

1 **Assessing the impact of forest management and climate on a peatland under Scots pine monoculture**  
2 **using a multidisciplinary approach**

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17

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

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

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

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

52  
53 **1. Introduction**

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

65 Insufficient awareness of the ecological importance of peatlands has led to them being treated as  
66 wastelands and drained for hundreds of years to obtain land for agriculture, and forestry or exploited  
67 commercially as an energy resource (Joosten et al., 2012; Łuców et al., 2022; Paavilainen and Päivänen,  
68 1995). Many of these areas have also had to adapt to a changing environment resulting from the use of  
69 various forest management techniques, e.g., the replacement of mixed forests with more easily managed  
70 monoculture forests (plantations) (Lee et al., 2023; Łuców et al., 2021; Słowiński et al., 2019). Mixed  
71 forests, through greater biodiversity, are more resilient and better able to adapt to environmental change

72 (Bauhus et al., 2017; Messier et al., 2022), providing a more comprehensive range of ecosystem services  
73 (Felton et al., 2016; Huuskonen et al., 2021).

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

88 The history of peatlands' development can be traced using palaeoecological analyses, which allow  
89 numerous reconstructions of past environmental conditions, including climate change (Lamentowicz et al.,  
90 2015; Mauquoy and Yeloff, 2008). These include reconstructions of vegetation changes in the peatland and  
91 its surroundings, changes in the water table, and reconstructions of past fire activity (Gałka et al., 2022;  
92 Kołaczek et al., 2018; Marcisz et al., 2020b, 2017; Mroczkowska et al., 2021). Peat archive records contain  
93 a wide range of preserved micro- and macrofossils for example, pollen, spores, microbial remains, and  
94 charcoal are deposited in situ and brought in by wind or water (Godwin, 1981). While paleoenvironmental  
95 reconstructions based on peat records have become common, few studies integrate palaeoecological data  
96 with other methods. For example, studies that combine palaeoecological and dendrochronological records,  
97 including dendroclimatic reconstructions based on analysis of the annual growth of tree rings, are still  
98 relatively rare (Ballesteros-Cánovas et al., 2022; Beaulne et al., 2021a; Dinella et al., 2021; Edvardsson et  
99 al., 2022, 2019, 2016; González de Andrés et al., 2022; Kuosmanen et al., 2020; Lamentowicz et al., 2009b).  
100 Yet, combining peat records with dendrochronological data can benefit interpretations of trees and forest  
101 resilience and resistance to disturbances compared to local environmental changes recorded in peat. Such a  
102 view of past environmental changes through several proxies and other archive types is fundamental and will  
103 be helpful for forest management and nature conservation in the future. To assess the current state of the  
104 peatland, we also included remote sensing data in the analysis. Remote sensing methods have been applied  
105 to study wetland conditions for over 50 years and are currently regarded as one of the most useful methods

106 in this research area (FAO, 2020; Guo et al., 2017). Remote sensing technologies enable the remote and  
107 non-invasive acquisition of information about the research object using specialized sensors, typically  
108 mounted aboard satellites or aircraft. In this study, data obtained from a multisensor aerial platform were  
109 used to assess the extent of peatland, the identification of drainage ditches, and the current vegetation  
110 condition.

111 Our study aims to assess the impact of forest management (introduction of pine monoculture) and  
112 changing climate on the vegetation, as well as hydrological, and trophic conditions of a peatland in CE  
113 Europe by integrating various data sources - palaeoecology, dendrochronology, remote sensing, and  
114 historical information. We assumed that the introduction of pine monoculture led to changes in the species  
115 composition of peatlands in favor of *Sphagnum* mosses, as well as to the stabilization of the water table. We  
116 also undertook to confirm whether peatlands register and respond to extreme events, both *in situ* and in the  
117 immediate environment. We assumed that the disturbances that occurred in the monoculture forest would  
118 be recorded in the tree rings (annual growths) record of Scots pine (*Pinus sylvestris* L.) and would confirm  
119 and complement the palaeoecological reconstruction of the peatland. Thus, we have identified peat layers  
120 corresponding to the occurrence of extremes known from historical sources and compared  
121 dendrochronological (dendroclimatic) data with them.

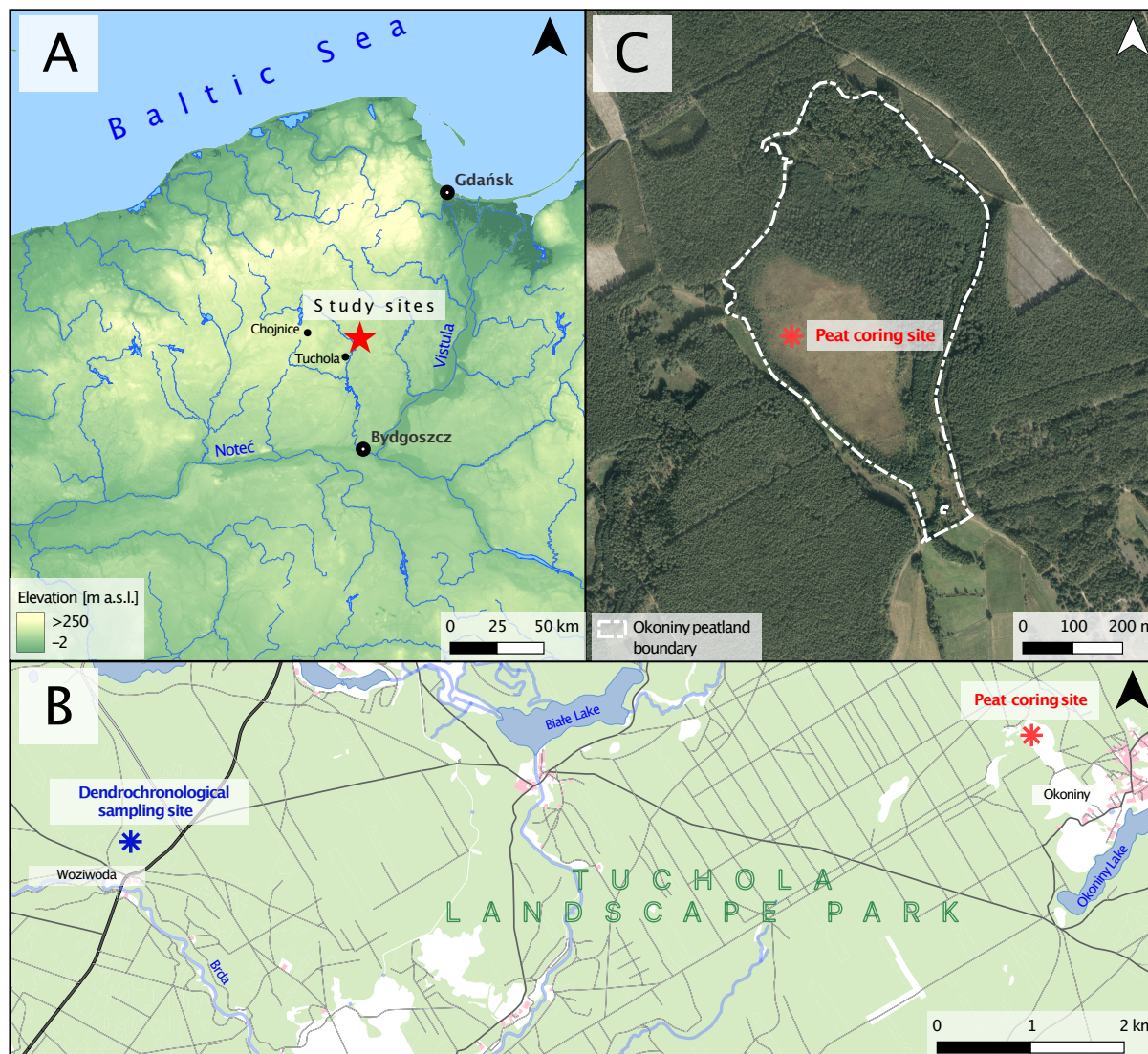
122

## 123 2. Materials and methods

### 124 2.1. Study site

125 The Okoniny peatland (53°40'52"–53°41'21"N 18°03'09"–18°03'40"E according to standard WGS  
126 84) is located in northern Poland, about 60 km north of Bydgoszcz and about 20 km northeast of Tuchola  
127 (Fig. 1). The study area is located within the Tuchola Pinewoods mesoregion (Kondracki, 2001), close to  
128 the Pomeranian ice margin of the Vistulian Glaciation dated to ca. 17,000–16,000 cal. BP (Marks, 2012).  
129 The entire area of the Tuchola Pinewoods is a young glacial landscape covered by glacial till, sand, and  
130 numerous depressions and other forms originating from melting dead ice (Błaszkiwicz et al., 2015). Based  
131 on the analysis of remote sensing data, it was determined that the surface area of the peatland is 27.08  
132 hectares, with approximately 7.00 hectares designated as non-forested area. The direct catchment area of  
133 the peatland covers a surface of 33.23 hectares. The current elevation of the peatland is around 119 m asl,  
134 with the highest elevated area within the direct catchment reaching around 128 m asl. It is part of a protected  
135 area (Regulation No. 64/97, 1997), included within the boundaries of the Tuchola Landscape Park (created  
136 in 1985). Moreover, since 2008 the entire complex of the Tuchola Pinewoods has been included on the  
137 Natura 2000 list as a Special Protection Area. Since 2010, it has been listed as a UNESCO Biosphere  
138 Reserve (UNESCO, 2024).





139  
 140 Figure 1. Location of the study area. (A) Location on a map of north-western Poland. (B) Location of the  
 141 two study sites – dendrochronological sampling site and peat coring site. (C) Okoniny peatland sampling  
 142 site with current peatland boundaries.

143  
 144 The Okoniny peatland is located in a temperate latitude zone, with a transitional climate influenced  
 145 by continental air masses from eastern Europe and oceanic air masses from the Atlantic Ocean (Beck et al.,  
 146 2018). According to climate data obtained from the Institute of Meteorology and Water Management for the  
 147 meteorological station in Chojnice (35 km west of the study area) for the period between 1991-2020, the  
 148 coldest month is January with an average temperature of -1.5 °C, the warmest month is July with an average  
 149 temperature of 18.0 °C. Between 1961-1990, both January and July were cooler by 1.6 °C compared to  
 150 1991-2020. The average annual temperature increased from 6.9 °C in 1951-1990 to 8.1 °C in 1991-2020. In

151 terms of precipitation, February has the least amount with an average of 31.1 mm for the period 1991-2020,  
 152 and July has the most with an average of 80.7 mm for the period 1991-2020. Compared to 1951-1990, the  
 153 average precipitation for February increased by 7.7 mm and for July decreased by 4.1 mm. Mean annual  
 154 rainfall increased from 558.1 mm for 1951-1990 to 612.4 mm for 1991-2020.

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

159

## 160 2.2. Peat and tree core sampling

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

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

172

## 173 2.3. Radiocarbon dating and chronology

174 Ten samples containing *Sphagnum* stems and leaves were used for accelerator mass spectroscopy  
 175 (AMS) <sup>14</sup>C dating of the entire length of the profile. The survey was conducted at the Poznan Radiocarbon  
 176 Laboratory in Poland (laboratory code marked Poz; Tab. 1). The IntCal20 (Reimer et al., 2020) and  
 177 Bomb21NH1 (Hua et al., 2021) atmospheric curves were used to calibrate the dates.

178

179 Table 1. The list of radiocarbon dates from Okoniny peatland with calibration in the OxCal v4.4.4 software  
 180 using the 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

181  
182 The absolute chronology of the entire core was based on a Bayesian age-depth model using OxCal  
183 v4.4.4 (Bronk Ramsey, 2021). The *P\_Sequence* command with a parameter  $k$  of  $0.1 \text{ cm}^{-1}$  was used to  
184 calculate the model, assuming  $\log_{10}(k/k_0) = 2$ , and interpolation = 1 cm. The most pronounced change in  
185 peat composition, as manifested by changes in pollen concentration, testate amoeba species composition  
186 and species composition of plant macrofossils, which may signal changes in peat accumulation rates, was  
187 input using the *Boundary* command at a depth of 66 cm. For better readability of the age-depth model, mean  
188 values ( $\mu$ ) were introduced and used to illustrate the modeled age.

189

#### 190 2.4. Peat properties and carbon accumulation rate

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

203

## 204 **2.5. Plant macrofossil analysis**

205 The analysis of plant macrofossils was carried out using the modified protocol of Mauquoy et al., 2010.  
206 Each sample of approximately 5cm<sup>3</sup> was wet sieved (mesh diameter: 200 µm). The generalized content of  
207 the sample was estimated in percentage using a binocular microscope. Fruits, seeds, caryopses, achenes,  
208 perigynia, bud scales, catkin scales, whole preserved leaves, whole preserved needles, cones, anthers,  
209 sporangia, opercula, fungi sclerotia, and wood pieces were counted as total numbers in each sample. The  
210 tissues of monocotyledon species and moss leaves (brown and *Sphagnum* mosses) were identified on slides  
211 using a magnification of ×200 and ×400. The material was compared with the guides (Anderberg, 1994;  
212 Berggren, 1969; Bojňanský and Fargašová, 2007; Mauquoy and van Geel, 2007). The diagram for the  
213 analyzed proxy was plotted using the riojaPlot package for R (plant macrofossils) (Juggins, 2023).

214

## 215 **2.6. Testate amoebae analysis**

216 Samples for testate amoeba analysis (volume: ca. 5cm<sup>3</sup>) were washed under 300 µm sieves following  
217 the method described by Booth et al. (2010). Testate amoebae were analyzed under a light microscope with  
218 ×200 and ×400 magnifications until the sum of 100 tests per sample was reached (Payne and Mitchell,  
219 2009). Several keys and taxonomic monographs (Clarke, 2003; Mazei and Tsyganov, 2006; Meisterfeld,  
220 2001; Ogden and Hedley, 1980) as well as online resources (Siemensma, 2023) were used to achieve the  
221 highest possible taxonomic resolution. The results of a testate amoebae analysis were used for the  
222 quantitative depth-to-water table (DWT) and pH reconstructions. Both the full diagram and the  
223 reconstructions were performed in C2 software (Juggins, 2007) using the European training set (Amesbury  
224 et al., 2016).

225  
226 **2.7. Pollen and non-pollen palynomorphs**  
227 Samples for palynological analysis (volume: 2 cm<sup>3</sup>) were prepared using standard laboratory  
228 procedures (Berglund and Ralska-Jasiewiczowa, 1986). To remove the carbonates, samples were treated  
229 with 10% hydrochloric acid. This step was followed by digestion in hot 10% potassium hydroxide (to  
230 remove humic compounds) and soaking in 40% hydrofluoric acid for 24 h (to remove the mineral fraction).  
231 Next, acetolysis was carried out. Three *Lycopodium* tablets (Batch 280521291, containing 18407 spores per  
232 tablet; produced by Lund University) were added to each sample during the laboratory procedures for the  
233 calculation of microfossil concentration (Stockmarr, 1971). Pollen, spores, and selected non-pollen  
234 palynomorphs (NPPs) were counted under an upright microscope (Zeiss Axio SCOPE A1) until the number  
235 of total pollen sum (TPS) grains in each sample reached at least 500, apart from 23 samples in which pollen  
236 concentrations were very low. Sporomorphs were identified with the assistance of atlases, keys (Beug, 2004;  
237 Moore et al., 1991), various publications, and the image database in the case of NPPs, for which there are  
238 no atlases (Miola, 2012; Shumilovskikh et al., 2022; Shumilovskikh and van Geel, 2020). The results of the  
239 palynological analysis were expressed as percentages, calculations are based on the ratio of an individual  
240 taxon to the TPS, i.e., the sum of AP (arboreal pollen) and NAP (non-arboreal pollen), excluding aquatic  
241 and wetland plants (together with Cyperaceae and Ericaceae), cryptogams, and fungi. The diagram for the  
242 analyzed proxy was plotted using Tilia/Tilia graph software (pollen) (Grimm, 1992, 1991).

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  
246 number of charcoal particles and *Lycopodium* spores counted together, exceeded 200 (Finsinger and Tinner,  
247 2005; 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  
251 more visible contrast between the charcoal and the remaining organic matter following the method described  
252 by 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. Tree core chronology construction**

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

274

## 275 **2.10. Dendroclimatological and pointer years analysis**

276 The 'chron' function from 'dplr' package allowed for the making of a residual chronology, which was  
277 used for climate-growth analysis. The 'dcc' function and its moving response (25-yr window) function  
278 method were used to determine the effects of climate conditions on the growth of Scots pine using the  
279 'treeclim' package (Zang and Biondi, 2015) version 2.0.6.0 in R (R Core Team, 2022). This package allows  
280 the use of the bootstrap procedure to test the significance and stability of the coefficients of determination  
281 ( $r^2$ ) over a set period (Guiot, 1991). Monthly mean air temperature (TEMP) and total monthly precipitation  
282 (PREC) were used to analyze climate-growth for the period 1920-2022 (Klein Tank et al., 2002). Climate  
283 data were acquired via Climate Explorer (Trouet and van Oldenborgh, 2013) and calculated from the  
284 monthly gridded observational dataset E OBS v. 25.0e (Haylock et al., 2008) obtained for the 17.75-18.00°E  
285 and 53.50-53.75°N grid.

286 The Becker algorithm (Becker et al., 1994) was used to determine the pointer years in the Woziwoda  
287 chronology. Calculations were made using the 'dplr' package in R and the 'pointer' function (Bunn, 2008).  
288 Pointer years were calculated using adjustable thresholds of relative variation in radial growth set to a 10-  
289 year time window and the number of series exhibiting a similar incremental growth pattern. The main  
290 criterion for determining pointer years was the occurrence of unidirectional changes (i.e., a decrease or

291 increase in the number of annual rings) in a minimum of 85% of the tested sequences of annual increments  
292 observed in a group of trees at the Woziwoda site.

293

#### 294 **2.11. Acquisition and post-processing of remote sensing data**

295 The analysis of the current state of Okoniny peatland was conducted using airborne remote sensing  
296 data. The data were acquired through a multisensor aerial platform by the MGGP Aero company on March  
297 25, 2022 (leaf-off collection) and July 20, 2022, one of the warmest days of the year, which was particularly  
298 important for acquiring thermal data (leaf-on collection). Multispectral images (acquired with the IXM-100  
299 camera) and Airborne Laser Scanning data (ALS; acquired with the Riegl VQ780-II scanner) were obtained  
300 in the leaf-off season. Subsequently, during the vegetation season, the dataset was enhanced by acquiring  
301 hyperspectral data (collected using the HySpex VS-725 scanner) and thermal data (obtained with the  
302 InfraTEC 9400 camera). Based on the multispectral images, an orthophotomap was generated with a Ground  
303 Sampling Distance (GSD) of 10 cm. Hyperspectral data were used to create a mosaic consisting of 430  
304 bands (in the range from 400 to 2500 nm), ALS data were applied for the development of a Digital Terrain  
305 Model (DTM), and thermal data were used to produce a land surface temperature (LST) mosaic. Thermal  
306 and hyperspectral mosaics and DTM were prepared with GSD = 1 m.

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

318

#### 319 **2.12. Historical and cartographic information**

320 Several historical cartographic studies were used to assess changes to the peatland and its surroundings.  
321 The oldest of the materials used is the Schrötter-Engelhardt map of 1803. Work on creating the map began  
322 in 1796 under the leadership of the Prussian government minister Friedrich Leopold von Schrötter (1743-  
323 1815) and topographer Friedrich Bernhard Engelhardt (1768-1854). The manuscript was produced at a scale  
324 of 1:50,000. Still, due to the concerns of the Prussian army command about the map being too detailed and

325 capable of being used by enemy armies, a generalized version was eventually published at a scale of  
326 1:150,000. A larger-scale version of the map was not available until the 1920s (Jäger, 1982, 1981). In this  
327 article, the generalized version of the map is interpreted.

328 The Prussian topographic map Messtischblatt of 1874 on a scale of 1:25 000, sheet No. 982, Zalesie  
329 section, was also analyzed. and the Detailed Map of Poland issued by the Military Geographical Institute in  
330 1933 at a scale of 1:25,000, PAN map sheet 34 - SLUP 26 - B (Linsk). In addition, a geological-agricultural  
331 map compiled between 1899 and 1900 on the topographic Messtischblatt of 1874 was considered. The  
332 Prussian Geological Survey produced the map (Königlich-Preußische Geologische Landesanstalt) and  
333 provides information on alluvial and diluvial deposits covering the area under study. The maps show the  
334 changes in the peat bog and its surroundings from the early 19th century to the 1930s. Aerial images from  
335 1964, 1984, and 1997 obtained from the Central Office of Geodesy and Cartography were also used for the  
336 same purpose (license no. DIO.7211.457.2023\_PL\_N).

337 Insect outbreak data are based on the literature (Orłowicz, 1924; Schütte, 1893; Wilson, 2012).

338

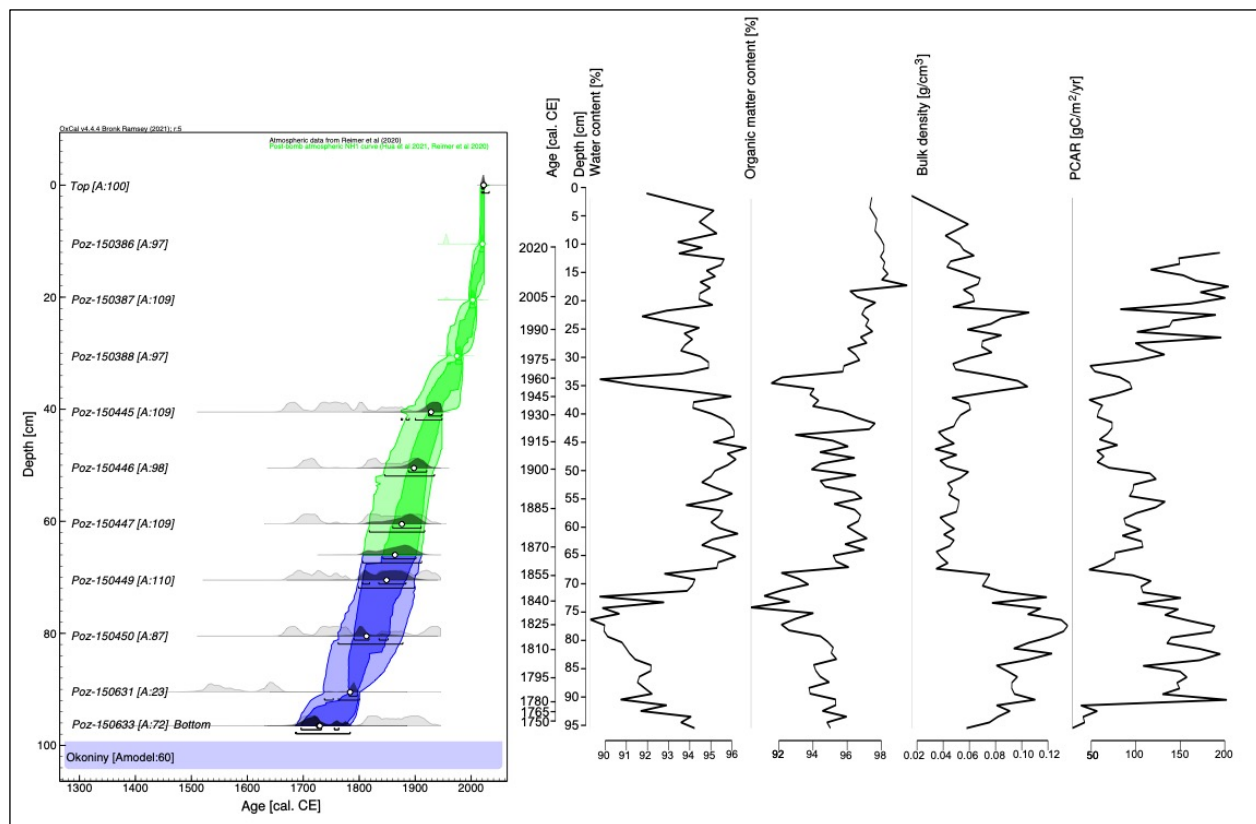
### 339 **3. Results and interpretation**

#### 340 **3.1. Age-depth model and peat accumulation rate**

341 The age-depth model showed a model agreement index ( $A_{\text{model}}$ ) of 60% (Fig. 2), precisely at the limit  
342 of the recommended minimum for its reliability (60% according to Bronk Ramsey, 2008). The model  
343 spanned the period of ca. 282 years, with a maximum uncertainty of ca. 30 years (mostly in the section of  
344 ca. 1883-1783 cal. CE). Most of the core consisted of well-preserved *Sphagnum* peat, while the lower part  
345 consisted of sedge peat. The peat accumulation rate averaged 3.6 mm/yr, with the highest values associated  
346 with the undecomposed acrotelm zone. The upper layers located between 0 and 11 cm were excluded from  
347 the analysis of peat accumulation rates. The fastest rate was 0.71 cm/yr (at 11.5 cm), and the slowest was  
348 0.1 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  
349 of 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  
350 and 30 cm. In the upper part between 29 and 0 cm, it was 0.06 g/cm<sup>3</sup>. Similarly, this upper, undecomposed  
351 layer was excluded from the peat carbon accumulation rate (PCAR) analysis. For the rest of the core (11-  
352 96 cm), PCAR averaged 112 gC/m<sup>2</sup>/yr. The mean water content of the wet sample was 93.8%, and the mean  
353 organic matter content of the dry sample was 95.5%.

354





355  
 356 Figure 2.  $^{14}\text{C}$  age-depth model of the Okoniny peat profile. Water content, organic matter content, bulk  
 357 density, and PCAR are also marked.

358

### 359 3.2. Palaeoecological analyses

#### 360 3.2.1. Phase 1 (~1726–1838, 96–74 cm): wet conditions and low human impact

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

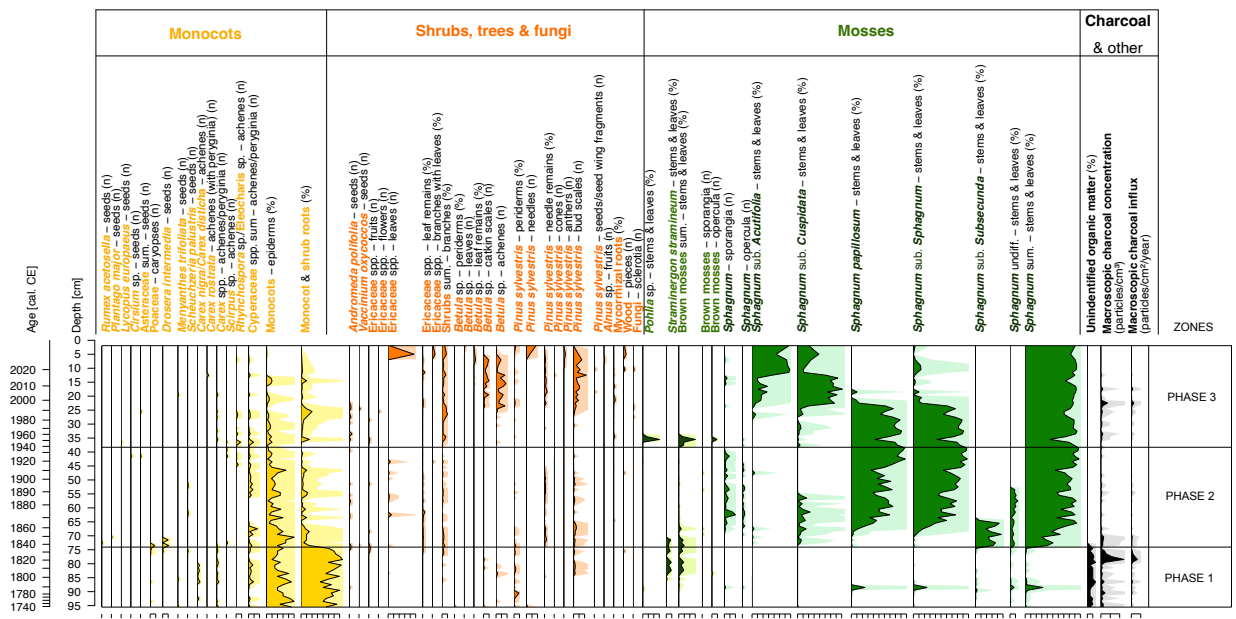
370 This phase was also characterized by the brown moss *Straminergon stramineum* (max. 9% of the  
 371 subsample content) (Fig. 3). This species occurs in a wide range of habitats (Hedenäs, 1993) but is most  
 372 common in wet, moderately acidic habitats (Blockeel, 2010). *Straminergon stramineum* is usually found as

373 scattered stems or small patches among other mosses but occasionally forms scattered mats, sometimes  
 374 partially submerged in water, next to lakes, on the edges of peat bogs or in lakeside marshes (Hill and  
 375 Blockeel, 2014).

376 This phase of peatland development was characterized by a very low concentration of testate amoebae  
 377 in the samples. *Centropyxis aculeata* was the most abundant species (Fig. 4). The dominance of plagiostomic  
 378 species from the genus *Centropyxis* may point to the presence of mineral input into the peatland  
 379 (Lamentowicz et al., 2009a; Marcisz et al., 2020a). The water level in the peatland was quite unstable and  
 380 fluctuated between 4.3 and 16.5 cm below the ground and the pH value ranged between 4.5 and 5.2, but due  
 381 to the low number of identified tests, these reconstructions should be viewed with caution (Fig. 4).

382 The surrounding vegetation was characterized by the dominance of forests, as evidenced by the high  
 383 proportion of arboreal pollen (AP) (83.6-91.1%) in total pollen content (TP) (Fig. 5). The main species  
 384 recorded were *Pinus sylvestris* (62.6-81.3% AP) and *Betula* (6.8-16.0% AP), with admixtures of *Alnus* (2.5-  
 385 7.7% AP), *Quercus* (1.8-8.1% AP), *Corylus avellana* (0.6-3.8% AP), *Carpinus betulus* (0-3.4% AP) and  
 386 *Fagus sylvatica* (0.4-3.3% AP). Values of Cerealia pollen sum (0-7.8% TP) with *Centaurea cyanus*, a crop  
 387 weed, indicated a stable presence of cultivated fields.

388



389  
 390 Figure 3. Diagram showing macrofossil percentages, macroscopic charcoal concentrations, and influx as a  
 391 local fires proxy. 10 times exaggeration is marked.

392  
 393 This phase also had the highest influx of macroscopic charcoal (MAC) of all three distinguished  
 394 phases (Fig. 3). Towards the end of the phase, at depths of 79.5 and 78.5 cm (1st half of the 1820s according



408 Figure 5. Pollen diagram with selected taxa presented (list of taxa presented in the associated open dataset).  
409 Pollen percentages are shown in black, and 10 times exaggeration is marked. Microscopic charcoal  
410 concentrations and influx as an extra-local fires proxy are also presented.

411  
412 **3.2.2. Phase 2: (~1838–1945, 74–37 cm): stabilization of water table and increase in acidity, a**  
413 **transition from mixed forest to pine monoculture and agricultural development**

414  
415 The local vegetation (Fig. 3) in this phase was dominated by *Sphagnum*, first by the subgenus  
416 *Subsecunda*, then for most of this period by *Sphagnum papillosum*. *S. papillosum* occupies the more  
417 oligotrophic lawns with a preference for open space (Clymo and Hayward, 1982; Laine et al., 2018). Along  
418 with the appearance of *Sphagnum* from the subgenus *Subsecunda*, *Drosera intermedia* was also recorded.  
419 Currently, in Poland, it is a very rare species, found in dispersed peatlands (Mirek et al., 2006). Individuals  
420 often stand in the water even throughout the season. *Andromeda polifolia* also appeared in this phase.  
421 Initially, the presence of *Sphagnum* was accompanied by *Straminergon stramineum* (max. 10%), but later it  
422 disappeared completely. By the beginning of the twentieth century, a relatively high proportion of  
423 monocotyledonous plants was also observed, represented in the samples by their epidermis, averaging about  
424 20% in a sample, with a much higher proportion in the early stages. All these taxa indicate an intermediate  
425 environment between a shallow lake and a moss peatland.

426 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),  
427 the water table level increased and stabilized at a high level, reaching a maximum of 6.8 cm at 47.5 cm,  
428 1907 cal. CE (Fig. 4). The abundance of individual testate amoeba species also increased. Initially, *C.*  
429 *aculeata* dominated, but later *Amphitrema wrightianum* and *Hyalosphenia papilo*, mixotrophic taxa that  
430 contain endosymbiotic photosynthetic algae, begin to prevail (Lamentowicz and Mitchell, 2005a; Marcisz  
431 et al., 2020a) (Fig. 4). Subsequently, the proportion of *A. wrightianum* and *H. papilo* begun to decline in  
432 favour of *Archerella flavum* and *Hyalosphenia elegans* (Fig. 4). All four species are associated with the  
433 presence of *Sphagnum*, with *A. flavum* and *A. wrightianum* tolerating very wet or even submerged  
434 *Sphagnum* habitats, which corresponds to a stably high-water table. Then, from the mid-1880s for another  
435 ca. 20 years, *C. aculeata* again became dominant. After this period, species associated with *Sphagnum*–*A.*  
436 *wrightianum*, *A. flavum* and *Heleopera sphagni* – began to dominate again. During this phase, further  
437 acidification of the site was noted through a drop in the pH value from the initial 4.8 to 4.1 (Fig. 4).

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

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

446  
447 **3.2.3. Phase 3: (~1945–present, 37–0 cm): Lowering of the groundwater table, further afforestation**  
448 **with *Pinus sylvestris*, a succession of *Betula***

449  
450 The local vegetation (Fig. 3) underwent several changes during this phase. Although *Sphagnum*  
451 dominated for the entire time, the subgenus *Sphagnum* receded in favour of first the subgenus *Cuspidata*  
452 and then the subgenus *Acutifolia*. The beginning of the phase was marked by *Pohlia nutans*, which can win  
453 the competition in unstable habitat conditions, such as during the dry season (Boulc'h et al., 2020). Its  
454 occurrence correlated with the presence of *Phryganella acropodia* among testate amoebae (Fig. 4), which  
455 is an indicator of low water levels in *Sphagnum* peatland (Diaconu et al., 2017; Lamentowicz and Mitchell,  
456 2005b).

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

467 On a regional scale, there is an increase in the relative abundance of *Pinus* pollen in the TP, from about  
468 46% at the beginning of the phase to about 85% today as an effect of afforestation (Fig. 5). *Betula* pollen  
469 share has an apparent increase, from 0,7-11,3% in the second phase to 5,6-32,5%. The increased percentage  
470 of *Betula* pollen, combined with macroscopic remains in the form of achenes and catkin scales, indicates  
471 the intensive succession of this species on the peatland surface. The ruderal species *Urtica* and *Artemisia*  
472 were also more strongly manifested. The average proportion of *Urtica* pollen in the TPS increased distinctly  
473 (from 0-0.7% to 0-2.9%). The percentage of Cerealia in TP has decreased significantly, from nearly 20% in  
474 the early 1920s to just over 1% today.

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

477

478 **3.3. Dendrochronological and pointer years analysis**

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

487 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

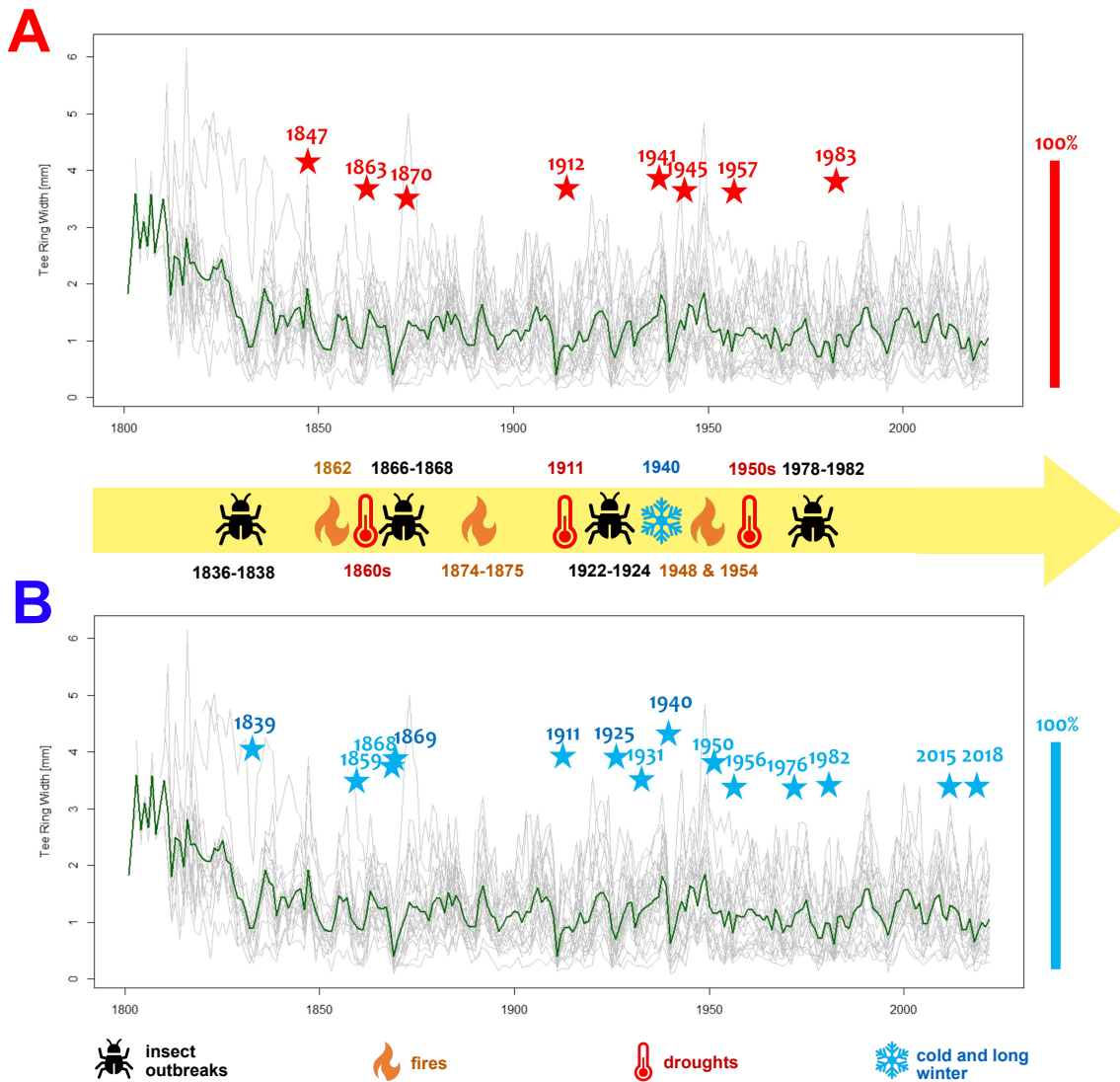
488

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

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

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

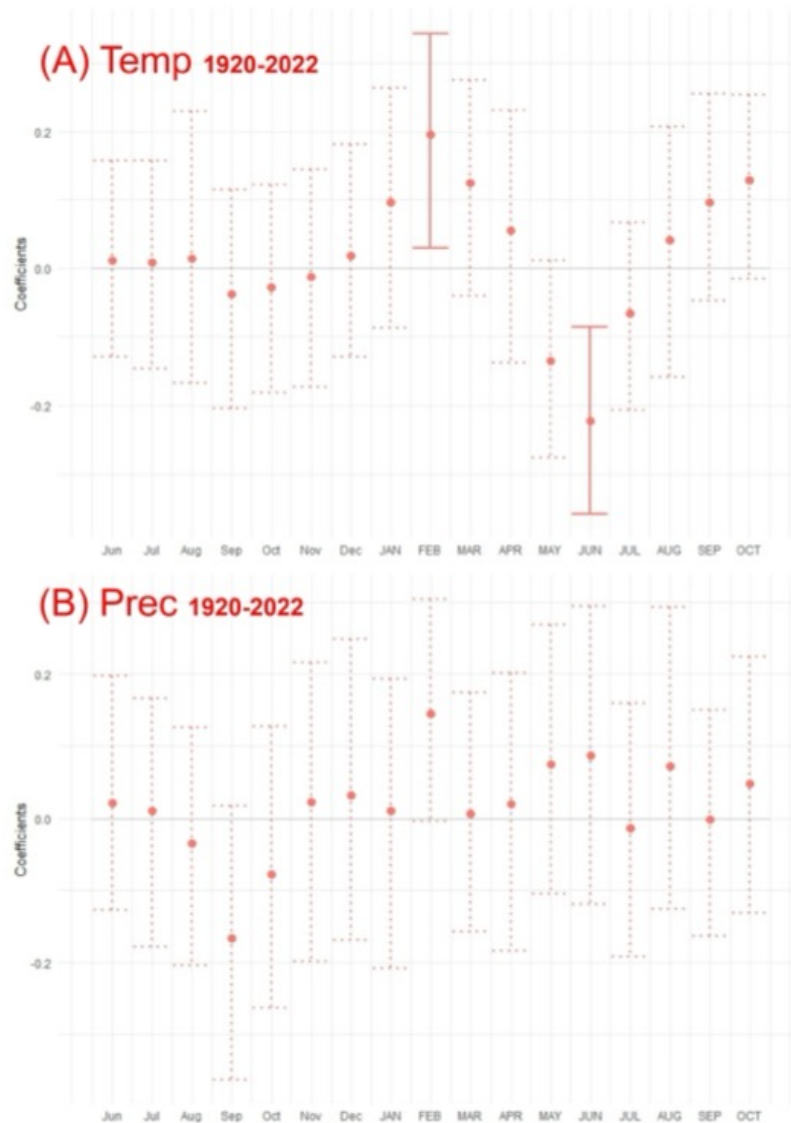
503 For Woziwoda site 8 positive and 13 negative pointer years were identified for the period 1814-  
 504 2022 (with a minimum sample depth of 10 trees) (Fig. 6). The most pronounced positive pointer years with  
 505 more than 90% tree response were as follows: 1847, 1863, 1912, 1941, 1945, 1957, and 1983. The most  
 506 pronounced negative pointer years were: 1839, 1868, 1869, 1911, 1925, 1940, and 1950. Figure 6 provides  
 507 marks of pointer years together with meteorological and ecological characteristics.



508  
 509 Figure 6. The grey lines depict the individual tree ring series of each tree, while the green line represents  
 510 the average raw chronology of *Pinus sylvestris* L. at the Woziwoda site. Identified within the Scots pine



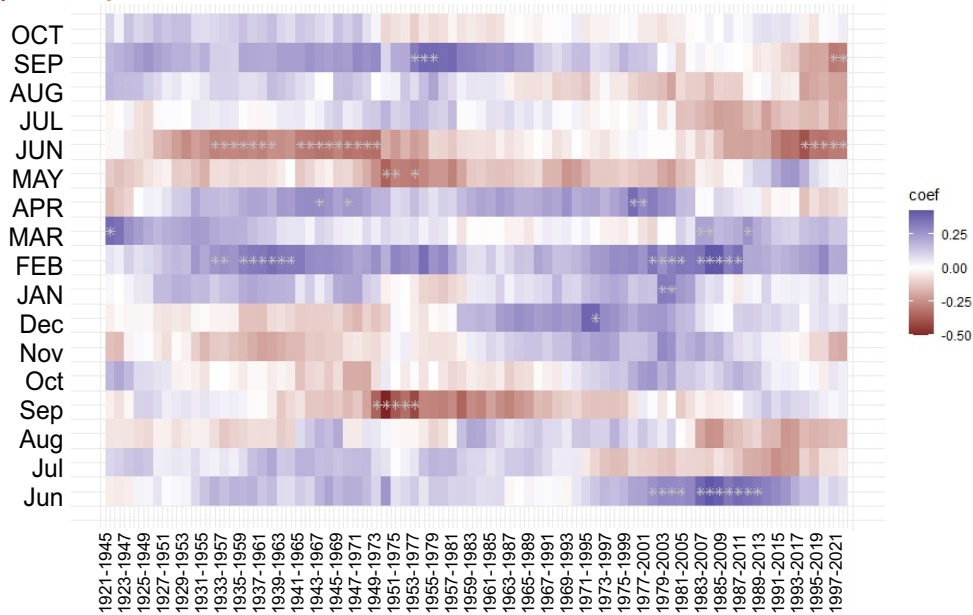
511 chronology from Woziwoda are pointer years, categorized as negative (NEG) (A) and positive (POS) (B).  
 512 These pointer years are highlighted with colored asterisks: red for positive pointer years and blue for  
 513 negative pointer years. The position of the asterisks refers to a scale of 0-100%. Information on extreme  
 514 phenomena is based on Orłowicz, 1924; Schütte, 1893, Broda 2000, Wilson 2012.



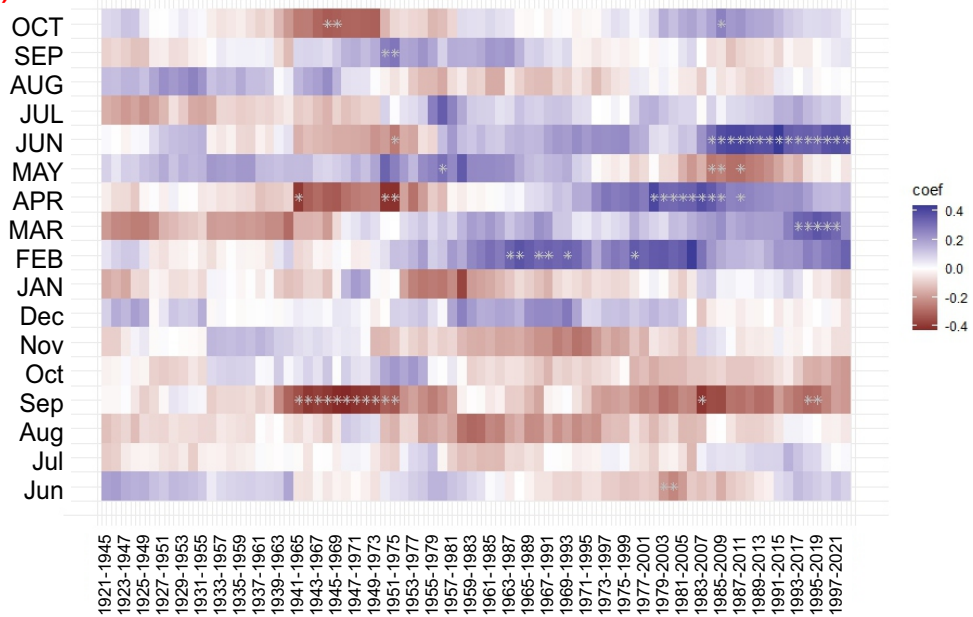
515  
 516 Figure 7. Response function coefficients between residual *Pinus sylvestris* L. chronology and climate  
 517 variables: (A) mean air temperature (Temp), and (B) precipitation (Prec) for the period 1920–2022. Names  
 518 of the previous year’s months start with a lowercase letter. Solid lines represent significant coefficients at p  
 519 < 0.05.



(A) Temp



(B) Prec

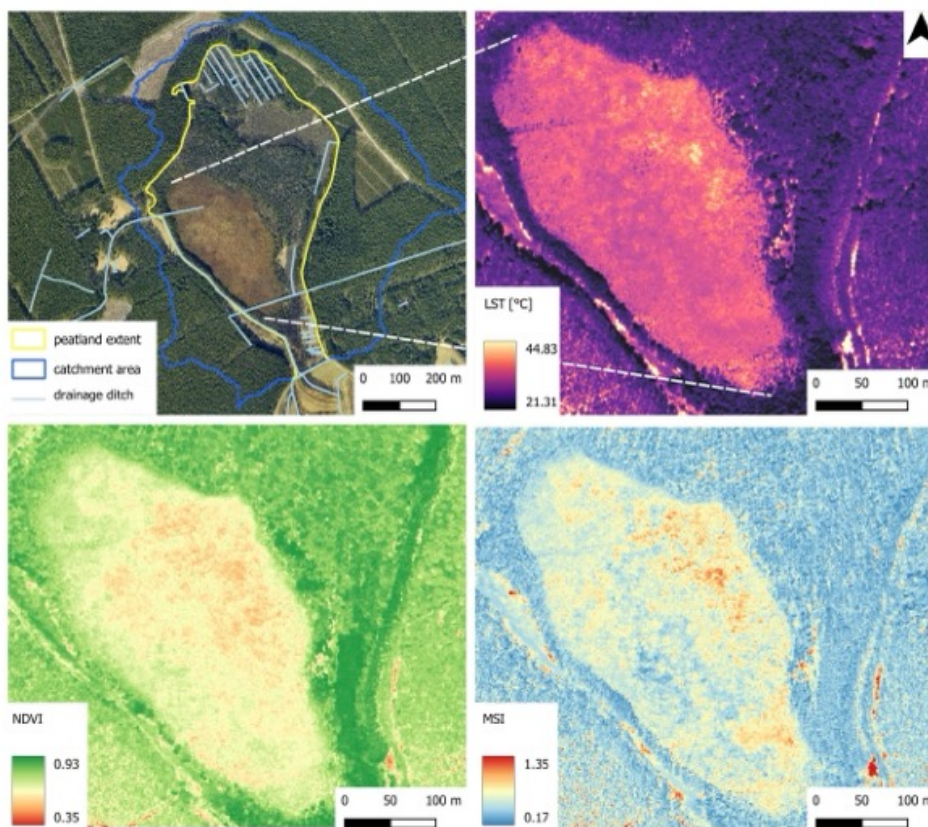


520  
 521 Figure 8. Moving response correlations (25-year window) between residual *Pinus sylvestris* L. chronology  
 522 and climate variables: (A) mean air temperature (Temp), and (B) precipitation (Prec) for the period 1920–  
 523 2022. The color code represents the response function coefficients. Significant correlations are indicated by  
 524 white asterisks.

525

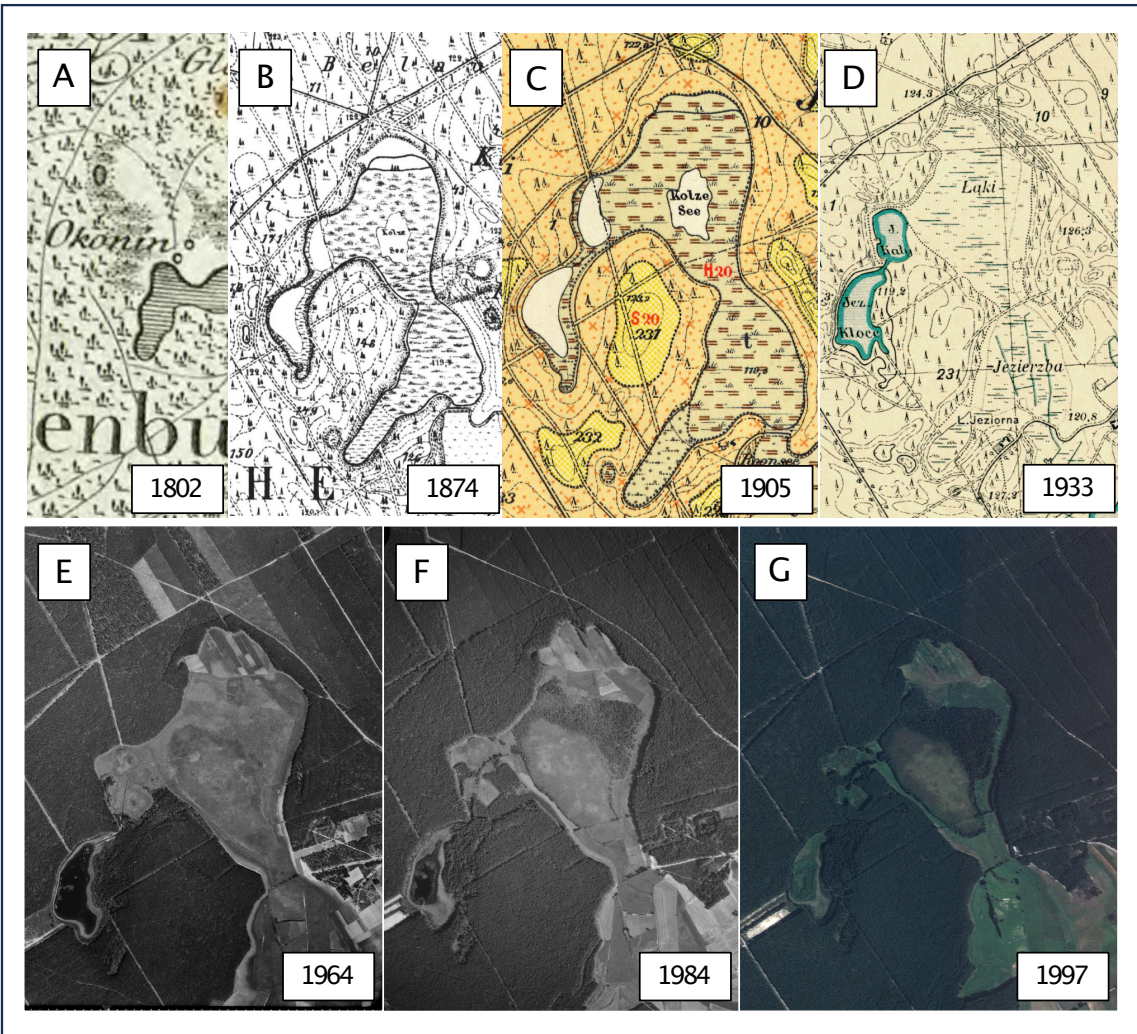
526 **3.4. The current state of the peatland based on remote sensing data analysis**

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



540  
541 Figure 9. Remote sensing characteristics of Okoniny peatland based on multisensorial airborne data acquired  
542 in 2022.  
543





545  
 546 Figure 10. Changes in the peatland and its surroundings since the beginning of the 19th century based on  
 547 historical maps and aerial images. (A) Schrötter-Engelhardt map 1:150 000 (1802), (B) Messtischblatt map  
 548 no. 982 1:25 000 (1874), (C) Prussian geological and agricultural map no. 2374 1:25 000 (1905), (D)  
 549 Detailed Map of Poland 1:25 000 (1933), (E) Aerial photograph from 1964, (F) Aerial photograph from  
 550 1984, (G) Aerial photograph from 1997. Maps no. A, B, C, and D are in the public domain. Aerial  
 551 photographs were obtained from © Central Office of Geodesy and Cartography in Poland, license no.  
 552 DIO.7211.457.2023\_PL\_N.

553  
 554 Analysis of historical materials (Fig. 10), including maps and airborne images, confirms the results  
 555 of the palaeoecological analysis. Both the Schrötter-Engelhardt map of 1802 and the Messtischblatt of 1874  
 556 indicate the existence of a small lake in the coring area. Again, however, it should be noted that the Schrötter-  
 557 Engelhardt map is a highly generalized study and does not give much information about the surroundings

558 of today's peatland, other than that we are dealing with an area with the character of a dense forest complex  
559 with wetlands in isolated places. Messtischblatt allows us to better interpret the surroundings of the analyzed  
560 modern peatland at the time in which the map was prepared. A small lake named "Kolze See" is observed  
561 in an advanced stage of development, i.e., progressive overgrowth. This lake is located in the surroundings  
562 of wetlands (Bruch in German) somewhat distant heathland (Heide in German) and wasteland (Ödland in  
563 German) (the original nomenclature of the map legend was adopted). This lake and two other lakes close  
564 by are enclosed within a single catchment area. To the south, the area of the current peatland was adjacent  
565 to an open, extensive meadow.

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

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

581 Aerial photos document subsequent changes in the ecosystem. The 1964 photo shows the northern part  
582 of today's peatland's agricultural use (regular surface layout). Lake Kały, located nearby, became completely  
583 overgrown, and its area was later dug by a drainage ditch, brought to the studied peat bog. The surrounding  
584 area of the peatland is dominated by dense forest with occasional open clear-cutting areas. A photo from  
585 1984 documents the succession of trees in the north-central part of the peatland. In the surrounding area,  
586 open forest areas have entirely disappeared. A photo from 1997 clearly shows the development of trees on  
587 the peatland, which have formed a dense block in its north-central part. A distinct area of *Sphagnum*-  
588 dominated peatland with a well-marked edge has also emerged. Currently, the northernmost part of the  
589 peatland is overgrown by pine; it is almost impossible to identify the maximum extent of the peatland surface  
590 in the field (Fig. 1).

591

## 592 4. Discussion

### 593 4.1. Exceptionally high peat accumulation rate

594 In the Okoniny peatland, a rapid rate of peat accumulation is observed, averaging 3.56 mm/yr, with a  
595 maximum value of 7.1 mm/yr at a depth between 11 and 12 cm. This accumulation rate is not commonly  
596 observed. There are only several peatlands in Poland for which higher accumulation rates were reported. In  
597 the Tuchola Pinewoods, these were Dury – 10 mm/yr (Pawlyta and Lamentowicz, 2010), Mukrza – 4.6  
598 mm/yr (Lamentowicz and Obremska, 2010), Jelenia Wyspa mire where the accumulation rates reached 0.4  
599 mm/yr for the first 3000 years but accelerated to 3 mm/yr in the last 150 years (Lamentowicz et al., 2007),  
600 and the Tuchola kettle-hole bog – 1.2 mm and after ca. 1320 cal. yr BP the accumulation rate dropped to 0.4  
601 mm/yr (Lamentowicz et al., 2008b). In other pine monocultures, such as the Noteć Forest, the Rzecin  
602 peatland stands out for its high accumulation rate – an average of 6.8 mm/yr in one profile and 7.5 mm/yr  
603 in the other one (Milecka et al., 2017). Peatlands in Tuchola Pinewoods, including Okoniny peatland,  
604 generally have a faster accumulation rate than peatlands located in other parts of Pomerania, especially small  
605 kettle-hole peatlands that accumulate carbon the fastest of all peatland types (Karpińska-Kołodziej et al.,  
606 2024). In Pomeranian peatlands, the highest accumulation rates were reported for the period between ca.  
607 150-1230 AD and reached 2.2 mm/yr in Stażki (Lamentowicz et al., 2008a), and 1.38 mm between 1830  
608 and 2006, although the highest accumulation rate was 5 mm/yr (during AD 840-860) in Słowińskie Błota  
609 raised bog (Lamentowicz et al., 2009b). At the Gołębiewo sites the maximum accumulation rate were 1.85  
610 mm/yr and 0.36 mm/yr (Pędziszewska and Latałowa, 2016). For many *Sphagnum*-dominated peatlands in  
611 other parts of Poland, the average PAR varied between 1.4-2.5 mm/yr (Gałka et al., 2015; Lamentowicz et  
612 al., 2020; M. Lamentowicz et al., 2015; Marcisz et al., 2020b). Such high accumulation rate values are also  
613 rare in other parts of the temperate climate zone of Europe. Teici bog (Latvia) showed similar accumulation  
614 rates - 3.5 mm/yr - from 1835 to 1965 AD and 10 mm/yr after 2000 (Stivrins et al., 2018). Okoniny peatland  
615 after 2000 (between 21.5 and 11.5 cm) recorded an accumulation of 5.7 mm/yr. Saxnäs mosse in Sweden  
616 showed an almost linear peat accumulation rate of 2-2.5 mm/yr (van der Linden et al., 2014). The maximum  
617 accumulation was recorded at around 2310-2250 cal on the Estonian Hara bog. BP (31-15 cm) reaching 2.4  
618 mm/yr (Łuców et al., 2022). A comparison with other regions of Poland and Europe shows that the  
619 exceptionally high accumulation rates at the analyzed site are worth highlighting.

620

### 621 4.2. Relationships between forest management and pollen analysis

#### 622 4.2.1. The complex history of the Tuchola Pinewoods and its influence on the forest

623 The results of pollen analysis of the collected core enabled us to illustrate how the forest was managed  
624 over the past 300 years. Due to political changes and several administrative decisions, the management

625 strategies of the Tuchola Pinewoods underwent vital changes. The consequences of the implementation of  
626 forest management techniques were visible in the palaeoecological record.

627 With the first partition of Poland in 1772 by Prussia, regulations for planned forest management began  
628 to be introduced. The main planting species was Scots pine, which over time began to dominate the forest,  
629 replacing deciduous admixture species. The region's forest cover and forest composition were also affected  
630 by later political and administrative developments. For more information on the history of forest  
631 management in the late 18th and early 19th centuries, see Supplementary File 1.

632 Our data confirm an increase in the proportion of pine pollen in the forest composition and a decrease  
633 in the proportion of pollen of other species. From the 1730s to the mid-1860s, the share of pine pollen in  
634 the pollen of all trees increased from about 60% to about 90%. Our pollen diagram shows the rapid increase  
635 in *Pinus sylvestris* pollen percentage after 1850. It can, therefore, be assumed that this resulted from *Pinus*  
636 *sylyestris* introduced by mass monoculture plantings in the early 1830s reaching reproductive capacity. Pine  
637 usually reaches sexual maturity between 10 and 15 years (Sullivan, 1993), although the threshold age has  
638 been set at 25 years (Matthias and Giesecke, 2014). The decline in the share of deciduous species and the  
639 increase in the share of Scots pine in the landscape began in Poland with the formation of the state. However,  
640 at that time, it was associated with the expansion of agriculture and the harvesting of preferred species such  
641 as *Carpinus betulus* (Czerwiński et al., 2021) Nevertheless, in the Prussian partition, planned forest  
642 management permanently changed the composition of Polish largest forest complexes, which were  
643 dominated by easy-to-grow pine (Broda, 1993) (see Supplementary File 1). A dynamic increase in the share  
644 of pine pollen until the 1860s in the Tuchola Pinewoods was also recorded at the Czechowskie Lake  
645 (Słowiński et al., 2019). An increase in pine pollen percentage since the 19th century was also shown in  
646 pollen diagrams of other sites from Pomerania – Stażki (Lamentowicz et al., 2008a), Słowińskie Błota  
647 (Lamentowicz et al., 2009b) – and in other monoculture plantation complexes from the Prussian partitioning  
648 area – Rzecin peatland in the Noteć Forest (Milecka et al., 2017).

649 Although attempts were undertaken to correct earlier mistakes, this did not stop the massive  
650 deforestation (among other consequences of war events and administrative regulations on settlement, more  
651 in Supplementary File 1). Until the 1870s, the feudal system was still mixed with capitalist components, but  
652 from the 1870s onward, under monopoly capitalism, timber trade and processing began to reach a significant  
653 size (Broda, 2000). However, it has been noted that forests regulate air temperature, store water in the soil  
654 more efficiently, and reduce wind speed, preventing soil erosion, which can help local agriculture face  
655 difficult environmental conditions (Wilson, 2012). For this reason, as early as the 1870s, the state  
656 administration encouraged landowners to protect forest stands on their lands and establish forestry  
657 cooperatives. The government also guaranteed funds for the reforestation of private and municipal lands. In  
658 the mid-1870s, the Landtag set aside a budget for the purchase and reforestation of wasteland by the state.



659 However, these funds were used to a small extent, although this somewhat reduced the share of forested  
660 private property (Broda, 2000; Wilson, 2012). In 1886, the Royal Settlement Commission (in German:  
661 Königliche Ansiedlungskommission) was established to buy up the estates of impoverished Polish nobility  
662 to acquire agricultural land for German settlers (Wilson, 2012).

663 At the end of the 19th century, Tuchola Pinewoods became the largest timber production hub in the  
664 Prussian partition. The Bydgoszcz timber industry region also played a major role in wood processing. The  
665 first steam sawmill in the Bydgoszcz region was built in 1873, and by 1913, there were 20 of them,  
666 processing some 500,000 m<sup>3</sup> of wood and employing more than 1,600 people (Broda, 2000). All this resulted  
667 in a significant decline in the share of tree pollen in the total pollen share in our diagram, to less than 60%  
668 by the late 1920s and early 1930s. At the same time, we have seen intensive agricultural development. At  
669 Okoniny, the proportion of Cerealia pollen doubled between ca. 1900 and 1920. This trend is also confirmed  
670 by pollen data from the site in Okoniny Nadjeziorne, on the other side of Okonińskie Lake (Tipton, 2023),  
671 as well as from Czechowskie Lake, about 25 km northeast of our site (Słowiński et al., 2019). Despite  
672 intensive deforestation in general, further afforestation with pine was also progressing. In 1893, pine forests  
673 accounted for 99% of all forests in Tuchola County (Szwankowski, 2005). Intense changes in forest  
674 management (pine dominance) and agricultural development (high percentage of Cerealia pollen) in the 19<sup>th</sup>  
675 century are also evident in records of profiles outside large, dense forest complexes – Kusowskie Bagno  
676 (Gałka et al., 2014), Linje mire (Marcisz et al., 2015).

677

#### 678 **4.2.2. Impact of forest management on peatland vegetation**

679 As a result of changes related to forest management, lake to peatland transition occurred rapidly. We  
680 assume that this was primarily the result of drainage, which was undertaken in the area at the end of the 19<sup>th</sup>  
681 century (see drainage ditches on the southern side and a dike in the middle part of the site on maps in Figure  
682 6), and secondly, to a lesser extent, the transition from mixed forests to pine monoculture. These activities  
683 contributed to an increase in the acidity of the peatland. Forest drainage is often associated with the  
684 acidification of surface waters (Miller et al., 1990). The introduction of forest drainage, on or near peatlands,  
685 to improve tree growth has been quite common in northern and northeastern Europe (Westman and Laiho,  
686 2003). The oxidation of organic sediments and the detachment of H<sup>+</sup> ions increase acidity (Ulrich, 1980).  
687 In addition, the supply of alkaline cations to the peat is impeded by drainage ditches (Minkkinen et al.,  
688 2008). However, the long-term consequences of drainage are devastating to peatlands, as they initiate  
689 vegetation succession, in which species typical of peatlands are replaced by forest vegetation (Laine et al.,  
690 1995). In the example of our palaeoecological data, the dynamic succession of pine and birch in the Okoniny  
691 peatland is evident, which is also supported by aerial imaging. As already mentioned, the successive decline  
692 in pH is also the result of the impact of pine plantations growing in catchments. A drop in pH in Okoniny

693 has likely enabled the rapid growth and expansion of *Sphagnum* and the peatland initiation. The crowns of  
694 forests, especially the needles, can increase the uptake of atmospheric pollutants such as sulfur and nitrogen  
695 components, contributing to the acidification of surface waters (Nisbet, 2001; Reynolds et al., 1994).  
696 Conifers also can capture ions of marine origin - Na and Mg cations. These, in turn, displace hydrogen and  
697 aluminium cations from the soil, leading to acid runoff from the forests along with surface runoff, which is  
698 known as the "sea-salt effect" (Drinan et al., 2013; Harriman et al., 2003; Reynolds et al., 1994). We  
699 observed the presence of *Pinus* needles at the beginning of phase 2 (from 1838 cal. CE), at the transition  
700 from pond to peatland ecosystem. Moreover, *Pinus* stomata were also present in palynological samples at  
701 that time, pointing to more frequent needle falls. More pine trees in the Tuchola Pinewoods resulted in much  
702 higher amounts of needles and other pine fragments accumulating on the forest ground, leading to soil  
703 acidification. This, together with drier conditions, could quickly lead to acidification around the pond,  
704 forming perfect conditions for *Sphagnum* to encroach – first as a floating mat that successively overgrown  
705 the pond. We sampled the peat core close to the edge of the peatland, thus in the place where moss  
706 encroachment on the open water body began; therefore, we were able to track this succession in our record.  
707 This succession and disappearance of Lake Kolze are also clearly visible in historical maps (Figure 10).  
708 Other examples of quick encroachment of floating mats on the surface of the lake have been observed and  
709 mapped in other open water bodies in the Tuchola Pinewoods (Kowalewski, 2003; Kowalewski and  
710 Milecka, 2003) and other regions (Warner, 1993).

711

### 712 **4.3. Anomalies and extreme events**

#### 713 **4.3.1. The impact of droughts and fires on the forest and peatland**

714 Historical sources indicate that in the 18<sup>th</sup> and 19<sup>th</sup> centuries, the Tuchola Pinewoods were relatively  
715 often affected by droughts resulting in fires (Wilson, 2012). In 1781, there was a fire in Tuchola (ca. 16 km  
716 SW), during which a large part of the city with the church and town hall burned down, and in 1792, Starogard  
717 Gdański (ca. 42 km NE) burned almost to the ground (Orłowicz, 1924). Major fires also occurred in 1794,  
718 and 1807, when more than 34,000 hectares of forest burned (Orłowicz, 1924; Schütte, 1893). Fires in 1809,  
719 1810, 1812, 1813 and 1828 in the Świt forest district about 15 km from the study site were also recorded  
720 (Cyzman, 2008). Palaeoecological data, especially MIC, confirm high fire activity in the first decades of the  
721 19<sup>th</sup> century (a rapid increase). Słowiński et al. (2019) emphasized that data on fires before the 1830s,  
722 especially regarding their area, should be treated with caution due to the lack of accurate measurement  
723 techniques. In the Woziwoda Forest District, within which the Okoniny peatland is located, the forests of  
724 the Biała and Barłogi forest districts also burned in 1842 (Cyzman, 2008). Intense fires also appeared in the  
725 Tuchola Pinewoods between 1846 and 1848 (Orłowicz, 1924; Schütte, 1893).



726 Later, numerous fires were also reported in the Woziwoda Forest District. Between 1860 and 1889,  
727 310 fires were observed, destroying 4206 hectares of the forest (Orłowicz, 1924; Schütte, 1893). The highest  
728 number of fires in this period was registered in 1862-1864 and 1874-1875 when 3565 hectares of forest  
729 burned; altogether, nearly 85% of the area burned in 1860-1889 (Schütte, 1893). The largest area burned in  
730 1863 equaled 2333 hectares, including more than 1250 hectares in the Woziwoda forest district; altogether,  
731 25% of all the forest burned in 1860-1889 (Orłowicz, 1924; Schütte, 1893). Meteorological data confirm  
732 dry years in the period from 1862 to 1865. In 1862 and 1863, the annual precipitation in Bydgoszcz was  
733 only a little over 450 mm (Kirschenstein, 2005), and it was then that the largest number of hectares of forest  
734 in the known history of the Tuchola Forest burned (Dietze et al., 2019).

735 The number of fires can also be linked to political events (Orłowicz, 1924; Schütte, 1893; Wilson,  
736 2012). In 1901, in the nearby Trzebciny and Gołębek Forest Districts, a fire consumed 663 hectares of forest  
737 (there was a parallel children's strike in Września Province) (Orłowicz, 1924; Wilson, 2012). Fires could  
738 also be caused by agricultural activities and land preparation for crops (Poraj-Górska et al., 2017). By the  
739 1830s, charcoal production was widespread (McGrath et al., 2015), and forest burning was used to create  
740 heathlands for beekeeping (Bienias, 2009).

741 Fires of the 1860s provide a regional signal at another site in the Tuchola Pinewoods – Czechowskie  
742 Lake (Dietze et al., 2019). Increased fire activity in the mid-19<sup>th</sup> century was also observed at the Lake  
743 Jaczno site (Poraj-Górska et al., 2017). At the Okoniny peatland, MIC and MAC values decreased after  
744 1850, but at the same time, the water level stabilized and remained high. Fire activity remained low in areas  
745 where wet conditions prevailed, such as southern Finland (Väliranta et al., 2007) and eastern Estonia  
746 (Sillasoo et al., 2011).

747 In 1948, about 450 hectares of forest were burned near Osieczna, and in 1954, 80 hectares were burned  
748 near Ocypl (Cherek, 2007). Palaeoecological data record an increased MIC supply during this period. The  
749 first of these fires was also recorded in the sediments of Czechowskie Lake (Słowiński et al., 2019). The  
750 summer drought of 1921 occurred over a larger area of Europe, from Poland and the Czech Republic to the  
751 UK (van der Schrier et al., 2021). Summer droughts also affected the Tuchola Pinewoods in 1951 and 1959.  
752 In 1959 Bydgoszcz received only 37 mm of precipitation from August to October (Mitosek, 1960), and from  
753 1950 to 1958 Bydgoszcz received less than 500 mm of rain per year (Kirschenstein, 2005). Our  
754 palaeoecological data confirm droughts in the 1950s. There is a sharp increase in the proportion of  
755 *Phryganella acropodia* among the testate amoebae, an indicator of dry conditions (Diaconu et al., 2017) and  
756 an expansion of brown mosses in the form of *Pohlia nutans* (up to 30% of the peat sample composition) are  
757 also marked. Dendroclimatic data recorded the negative impact of climatic conditions on pine, especially  
758 strongly in 1950 and 1956.

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

769

#### 770 **4.3.2. Insect outbreaks and their impact on pine monoculture**

771 Palaeoecological studies based on the presence of insect head capsules and/or faeces, as well as other  
772 insect remains could be helpful, but these methods are rarely used (Bhiry and Filion, 1996; Lavoie et al.,  
773 2009; Simard et al., 2006; Waller, 2013). Often the main obstacle to performing this method is bad  
774 preservation of insect remains in peat. In the Okoniny peatland, we found no insect remains, even though  
775 quite a large sample volume has been analyzed for the plant macrofossil analysis. Therefore, we can interpret  
776 the effect of insect outbreaks using other sources of evidence.

777 The earliest information on insect outbreaks from the forests of the Tuchola Pinewoods under planned  
778 forest management dates back to 1836-1838. An infestation of ~~the~~ *Panolis flammea* occurred at that time  
779 (Schütte, 1893). The insects also attacked between 1866 and 1868. As a result of this infestation, 1380  
780 hectares of forest were destroyed in the Woziwoda forest district alone (Schütte, 1893). The pollen diagram  
781 from the Okoniny peatland documents the phenomenon in the 1860s with a decrease in *Pinus sylvestris*  
782 pollen and an increased presence of *Pinus stomata* that may indicate the event of the insect outbreak  
783 (Barabach, 2015). The needles that fell were partially decomposed and carried downwind to the peatland,  
784 where they were preserved (Słowiński et al., 2019). The same effect was noted in another closely located  
785 peatland in Okoniny Nadziejorne, where the 1866-1868 infestation also corresponds with increased numbers  
786 of *Pinus stomata* (Tipton, 2023). In 1855, *Lymantria monacha* appeared in large numbers but damaged only  
787 some of the younger stands (Schütte, 1893).

788 A serious incidence of *Panolis flammea* gradation also occurred in 1922-1924 (Kiełczewski, 1947;  
789 Mokrzecki, 1928). Between 1978 and 1985, with a peak in 1982, the forests of the northern part of the  
790 country were overrun by *Lymantria monacha*, and this was the largest infestation since the establishment of  
791 the National Forests in 1924, with salvage treatments covering more than 6.3 million hectares of forest over  
792 seven years (Broda, 2000; Jabłoński, 2015; Śliwa, 1989, 1987). Both major gradations are reflected in

793 palynological data, manifested by declines in the pollen percentage of trees, primarily *Pinus* and *Picea*. A  
794 decrease in conifer pollen during the gradation period has also been shown by studies of other sites in the  
795 Tuchola Pinewoods (Łuców et al., 2021; Tipton, 2023). Other pine monoculture in Poland, the Noteć Forest  
796 was also affected by gradation in 1922-1924, and this event manifested itself in palaeoecological data  
797 (Barabach, 2015; Lamentowicz et al., 2015; Milecka et al., 2017). Among other things, Barabach (2015)  
798 noted an increase in *Glomeromycota* fungal spores, which according to this author may indicate intense soil  
799 erosion caused by the felling of dead trees, and a marked increase in *Calluna* and Poaceae indicating an  
800 increase in the openness of the landscape. Lamentowicz et al. (2015) noted an increase in mineral content  
801 in the sediment as indicated by *Centropyxis platystoma*, which was confirmed by XMT analysis of the peat.  
802 Milecka et al. (2017) described higher ash and charcoal content in the sediments. Although the Tuchola  
803 Pinewoods and the Noteć Forest are in the region of highest risk of outbreaks, other areas of Poland were  
804 also affected, such as the Kampinos Forest in 1972 (Śliwa, 1974), or over the last decade, the Białowieża  
805 Primeval Forest (Grodzki, 2016; Kamińska et al., 2021).

806 It's difficult to assess unequivocally whether the gradations affected the immediate vicinity of the  
807 peatland, or whether this is a regional signal. Historic maps could be helpful, but these usually do not show  
808 the difference between old and new plantings (Barabach, 2012). However, dendrochronological data  
809 obtained from pine trees could help to reconstruct the extent of the outbreak. The main problem in  
810 monoculture forests though is that the forest is successively cut and new trees are planted regularly.  
811 However, for our dendrochronological record, we were able to obtain samples from the oldest pine trees in  
812 the area. The oldest trees in the region analyzed in this study were planted over 200 years ago in the close  
813 vicinity of the Woziwoda Forest District, after the introduction of the Prussian forest management strategies,  
814 and have been kept there by foresters for obtaining tree saplings and for monitoring. The influence of insect  
815 outbreaks has been recorded in these pine trees and we were able to track all the outbreak events in the  
816 wood. The first years after the gradations - 1839, 1869, 1925, and 1982 - manifested very strongly in the  
817 dendrochronological data as negative indicator years.

818

#### 819 **4.4. Current condition of the peatland vs. remote sensing and dendroclimatic data**

820 The assessed growth reactions of pine trees to climate factors at the Woziwoda site may be considered  
821 typical. The effect of February air temperatures on Scots pine growth in northern Poland was previously  
822 noted (Cedro, 2001; Cedro and Lamentowicz, 2011; Feliksik and Wilczyński, 2009; Koprowski et al., 2012,  
823 2011; Matulewski et al., 2019; Zielski, 1996; Zielski et al., 2010; Zielski and Sygit, 1998). Although the  
824 studied pines from Woziwoda showed a similar growth response to climate as other pines from northern  
825 Poland, their climate sensitivity was greater. The highest negative correlation for pine radial growth from  
826 the Woziwoda site was found with July's mean air temperature.

827 Another factor commonly affecting the radial growth of Scots pine, according to the literature, is pluvial  
828 conditions in February. This linkage was identified by Cedro (2001), Feliksik and Wilczyński (2009),  
829 Koprowski et al. (2011) in the Pomeranian region (Northern Poland). The present study confirmed a short-  
830 term relationship between pine radial growth and precipitation sums in February (Fig. 7). Late February and  
831 early March are when additional water is required due to the initiation of biochemical processes in trees  
832 (Przybylski, 1993). Additionally, in our study, a stronger dependence of pine radial growth on precipitation  
833 was demonstrated in June. A similar result for pine from northern Poland was obtained by Matulewski et al.  
834 (2019), Zielski and Barankiewicz (2000), where pine growth was threatened by a water deficit in the summer  
835 season. Increased pine demand for water occurs in June and July, the months of the most intense growth  
836 (Obmiński, 1970). At the same time, these are the months when droughts have become more frequent in  
837 recent years (Łabędzki, 2004; Spinoni et al., 2018). Our results confirm that within the temperature and  
838 monthly precipitation values typically observed in Central Europe, the primary environmental factor  
839 influencing the diversity of species growth in the near future will be the availability of water (Boczoń et al.,  
840 2017; Taeger et al., 2013). This availability is determined by the precipitation level and losses caused by  
841 evapotranspiration (Boczoń and Wróbel, 2015; Zajączkowski et al., 2013).

842 The higher climatic sensitivity of pines at the Woziwoda site was manifested also by a higher number  
843 of pointer years. The pointer years identified in this study are confirmed by earlier studies performed on  
844 pine trees in northern Poland for 1910-2014 (Matulewski et al., 2019; Zielski et al., 1998; Zielski and  
845 Barankiewicz, 2000). The years 1911, 1940, 1950, and 1982 attract particular attention. These are years in  
846 which dry and hot summers were recorded (Matulewski et al., 2019; Zielski, 1996).

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

853 Peatlands are also affected by accelerating climate change and on top of that they are at risk of losing  
854 their favourable environment, especially in *Pinus sylvestris* monoculture forests, which are particularly  
855 vulnerable to increasing extreme events. Studies conducted by various researchers confirm that remote  
856 sensing data, provide a valuable source of information about peatlands and help in monitoring their  
857 condition (Czapiewski and Szumińska, 2021; Kaplan et al., 2019; Lees et al., 2021; Rapinel et al., 2023).  
858 The analyses conducted in this study have demonstrated that multisensor airborne data can be successfully  
859 utilized to assess the current state of peatlands vegetation. Applying of simple remote sensing indices  
860 enabled the detection of spatial differences in the condition and water stress of vegetation in the Okoniny

861 peatland. According to Rastogi et al. (2019), NDVI values for peatland vegetation may decrease in areas  
862 affected by stress factors such as warming and reduced precipitation. Moreover, NDVI values for healthy  
863 Sphagnum moss in peatland usually range from 0.8 to 0.9 during the summer, but they are also species-  
864 dependent (Harris, 2008; Letendre et al., 2008; Péli et al., 2015). Consequently, the values of NDVI observed  
865 in this study (averaging 0.65) may indicate a prevailing drought situation in certain areas of the Okoniny  
866 peatland. Comparable findings can be drawn from the spatial variation of MSI values presented in this study.  
867 Harris et al. (2006, 2005) demonstrated that MSI is significantly correlated with near-surface moisture  
868 condition of Sphagnum moss. Despite the wide application of optical data and spectral indices in assessing  
869 peatland conditions, Gerhards (2018) found that spectral indices may only be useful under conditions of  
870 severe or prolonged water stress. For the pre-visual detection of initial vegetation water stress symptoms,  
871 temperature-based indices are most suitable, exemplified by the LST index used in this study. Although  
872 aerial thermal data has been previously applied in peatland research (Kopeć et al., 2016), further research  
873 into the potential use of airborne thermal data in assessing peatland vegetation conditions is recommended.  
874 To date, there have been few works in Poland using spectral data in peatland monitoring (Bandopadhyay et  
875 al., 2021, 2019). However, none has attempted to collate palaeoecological, dendrochronological, and remote  
876 sensing data.

877

## 878 5. Conclusions

879 Our data show that peatlands are highly sensitive to the progressive rise in Earth's temperatures and  
880 changing precipitation regimes. Groundwater levels have dropped dramatically in recent years, causing  
881 intense heating of the peatland surface in summer and stressing peat-forming vegetation to water scarcity.  
882 The pine monocultures surrounding the peatlands are also sensitive to climate change. They are currently  
883 responding very strongly to summer precipitation deficiency, and these data fit into dendrological predictive  
884 models. Planned forest management has permanently changed the composition of the forest. Deciduous tree  
885 species such as *Quercus*, *Fagus*, *Carpinus*, and *Corylus avellana* have almost disappeared. Forest  
886 management has also contributed to increased acidity in the peatland, and thus the rapid development of  
887 *Sphagnum* specialized for life in acidic conditions. After the expansion of *Sphagnum*, the water level in the  
888 peatland stabilized. Peatlands are also valuable archives of past climatic anomalies and catastrophic events.  
889 Pest gradations are recorded, among other things, by the presence of *Pinus* stomata, and periods of drought  
890 by an increase in the values of coprophilous fungi. These events correspond with dendrochronological  
891 records. There is a strong correlation between the first years after hailstorms and smaller increments of tree  
892 rings. Our study shows that the combining of different data (palaeoecological, dendrochronological, remote  
893 sensing and historical) can complement each other and create a more complete picture of past environmental  
894 changes and expand knowledge of best practices for local (Konczal et al., 2024) and global (Joosten, 2021)

895 recommendations for peatland conservation in forests. Healthy wetlands could be key to protecting forests  
896 and slowing the transformation of forests caused by climate change (Marcisz et al., 2024). The results are  
897 essential for peatland conservation in planned forest management.

898

#### 899 **Competing interests**

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

901

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912

#### 913 **Data availability**

914 All data associated with this article are openly available on Mendeley Data repository under the DOI:  
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916

#### 917 **Authors contribution**

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

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

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

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

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

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

928 DJ – laboratory analyses (dendrochronology), data interpretation

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

931

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