The pine  
932 monocultures surrounding the peatlands are also sensitive to climate change. They are currently responding  
933 very strongly to summer precipitation deficiency, and these data fit into dendrological predictive models.  
934 Planned forest management has permanently changed the composition of the forest. Deciduous tree species  
935 such as *Quercus*, *Fagus*, *Carpinus*, and *Corylus avellana* have almost completely disappeared. Forest  
936 management has also contributed to an increase in acidity in the peatland, and thus the rapid development  
937 of *Sphagnum* specialized for life in acidic conditions. After the expansion of *Sphagnum*, the water level in  
938 the peatland stabilized. Peatlands are also valuable archives of past climatic anomalies and catastrophic  
939 events. Pest gradations are recorded, among other things, by the presence of *Pinus* stomata, and periods of  
940 drought by an increase in the concentration of coprophilous fungi. These events correspond with  
941 dendrochronological records. There is a strong correlation between the first years after hailstorms and  
942 smaller increments of tree rings. Our study shows that palaeoecological and dendrochronological data can  
943 complement each other and create a more complete picture of past environmental changes and expand  
944 knowledge of best practices for local (Konczal et al., 2024) and global (Joosten, 2021) recommendations  
945 for peatland conservation in forests. Healthy wetlands could be key to protecting forests and slowing the  
946 transformation of forests caused by climate change (Marcisz et al., 2024). The results are important for  
947 peatland conservation in the context of planned forest management.

948

## 949 **Competing interests**

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

951

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962

#### 963 **Authors contribution**

964 MB – fieldwork, laboratory analyses (bulk density, carbon accumulation, plant macrofossils, selection of  
965 plant macrofossils for AMS radiocarbon dating), age-depth modelling, data interpretation, visualization,  
966 writing (original draft)

967 ML – fieldwork, support in plant macrofossil analysis, data interpretation, writing (commenting and editing)

968 PK – fieldwork, laboratory analyses (pollen and spores), age-depth modelling, data interpretation,  
969 visualization, writing (commenting and editing)

970 DW – laboratory analyses (testate amoebae), testate amoeba-based reconstructions, data interpretation

971 PM – fieldwork, laboratory analyses (dendrochronology), data interpretation, visualization, writing  
972 (commenting and editing)

973 DK, MW – fieldwork, remote sensing analyses and interpretation, writing (commenting and editing)

974 DJ – laboratory analyses (dendrochronology), data interpretation

975 KM – funding acquisition, conceptualization, fieldwork, laboratory analyses (charcoal), testate amoeba-  
976 based reconstructions, data interpretation, visualization, writing (commenting and editing)

977

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