

# Testate amoebae as indicators of critical transitions in historical forest management: A case study of Scots pine monoculture

The Holocene  
1–12

© The Author(s) 2026



Article reuse guidelines:

sagepub.com/journals-permissions

DOI: 10.1177/09596836261422219

journals.sagepub.com/home/hol



Jay Tipton,<sup>1</sup> Katarzyna Marcisz,<sup>2</sup> Dominika Łuców,<sup>3</sup> Milena Obremska<sup>4</sup> and Mariusz Lamentowicz<sup>2</sup>

## Abstract

Peatlands are susceptible not only to direct disturbance, but also to indirect changes in their surroundings, including land management. Changes in agricultural practices or forest management can significantly influence peatland functioning, for example, their trophic status or surface vegetation. Here, we investigate the effects of planned forestry on two *Sphagnum*-dominated peatlands in northern Poland's Tuchola Forest. We use testate amoebae and compare them to available pollen and historical data to reconstruct past environmental conditions and assess anthropogenic pressure. The Tuchola Forest has undergone significant transformations as a result of human activities, notably during Prussia's promotion of pine monoculture in the 19th century. We hypothesized that forest management activities and other related disturbances have led to wetland acidification and water table alterations. Our results show that these changes have had profound effects on both peatlands. Radiocarbon dating revealed a correlation between forest management practices and peatland dynamics. Quantitative reconstructions based on testate amoebae showed that, as a result of the introduced pine monoculture, both peatlands experienced rapid acidification (pH levels dropping from ca. 6.2 to 3.5) and water table lowering of over 15 cm. The predominance of pine monoculture has not only reduced biodiversity but also enhanced the susceptibility of the forest to fires and pest outbreaks, further affecting peatland conditions. These findings contribute to understanding of how historical land-use changes continue to influence present-day peatland dynamics, offering insights into restoration and conservation efforts in forested peatland landscapes.

## Keywords

bioindication, historical data, palaeoecology, peatlands, *Pinus sylvestris*, Poland, *Sphagnum*

Received 15 September 2025; revised manuscript accepted 12 January 2026

## Introduction

Peatlands are crucial ecosystems that offer a variety of benefits including carbon sequestration and storage, biodiversity support, ecosystem services, and historical preservation. One of their most important benefits is the ability to store massive amounts of carbon (Loisel et al., 2021). Peatlands cover only 3% of the Earth's surface, an estimated 4 million km<sup>2</sup>, but they store approximately one-third of the world's soil carbon, making them the world's largest terrestrial carbon stock (Frolking et al., 2011). Peatlands worldwide are severely threatened primarily by human activities, including drainage, agriculture, land-use changes, forest and land management and peat harvesting for fuel and horticulture (Frolking et al., 2011). These actions result in the degradation and destruction of peatland ecosystems, releasing substantial stored carbon into the atmosphere and contributing to global climate change (IPCC, 2021). Approximately 11–15% of global peatlands have been degraded and drained, particularly for agriculture, forestry, energy and infrastructure (FAO, 2022). Drainage exposes peat to air, causing it to oxidize and decay, leading to the emission of carbon dioxide and other greenhouse gases, with agriculture responsible for about 50% of this usage (Gorham, 1991). This degradation accounts for nearly 5% of all global anthropogenic greenhouse gas emissions (IPCC, 2014). European peatlands have increasingly become drier over the past three centuries, further exacerbating greenhouse gas emissions and adverse effects (Swindles et al., 2019).

Climate change, marked by rising temperatures and shifting precipitation patterns, poses an escalating threat, altering peatlands' hydrology, vegetation and carbon storage potential (IPCC, 2021; Loisel et al., 2021). It may also increase the frequency and severity of peatland-damaging wildfires (Che Azmi et al., 2021; Sim et al., 2023). In Poland, peatlands face these global threats alongside country-specific challenges, including a lack of mowing, agricultural restructuring, increased nutrient input, infrastructural development, hydro-engineering projects, river management, and insufficient knowledge about peatland diversity and eco-hydrological functioning (Kotowski et al., 2017). Hydrological

<sup>1</sup>Faculty of Biology, Adam Mickiewicz University, Poznań, Poland

<sup>2</sup>Climate Change Ecology Research Unit, Faculty of Geographical and Geological Sciences, Adam Mickiewicz University, Poznań, Poland

<sup>3</sup>Institute of Geography and Spatial Organization, Polish Academy of Sciences, Warsaw, Poland

<sup>4</sup>Institute of Geological Sciences, Polish Academy of Sciences, Warsaw, Poland

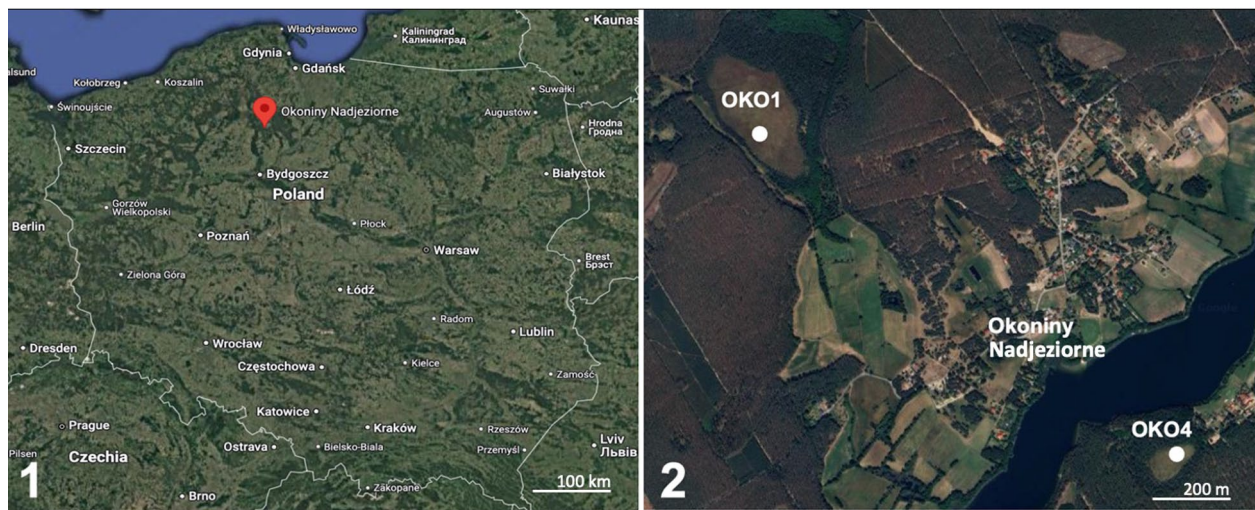
## Corresponding authors:

Jay Tipton, Faculty of Biology, Adam Mickiewicz University, ul. Uniwersytetu Poznańskiego 6, 61-614 Poznań, Poland.

Email: jaytipto@gmail.com

Katarzyna Marcisz, Faculty of Geographical and Geological Sciences, Adam Mickiewicz University, ul. Krygowskiego 10, 61-680 Poznań, Poland.

Email: marcisz@amu.edu.pl



**Figure 1.** Location of core sampling areas – OKO1 and OKO4 – within Poland.

Source: Google Maps, 2023 [Maps of the Area of (1) Poland, (2) Okoniny Nadziejorne in the Tuchola Forest].

conditions in Polish peatlands are considered ‘bad’ or ‘inadequate’ in 48% of raised bogs, 43% of transition mires and quaking bogs and 41% of alkaline fens. Drainage systems are negatively affecting 41% of raised bogs, 45% of transition mires and quaking bogs and 63% of alkaline fens (Institute for Nature Conservation, 2015). These problems are also visible in peatlands located within forest complexes that, in Poland, are managed by the State Forests. One of the most common managed forest complexes in Poland are pine monocultures that cover large areas. The three largest pine monocultures are the Noteć Forest, the Dolnośląskie Forest and the Tuchola Forest, covering the area of ca. 137,000, 165,000 and 300 000 ha, respectively. Peatlands are a common feature in young glacial landscapes such as the Tuchola Forest studied in this contribution, and several studies investigated their response to local environmental changes – both natural and anthropogenic (Bąk et al., 2024; Lamentowicz et al., 2006; Słowiński et al., 2019). Over the last 300 years, peatlands have undergone substantial changes all across Europe as a consequence of rising human impact which resulted in lowering of water tables and change in vegetation cover (Harenda et al., 2018; Lamentowicz et al., 2019; Longman et al., 2021; Swindles et al., 2019; Wochal et al., 2025). However, response of peatlands related to introduction of specific management practices remains understudied (Kreyling et al., 2021; Suetovienė and Dabašinskas, 2025). To understand the response of peatlands to specific management factors it is necessary to study long-term local environmental changes on well-selected sites that were affected by the mentioned management practices (Bąk et al., 2024, 2025). Only long-term reconstructions can help assess these changes and suggest how to handle management of peatlands under current anthropogenic climate change conditions (Chambers, 2022; Gillson and Marchant, 2014; Marcisz et al., 2022; Whitlock et al., 2018).

Palaeoecological studies have contributed to the understanding of peatland evolution, including the origin and development of different types of peatlands and their responses to environmental change, such as changes in climate and land use (Chambers et al., 2012; Lamentowicz et al., 2025; Warner, 1990). Techniques such as pollen analysis, plant macrofossil analysis, and testate amoeba analysis have been used to reconstruct past vegetation and hydrological changes in peatlands (Connor et al., 2018; Lamentowicz et al., 2025; Marcisz et al., 2020; Mauquoy and Barber, 2002). Among several proxies often studied in palaeoecology, testate amoebae (TA) are essential indicators of environmental change. Testate amoebae are a group of unicellular protists that are characterized by the presence of a shell, or test, which encases and protects the cell (Meisterfeld, 2000). These

organisms are primarily found in soil, peatlands, freshwater and mosses, where they play a crucial role in microbial food webs and nutrient cycling (Jassey et al., 2012, 2013; Wilkinson and Mitchell, 2010). The TA shells are decay-resistant; therefore, they are well preserved in peat and are commonly used to reconstruct past hydrological dynamics in peatlands (Mitchell et al., 2008). Their diversity and abundance in peatlands can be correlated with measures of peatland degradation like vegetation cover, water table depth, and carbon accumulation rate (Charman, 2001). Additionally, they are sensitive to human disturbance that influences hydrological state of the peatland, responding to drainage, peat extraction, and other land-use changes, making them valuable in assessing the quality and integrity of peatlands (Marcisz et al., 2020). All of this has led to the study of TA developing into an advantageous tool for reconstructing past and present peatland conditions and as a reliable gauge for evaluating the quality and structure of these ecosystems, as well as peatland health and restoration success (Mitchell et al., 2008).

In this study we aim to identify the effects of planned monoculture forestry on peatlands in the Tuchola Forest in northern Poland. This local-scale investigation of the timing of peatland’s response to hydrological and trophic changes focuses on individual peatlands affected by the forestry. Until now, most of palaeoecological case studies published from the area are based on investigations of single cores; here we broadened our analyses by comparing two individual peat cores. We selected to study peatlands that underwent similar human impact to compare if the response is unified across this portion of the Tuchola Forest. Working on two cores enables obtaining more detailed, independent and objective picture of changes and assessing the synchronicity of response to introduced management. We hypothesized that changes in forest management activities, as well as frequent fires in the region, affected peatlands by causing wetland acidification and a decrease in the water table, modification of peatland vegetation, and alternation of testate amoeba communities.

## Study sites and historical background

### Study sites description

The investigated sites are two *Sphagnum*-dominated peatlands near Okoniny Nadziejorne (Figure 1), a small settlement located inside the Tuchola Forest, referred to as Tuchola Pinewoods or Tuchola Conifer Woods, which is an extensive forested area dominated by pine. It is positioned between the Brda and Wda Rivers,

within the Gdańsk Pomerania region. Peatlands are situated 1.8 km apart, on the opposite sides of the Okonińskie Lake, and are both covered with various species of *Sphagnum* and vascular vegetation like *Andromeda polifolia*, *Carex* spp., *Eriophorum angustifolium*, *Eriophorum vaginatum* or *Vaccinium oxycoccus* (Bąk et al., 2024). Both peatlands possess diverse surface morphology with macroforms typical of *Sphagnum* peatlands – lawns, hummocks and pools. Some trees are present on the surface of the peatlands, especially along the edges, including *Pinus sylvestris* and *Betula pendula/pubescens*.

The study sites are located in the Tuchola Forest Biosphere Reserve (est. June 10, 2010), a vast forest complex, encompassing diverse natural habitats including pine and deciduous forests, heathlands, *Lobelia* lakes, dystrophic lakes with stonewort meadows and peatlands. Moreover, since December 2024, both investigated peatlands are legally protected as nature reserves (RDOŚ Bydgoszcz, 2024).

The local human population was sparse, even up to the end of the 18<sup>th</sup> century. The agriculture was growing in the 18<sup>th</sup> century and local forests – dominated by Scots pine with an admixture of broadleaf species like oak or hornbeam – were cut (Lamentowicz et al., 2008a). However, the local population grew in the second half of the 19<sup>th</sup> century and at the beginning of the 20<sup>th</sup> century towing to a rapid development of timber production. After acquiring of the land into Prussian borders in 1772, this region was designated for Scots pine plantation and by the end of 19<sup>th</sup> century almost 99% of the area was planted with Scots pine, several large mills were actively working, and many wetlands were drained (Bąk et al., 2024; Giętkowski, 2009; Łuców et al., 2021; Słowiński et al., 2019). This drastic change in forest management influenced the economy of the region, and now the forestry is especially important for local communities. Even though the economy grew, the human population in the Tuchola Forest was still sparse compared to other regions. Presently, the population density remains low, particularly in the forested regions. In recent years, agritourism has emerged as a thriving sector, and there are opportunities for local craft development based on timber processing.

The Tuchola Forest area experiences an average annual rainfall of 600 mm. Typically, the wettest month is July, with an average rainfall of approximately 200 mm, while August and September are the driest months. Owing to the rains, flooding of the mires typically occurs annually in the spring (Lamentowicz and Mitchell, 2007). In January and July, the average temperatures are −1.6°C and +18.7°C, respectively (Climate Data, 2026). According to palaeoecological records, lakes were present in these areas for much of the Holocene period. Today, many of the peatlands in the region are *Sphagnum*-dominated (Boiński, 1980; Boiński and Boińska, 1993; Lamentowicz and Mitchell, 2007).

### The history of forest management of the Tuchola Forest

It is essential to review and summarize the past and present management activities in the Tuchola Forest. Słowiński et al. (2019) provide invaluable information in piecing together the history of forest management in the Tuchola Forest, which has undergone multiple changes since the 14<sup>th</sup> century. The 14<sup>th</sup> century began the certification of town locations in the region, following mediaeval laws governing town privileges. From 1308 to 1466, Pomerania (the region Tuchola Forest is located in) was under the rule of the State of the Teutonic Order. From 1466 to 1772, the Polish state governed the area. Until the mid-18<sup>th</sup> century, the forests in the Tuchola Forest area consisted predominantly of oak, hornbeam, and other deciduous trees such as *Fraxinus*, *Ulmus*, *Tilia* and *Fagus* (Słowiński et al., 2019). The forests served primarily as a source of bedding and grazing for cattle, sheep and swine. Additionally, they were utilized for timber extraction to meet various living needs, including house construction and firewood (Broda, 2000; McGrath et al., 2015). Deforestation occurred to fulfil the demands of industries such as beekeeping, glassworks, charcoal

production, and potash production. It primarily affected areas with a high proportion of deciduous trees, particularly where oak and hornbeam accounted for more than 35% of the forest composition. Once the local forest resources were depleted, the deforested areas were repurposed for agricultural activities, as indicated by the increase in species indicative of human presence (Broda, 2000<sup>th</sup>). From the late 18<sup>th</sup> century to the early 20<sup>th</sup> century, Poland was under the occupation of Prussia, which led to introducing a new forest management system. In 1782, King Fredrik of Prussia issued an order titled ‘On the development of the Tuchola Forest’ which marked the beginning of transformative changes in the region. This order prompted the establishment of eight administrative areas within the Tuchola Forest, each encompassing approximately 6000 ha (Jażdżewski, 2008).

To facilitate effective planning for wood harvesting, the Prussians created detailed maps. These maps divided the individual Tuchola Forest districts into sections specifically designated for annual wood harvesting. The spatial division projects, initiated in 1790, aimed to establish uniform and compact forest complexes within the Tuchola Forest. Economic roads and branch lines were incorporated into the plans to ensure efficient forest management (Słowiński et al., 2019). In 1799, the Prussian government issued a decree that mandated the measurement of all forest areas acquired during the partitions. This assessment took into consideration factors such as species composition, age, proposed deforestation size, and loads associated with forest resources (Jażdżewski, 2008). During this time, deforestation in the Tuchola Forest area gained momentum. The region became the primary timber supplier to the Prussian market by the end of the 19<sup>th</sup> century. This significant transformation is evident in the pollen record, which shows a simultaneous decrease in deciduous trees and an increase in pine starting from the 18<sup>th</sup> century (Słowiński et al., 2019). The proliferation of pine was facilitated by the establishment of monocultures of this species (Giętkowski, 2009; Ott et al., 2018).

The Prussians referred to present-day Tuchola Forest as Tuchel Heath (in German: *Tucheler Heide*). During the late 19<sup>th</sup> century (1878–1880), a Prussian legislative body considered implementing legal measures to limit public access to timberlands to improve forest management and facilitate private hunting. The chief forester of the Woziwoda forest district at that time authored a book detailing the successful revival of local state forests since the 1850s. His book stated that the introduction of rational forestry practices brought transformative changes to the region, leading to increased productivity and a more prosperous landscape (Wilson, 2012).

According to the Eastern Marches Society, the state forests in the district doubled in size between 1867 and 1911, covering an additional 180,000 hectares. The number of forest districts and inspectorates also increased during this period, reflecting the expansion and administration of the local state forests. In the Tuchola Forest alone, the state’s landholdings doubled, encompassing two-thirds of the land, and the number of forest districts expanded from 9 to 23 (between 1886 and 1913). This growth required the deployment of additional personnel to the region, resulting in a doubling of forestry officials from the 1890s to over 200 by 1901 (Wilson, 2012). By 1913, the Tuchola Forest area included 20 large steam sawmills, signifying the extent of timber production in that period (Broda, 2000). During the transition from the 19<sup>th</sup> to the 20<sup>th</sup> century, a shift in Prussian policy led to the conversion of previously agricultural lands into pine forests (Szneider and Krysiak, 2024). Since the mid-20<sup>th</sup> century, the Tuchola Forest has been under the management of the Polish State Forestry. Policy has primarily focussed on the establishment of pine monocultures. This policy helps generate profit from the timber but comes with the cost of susceptibility to ecological disturbances. Today, central part of the Tuchola Forest is protected within the borders of the Tuchola Forest National Park.

By 1893, over 99% of the forests in the Tuchola County have been replanted with Scots pine (Giętkowski, 2009; Ott et al.,

2018). Since then, the forest districts have remained unchanged, with the area still predominantly covered by pine forests. In recent decades the levels of *Pinus sylvestris* have rapidly increased to their present-day high levels, starting around ~1980. However, because of the domination of one species, the Tuchola Forest is more vulnerable to events like insect outbreaks and fires (Słowiński et al., 2019), which have been confirmed during the past 100 years (Mokrzecki, 1928; Seidl et al., 2017). Additionally, monocultures are less resistant to sudden shifts in climate change (Leuschner and Ellenberg, 2017; Thurm et al., 2016). These monocultures and their lowered resistance to threats and climate change, can in turn affect the peatlands located inside the forests (Bąk et al., 2024, 2025).

## Methodology

### Field work

Two peat cores, named ‘Okoniny 1’ (OKO1, 53°41′00.3″N, 18°03′20.3″E) and ‘Okoniny 4’ (OKO4, 53°40′28.4″N, 18°04′39.8″E), were extracted for analysis from two distinct mires near Okoniny Nadjeziorne village (Figure 1). OKO1 was collected on January 7, 2022, and OKO4 was taken on March 4, 2022. The cores were sampled from a *Sphagnum* lawn (OKO1) and *Sphagnum* floating mat of the kettle hole mire (OKO4). Both cores – undisturbed monoliths – were sampled using Wardenaar corer (size: 10 cm × 10 cm × 1 m, Wardenaar (1987)).

### Laboratory preparation and testate amoeba analysis

The OKO1 core was 82 cm long while the OKO4 core was 84 cm long. Both cores had a visible zonation with undecomposed *Sphagnum* peat on top and decomposed peat with vascular plants and unidentifiable organic matter at the bottom. The division between these two peat types was clear after sampling the peat cores – it was visible at 36 cm in OKO1 and 48 cm in OKO4. Each core was cut into 2 cm slices, equalling 41 (OKO1) and 42 (OKO4) samples, respectively. The peat samples were then transferred into small plastic bags which were labelled and subsequently refrigerated. Samples for testate amoeba analysis were prepared according to the published methodology (Booth et al., 2010): they were sieved through a 300-µm mesh and the filtrate was used for the testate amoebae analysis. Testate amoebae were identified using atlases and online resources (Mazei and Tsyganov, 2006; Ogden and Hedley, 1980; Siemensma, 2025). The objective for each sample was to reach 100 testate amoeba tests (Payne and Mitchell, 2009), although for some samples the 100 mark was not reached, often simply because testate amoebae were absent. The minimum number of testate amoebae counted was 53. Some samples required only one microscope slide, while others required two or three. If 100 testate amoebae were not counted after three slides, the counting for that sample stopped.

### Quantitative water table and pH reconstructions

The results of testate amoeba analysis were used for the quantitative depth-to-water table (DWT) and pH reconstructions, which were performed in C2 software (Juggins, 2007) and *rioja* R package (Juggins, 2015) using the European training set and the best-performing model weighted average with tolerance downweighting and inverse deshrinking (Amesbury et al., 2016) and transfer function quantitative approach (Juggins et al., 2012).

### Radiocarbon dating and peat accumulation rates

Peat dating was performed using the AMS radiocarbon method in the Poznań Radiocarbon Laboratory. The  $^{14}\text{C}$  was measured at

**Table 1.** Radiocarbon dating results.

| Sample name (core code and sample depth in cm) | Laboratory number | Age $^{14}\text{C}$ | Dated material        |
|------------------------------------------------|-------------------|---------------------|-----------------------|
| OKO1 80–82                                     | Poz-153679        | 770 ± 30 BP         | <i>Sphagnum</i> stems |
| OKO1 64–66                                     | Poz-153538        | 310 ± 30 BP         | <i>Sphagnum</i> stems |
| OKO1 40–42                                     | Poz-153148        | 100.05 ± 0.4 pMC    | <i>Sphagnum</i> stems |
| OKO1 20–22                                     | Poz-153149        | 104.45 ± 0.38 pMC   | <i>Sphagnum</i> stems |
| OKO4 82–84                                     | Poz-153150        | 335 ± 30 BP         | <i>Sphagnum</i> stems |
| OKO4 50–52                                     | Poz-153371        | 80 ± 30 BP          | <i>Sphagnum</i> stems |
| OKO4 34–36                                     | Poz-153460        | 185 ± 30 BP         | <i>Sphagnum</i> stems |
| OKO4 22–24                                     | Poz-153461        | 121.62 ± 0.33 pMC   | <i>Sphagnum</i> stems |

several depths to cover the whole peat profile for both OKO1 and OKO4. A total of eight samples were used for radiocarbon dating – four for OKO1 and four for OKO4 (Table 1). The age-depth model was calculated using the OxCal 4.4.4 software (Bronk Ramsey, 1995) applying the *P*-Sequence function with parameters:  $k_0=0.6$ ,  $\log_{10}(k/k_0)=1$ , and interpolation = 1 cm (Ramsey, 2008; Ramsey and Lee, 2013). The IntCal20 atmospheric curve was used as the calibration dataset (Reimer et al., 2020). Peat accumulation rates (PAR) were calculated for each of the peat cores based on the cores’ chronologies.

### Supporting historical and palynological data

For the interpretation of our data on local environmental changes in studied peatlands we used several supporting data sets. These helped us to link local changes recorded in peatlands to historical events and changes in the forest composition that were an effect of introduced monoculture forest management. Historical data are based on several sources: Orłowicz (1924), Wilson (2012), Broda (2003), Słowiński et al. (2019), and Bąk et al. (2024). Data on forest composition and vegetation changes in the area were based on Obremska (2006) – a palynological study from a nearby Mukrza peatland. This site is located 17.5 km south from OKO4 site and covers over 1000 years of the Tuchola Forest vegetation history.

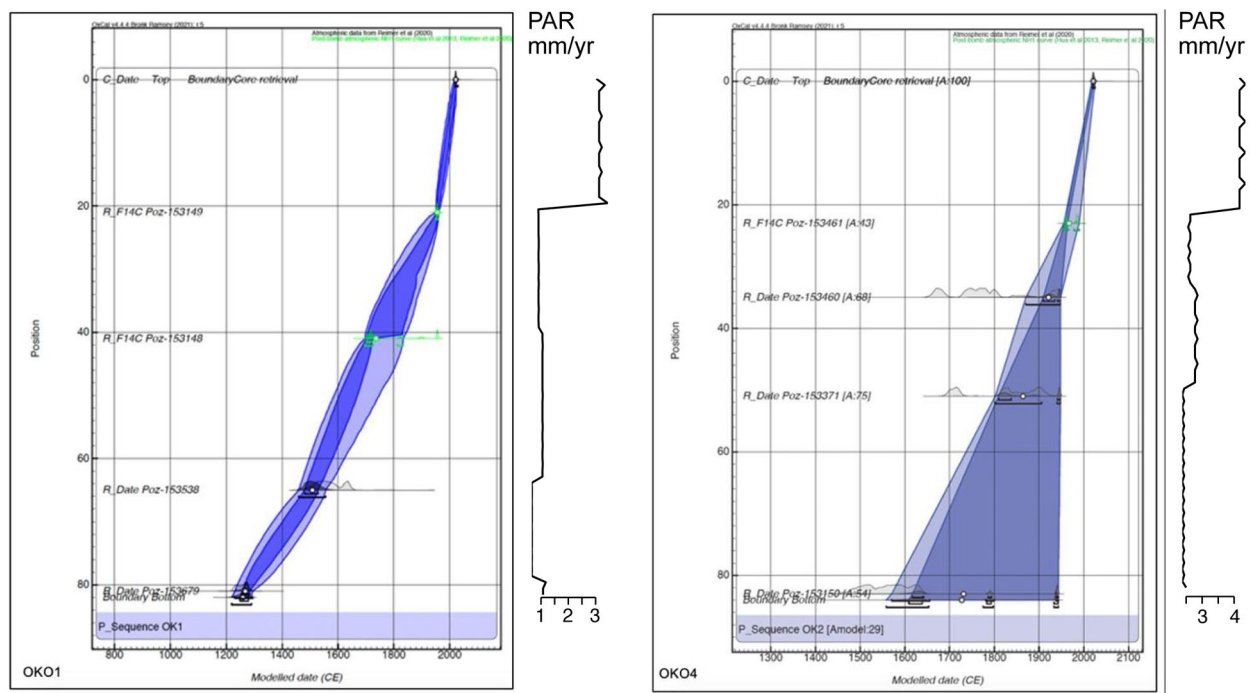
## Results

### Radiocarbon age-depth model and peat accumulation rates

Figure 2 shows the age-depth model of each peat core and calculated PAR values. The age-depth model output and PAR data can be assessed in Supplement 1. For OKO1, the year ca 1250 CE is listed at the beginning of the sampled core. By subtracting 1250 CE from 2022 CE, we conclude that the OKO1 core’s age is around 770 years. PAR values ranged throughout the core presenting mean values of mm/year equalling: 0.78 for zone 1, 1.0 for zone 3 and 2.3 for zone 3. For OKO4, the peat profile’s origin is around the year ca 1720 CE, resulting in the OKO4 core’s age being around 300 years. Therefore, PAR values were much higher for OKO4 than OKO1. The values ranged throughout the core presenting mean values mm/year equalling: 2.54 for zone 1, 3.1 for zone 3 and 4.2 for zone 3.

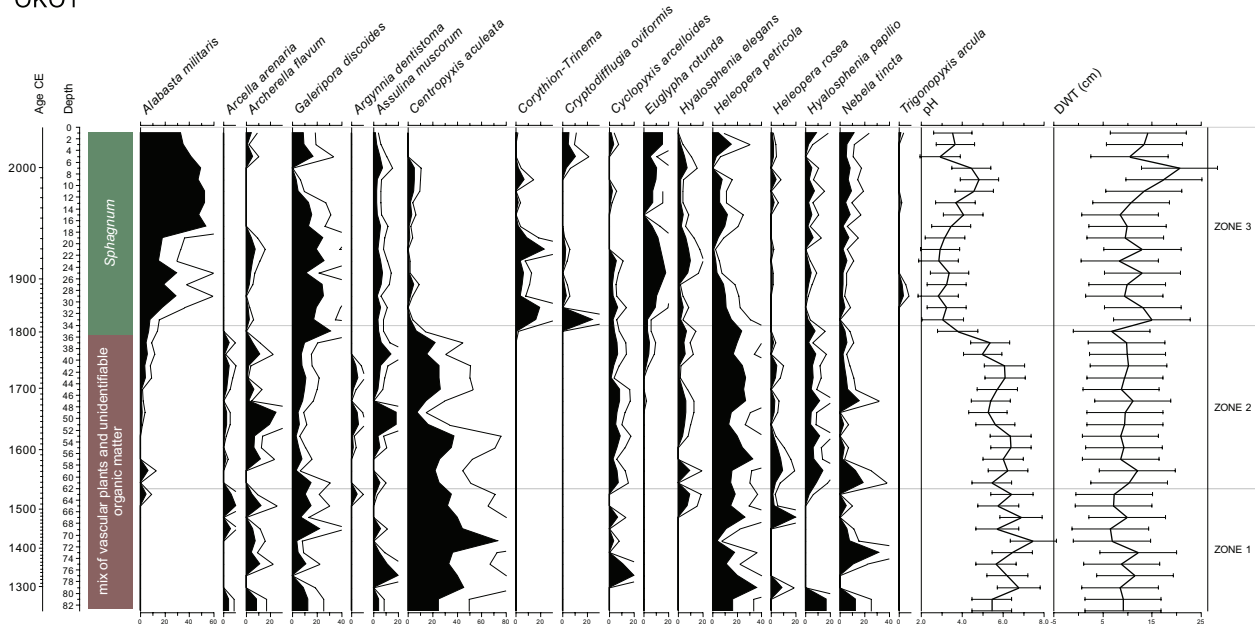
### Testate amoebae, hydrological and trophy reconstructions

**OKO1 profile.** Three zones make up the OKO1 water table which shows the testate amoebae (TA), pH, and depth-to-water-table (DWT) fluctuations (Figure 3). The TA data can be assessed in Supplement 1.



**Figure 2.** Age-depth models for OKO1 and OKO4 peat cores and associated peat accumulation rates (PAR).

#### OKO1



**Figure 3.** OKO1 testate amoebae % diagram and depth-to-water table (DWT) and pH reconstructions, as well as core lithology.

**Zone 1 (Depth: 84–62 cm, age: ~1250–1540 CE).** Thirteen species were found in zone 1 between 62 and 84 cm. The dominant species was *Centropyxis aculeata* which included occasional spikes of large numbers, totalling nearly 40% of all species. *Heleopera petricola* (17%) was also abundant. *Cyclopyxis arcelloides* (3.8%) and *Nebela tinctoria* (7.8%) experienced spikes at various depths in Zone 1. DWT in this zone ranges between 6 and 12 cm, with an average of 8.8 cm. The average pH is around 5, indicating minerotrophic conditions at the site.

**Zone 2 (Depth: 62–34 cm, age: ~1540–1810 CE).** Sixteen species were found in the second zone between 34 and 62 cm of depth. The two most abundant species were *C. aculeata* (21%) and *H. petricola* (21%), both of which saw patterns of persistent increases and decreases, however, maintaining a fair amount. *Galeripora discoides* (9%) was present throughout Zone 2.

*Hyalosphenia papilio* and *N. tinctoria* were both consistent through Zone 2 with occasional spikes in numbers. Water table in zone 2 ranges between 6 and 12 cm with an average of 9.55 cm. The pH levels are between 5 and 3 showing acidification of the peatland.

**Zone 3 (Depth: 34–0 cm, age: ~1810 CE–present).** Fifteen different testate amoeba species were found in zone 1. *Alabaster militaris* was the most dominant species making up nearly 33% of the total in this zone. It was found in great abundance near the surface but gradually decreased further in-depth, with two increase spikes around 24 and 28 cm. The second most common species was *G. discoides* (14% of the total) gradually increasing with depth. *Corythion-Trinema* displayed a few spikes of abundance at 22 and 36 cm. *Euglypha rotunda* showed consistent presence with moderate abundance, averaging around a count of 15 throughout the entire zone, equating to slightly over 10% of total

OKO4

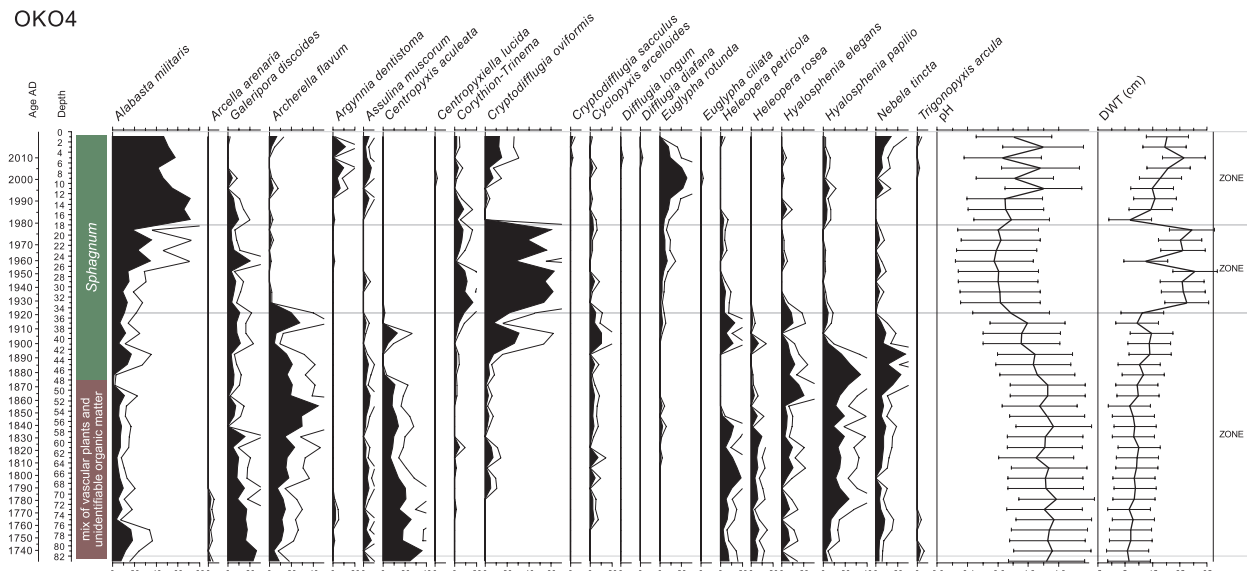


Figure 4. OKO4 testate amoebae % diagram and depth-to-water table (DWT) and pH reconstructions, as well as core lithology.

species. *Heleopera petricola* (7%) was also consistent in the zone, representing a valley curve with higher amounts near the surface before decreasing in the middle and then increasing towards the 30 cm mark. *H. papilio* and *N. tincta* were both present throughout the entire zone albeit in low numbers. The depth-to-water-table (DWT) for Zone 1 ranges between 8 and 14 cm with an average of 12.34 cm. The pH levels fluctuate averaging 4.07, which indicates acidic waters.

**OKO4 profile.** Three zones make up the OKO4 water table which shows the TA, pH and DWT fluctuations (Figure 4). The TA data can be assessed in Supplement 1.

**Zone 1 (Depth: 82–34 cm, age: ~1720–1920 CE).** Seventeen species were present in Zone 1. *Archerella flavum* spiked at the 38 cm mark. From there it continued to be the most prominent species in Zone 1 resulting in 17% of the species. The other three most common species include *G. discoides* (10%), *Centropyxis aculeata* (12%) and *H. papilio* (12%). *N. tincta* also saw a pattern of fluctuation, averaging 7% of all species. *A. militaris* continued to decrease in numbers, however, it stayed present throughout the water table. The DWT fluctuates between 6 and 12 cm with an average of 9.21 cm, while the average pH is 4.37, signifying an acidic environment.

**Zone 2 (Depth: 34–18 cm, age: ~1920–1980 CE).** Zone 2 experienced a decrease in the number of species with a total number of 15. *A. militaris* decreased in abundance in Zone 2, down to 20% of the total species. *G. discoides* (6%) were consistent in Zone 2 and experienced a spike in abundance at the 26 cm mark. *Cryptodiffugia oviformis* was the most common species, making up over half (52%) of all species. *Corythion-Trinema* accounted for 8% of the total species. The DWT in zone 2 ranges between 8 and 15 cm, averaging 11.44 cm. The pH levels average 3.81, indicating high acidity.

**Zone 3 (Depth: 18–0 cm, age: ~1980 CE-present).** Nineteen different testate amoeba species were found in zone 3 of OKO4. *A. militaris* was the most abundant species, comprising 56% of the particular total for the zone. The second most abundant (although far less than *A. militaris*) was *E. rotunda* (11%), which experienced its most significant spike at the 10 cm depth. After that, the species' numbers gradually declined further down the water table. On the other hand, *G. discoides* were rarely found in the first few centimetres of Zone 3 but started to grow towards the bottom. *C. oviformis* was also present at the very top and it experienced a large spike at centimetre 18. The DWT for Zone 3

of OKO4 ranges from between 8 and 21 cm with an average of 13.18 cm, while the pH level averages 4.09 which indicates acidic waters.

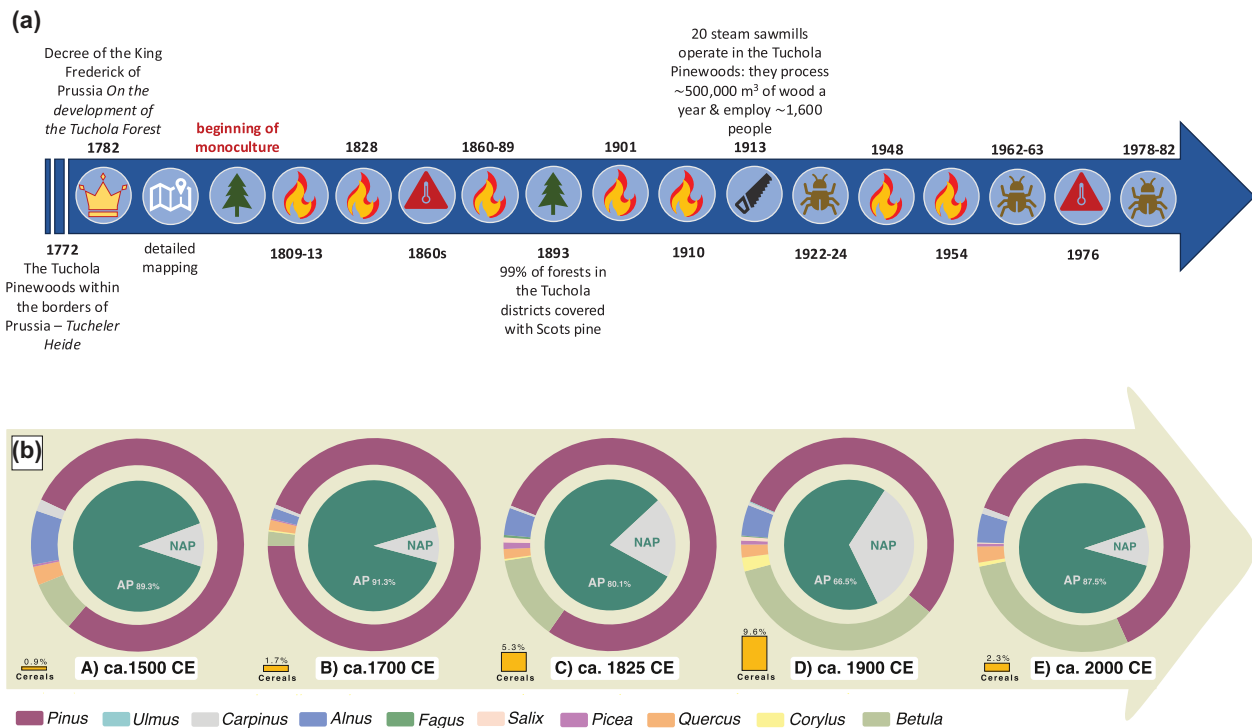
## Discussion

The hypothesis tested for this study is that changes in forest management activities in the Tuchola Forest, as well as frequent fires in the region, affected peatlands by causing wetland acidification and a decrease in the water table, modification of peatland vegetation, alternation of testate amoebae communities and a reduction of the carbon accumulation potential. Comparing with pollen data from the nearby Mukrza peatland and broad historical records we reconstruct environmental history of the region and the response of peatlands to introduced planned forest management.

### Environmental changes recorded in the peatland and the forest

The Tuchola Forest underwent a substantial change in forest composition that is visible in several published records (e.g. Bąk et al., 2024; Lamentowicz et al., 2008b; Łuców et al., 2021; Marcisz et al., 2025). Main disturbance events mentioned in historical sources are presented on a timeline in Figure 5a. Based on historical data and a detailed pollen record from the Mukrza peatland (Obremska, 2006) we can break the Tuchola Forest history into five distinct phases (A–E; see Figure 5b for summary of the Mukrza pollen record).

**Phase A: ~1250 to ~1700 CE (zones 1 and 2 in OKO1) – Stable conditions.** In this phase in local forests, drier habitats were covered by *Pinus sylvestris*, *Quercus* and *Carpinus betulus*, while *Betula* and *Alnus* occupied wetter habitats. Land-use changes occurred in the early 15th century and they were linked to increased human activities, resulting in a rise in pollen indicators. As an effect of expanding farmlands, the abundance of deciduous trees, particularly *Carpinus* and *Quercus*, gradually declined from approximately 35% to roughly 5% during this phase. Despite farming activities, the area was still densely forested and *Pinus sylvestris* was a dominant species. At that time, water tables in the peatland were relatively high, fluctuating slightly around 10 cm. Dominant TA species suggest water table fluctuations (*G. discoides*, Lamentowicz and Mitchell, 2005) and mineral matter input



**Figure 5.** (a) Historical data based on Orłowicz (1924), Wilson (2012) and Słowiński et al. (2019). (b) Summary of palynological data from nearby Mukrza peatland based on Obremska (2006).

into the site (*C. aculeata* and *C. arcelloides*, Marcisz et al., 2020) that would explain a slight opening of the landscape for agriculture.

**Phase B: ~1700 to ~1825 CE (zone 2 in OKO1, zone 1 in OKO4) – Agricultural activities in the peatlands area.** The pollen record for this phase shows a change in forest structure and the abundance of dominant pollen types changes. In general, within these 125 years a decline in arboreal pollen is noted and an increase in non-arboreal pollen (including cereals), highlighting expansion of croplands in the region (Wilson, 2012). The amount of *Betula* pollen increased but it may be related to local presence and expansion of this species on the peatland. In this period, a vital change was recorded in the OKO1 profile where a shift from minerotrophic fen to acidic *Sphagnum*-dominated peatland is noted at around 1780. This may be an effect of large drainage campaign undertaken at the northern side of the Okonińskie Lake with the aim to obtain more land for agriculture (Bąk et al., 2024). Water table in OKO1 dropped rapidly, and so did pH. These changes were not visible in OKO4 that was not affected by drainage in this period; therefore, it remained in stable trophic and hydrological state throughout phase B.

**Phase C: ~1825 to ~1900 CE (zone 3 in OKO1, zone 1 in OKO4) – Pine monoculture and increased agricultural activities.** This phase marks the most intensive and effective agricultural phase throughout the region history. After 1825, local communities continued to drain wetlands and other waterbodies, establishing croplands and turning the rest of the land into pine-dominated forest (Bąk et al., 2024; Słowiński et al., 2019; Wilson, 2012). The effect of drainage and water table lowering in the region are well visible in OKO1 profile. After the rapid fen-to-poor fen transition in phase B we can see that *Sphagnum* established on the site and the acidification process was completed. These changes were not visible in OKO4 that was not affected by drainage in this period; therefore, it remained in stable trophic and hydrological state throughout phase B.

**Phase D: ~1900 to ~2000 CE (zone 3 in OKO1, zones 2 and 3 in OKO4) – Planned forest management.** The 20th century marks the establishment of forest management practices in the region (Bąk et al., 2024). The expansion of agriculture is complete and the forests are now composed in 99% by pine (Wilson, 2012). Birch is common on the peatland surface and edges and on the edges of pine forest patches (Słowiński et al., 2019). Stable acidic conditions persist on OKO1, whereas OKO4 experiences a shift at the beginning of this phase – lowering of pH levels down to ca. 3.8 and drastic lowering of water table to 25 cm below ground level. The transformation of both sites from minerotrophic fens to *Sphagnum*-dominated poor fens is now complete. In time, when drainage is no longer effective, and the sandy areas of the Tuchola Forest do not support croplands in a good state, the agricultural areas decrease and the pine forest expands.

**Phase E: ~2000 CE onwards (zone 3 in OKO1, zone 3 in OKO4) – Climatic influence and changes in forest structure in 21st century.** Over the last 25 years forest managements practices continued as planned in phase D (Słowiński et al., 2019). When it comes to peatland's hydrology and trophy levels, in both sites some fluctuations of both parameters were noted. These may be related to climate change and related disturbances that are observed more often in the recent years – mainly strong winds, windthrows and even tornados (Łuców et al., 2021). These events interfere with forest management and force foresters to change their ways of managing the Tuchola Forest area – both forests and peatlands (Konczal et al., 2024).

#### Major historical events in the Tuchola Forest and their influence on peatlands

Figure 5a shows a timeline of some of the major events that took place in the Tuchola Forest, particularly forest fires, dry periods and insect outbreaks. Prussia, which controlled this region for a couple of 100 years, established a pine monoculture in the Tuchola Forest in the mid-19th century. About a 100 years after Prussian

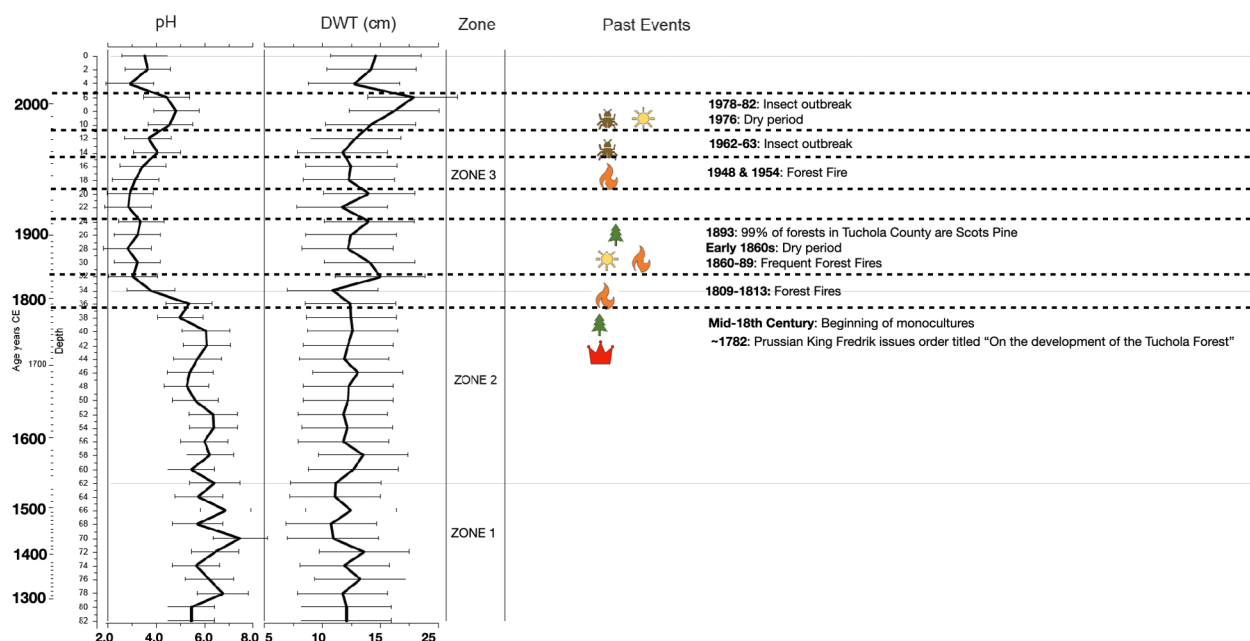


Figure 6. OKO1 major events in the Tuchola Forest.

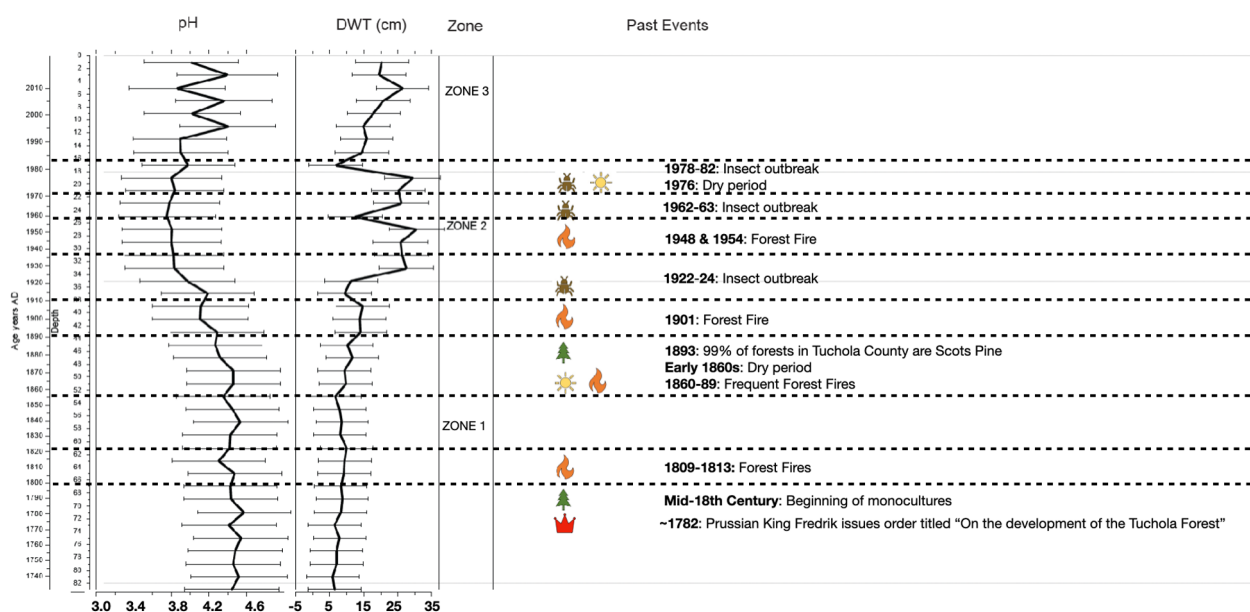


Figure 7. OKO4 major events in the Tuchola Forest.

King Fredrik issued his 1893 Tuchola Forest mandate, over 99% of forests in the Tuchola County – where our study sites are located – were Scots pine. Both before and after the Prussians took over management, forest fires were common in the Tuchola Forest (Cyzman and Oleksik-Tusińska, 2008).

Looking at our palaeoecological data, a change in forest management practices and an introduction of monoculture substantially influenced peatlands' water tables and acidity. In OKO1 and OKO4, the water tables were highest before the introduction of monoculture activity in the first half of the 19<sup>th</sup> century. They began to decrease and fluctuate more often at the onset of monoculture forests. In the years with droughts, insect outbreaks and fires, the DWT levels have decreased rapidly (Figures 5–7). This is likely due to sudden changes to the surrounding vegetation and climatic events resulting from these events, altering water retention abilities.

An increase in the acidification of OKO1 and OKO4 correlates almost directly with the onset of the Prussian monoculture activity and the King Frederik's decree to focus on zoning and managing the Tuchola Forest (Figures 5–7). By 1893, when 99% of the forests in the Tuchola County comprised almost exclusively *Pinus sylvestris*, pH levels in OKO1 and OKO4 reached high levels of acidity, which they have maintained until the present day. Scots pine is known to be a versatile species that has a tolerance for acidic soils, and through acidifying the soil it supports *Sphagnum* establishment in peatlands located in pine-dominated forests (Bağ et al., 2024, 2025; Wochal et al., 2025). This was also accelerated by the drainage of wetlands undertaken by local communities (Miller et al., 1990; Westman and Laiho, 2003). In recent years, OKO4 has seen pH spikes to more neutral levels but usually fluctuates back to acidic levels. However, the monocultures dominated by Scots pine contribute to

soil acidification and depletion, leading to diminished productivity and negative consequences for forest biodiversity, as well as the acidification of wetland areas (Bąk et al., 2024; Balto-dano, 2000; Lamentowicz et al. 2007; Rutkowska, 2019; Steckel et al., 2020).

Between 1860 and 1889, 310 fires were recorded in the Tuchola Forest, which destroyed over 4000 ha of forests (Orłowicz, 1924). Presently, the fires that occur there are ground fires and are smaller and less damaging (Adolf et al., 2018; Archibald et al., 2013). The Tuchola Forest experienced two periods of intense droughts – in the early 1860s and then again, a hundred years later in the 1970s (Kirschenstein, 2005; Schütte, 1893). Forest fires were so frequent that one German official stated, ‘It is truly a wonder of God that the region has not yet completely burned’. However, German foresters believed that the fires were not only a result of natural causes but also by the hands of native residents as a form of protest against Prussian rule. Although some local peasants did set fires for agricultural purposes, such as creating new pastures for their livestock or areas of heather for their bees, it was frequently suspected that political motivations lay behind the fires (Wilson, 2012). Other records from other parts of the Tuchola Forest show that forest management practices indeed protected the forest from frequent burning episodes (Marcisz et al., 2025). The Tuchola County and region around our study sites was also actively suppressing fires, not allowing them to spread and damage the forest stands (Bąk et al., 2024).

Additionally, there were significant insect outbreaks on numerous occasions – from 1922 to 1924, 1962 to 1963, and 1978 to 1982 (Kannenberga and Szramki, 2008; Kielczewski, 1947; Milecka et al., 2017). The prevalence of a single tree species or a uniform forest composition (monoculture) poses risks concerning beetle infestations as they are more vulnerable to insect outbreaks than mixed forests. This is because of the ease with which insects can spread from one tree to another, rapidly affecting the entire tree stand (Jactel et al., 2009; Kurz et al., 2008; Soja et al., 2007; Turetsky et al., 2012). Because of Tuchola Forest’s monoculture design, the area demonstrates low resistance to insect outbreaks. The most severe outbreak in the Tuchola Forest and Poland, in general, was that of the moth *Panolis flammea* (pine beauty) from 1922 to 1924 (Bąk et al., 2024, 2025; Broda, 2000; Mokrzecki, 1928). As a result of that outbreak, most of the Tuchola Forest was cut down (Broda, 2003). After this, there was a noticeable rise in tree planting. The extensive tree removal resulting from insect infestations and clear-cutting required reforestation efforts, almost exclusively focussed on Scots pine (Łuców et al., 2021). Between 1978 and 1985, unusual weather patterns including cold winters and shifts in water conditions led to a significant outbreak of *Lymantria monacha*, a moth commonly known as black arches. This outbreak, the most severe ever documented in the history of the Polish State Forests, affected various regions of Poland, particularly the northern and western areas, including the Tuchola Forest (Jabłoński, 2015; Śliwa, 1989). In recent years, however, the outbreaks are happening more often and seem to be more severe. The central part of the Tuchola Forest, including the Tuchola County, experienced a triple insect outbreak in spring 2024 when three different types of pests attacked pine stands between April and June (personal communication). This is posing a challenge to foresters and nature managers as they will have to include these catastrophic events in their management planning, looking for ways to minimize the damage caused by more frequent pest infestations (Bąk et al., 2025).

Abovementioned fires and pest infestations affected studied peatlands. Figures 6 and 7 for OKO1 and OKO4 divide the core samples into their three zones and line up the pH and DWT levels with years and the major events experienced in the Tuchola Forest. By visualizing all of the factors in this manner, we can better understand how past events affected pH and DWT as there are

notable changes in these parameters either exactly during or right after a major destructive event. For example, the dry period and insect outbreak that took place in the late 1970s and early 1980s correspond directly with a lowering in the water table and more acidic waters in OKO1. OKO4 saw a drop in DWT and a change in pH in the first half of the 20th century when Tuchola Forest experienced a series of forest fires and insect outbreaks between 1900 and 1954. Similar effect of local disturbance events was visible not only in other cores from Okoniny peatland, but also in dendrochronological record from the oldest pine trees in the Tuchola County (Bąk et al., 2024). This highlights the need for assessment of current forest management methods in order to reframe them to fit current environmental challenges related to progressing climate change and the legacy of past human activities and interventions. These challenges include water shortages, more frequently occurring droughts, strong winds and insect infestations. The new management plans should focus not only on financial benefits that come along with timber production, but also other components of this ecosystem, including various types of wetlands present in the landscape.

## Conclusions

- The afforestation efforts initiated in the 1850s to transform the Tuchola Forest, as described by the region’s chief forester in the late 1880s, represent a significant shift in forest management to enhance land productivity. These efforts, which prioritized monocultures of *Pinus sylvestris*, not only improved productivity but also influenced forest management practices across neighbouring regions. However, this shift towards single-species forestry lowered the forest’s resistance to climate change and environmental threats, such as fires and insect outbreaks, a trend substantiated by an increase in recorded environmentally destructive events since the advent of these monocultures.
- The influence of these forest management practices extended to the forest ecosystem’s peatlands, affecting peatland’s health – especially water table depth and pH levels. These changes are closely linked to the distribution of testate amoebae communities, which respond sensitively to alterations in wetness, acidity and mineral levels. The historical frequency of forest fires and subsequent environmental disturbances further exacerbated these changes, leading to observable shifts in peatland conditions in both investigated sites.
- The transformation of the Tuchola Forest highlights the intricate relationship between human-driven forest management strategies and their ecological consequences. While initial afforestation efforts were deemed successful in terms of productivity, they inadvertently introduced challenges related to forest vulnerability and peatland ecosystem dynamics. The study of testate amoeba communities within these peatlands has proven invaluable, offering insights into the long-term effects of forest management practices, and underscoring the need for a balanced approach to forestry that considers both productivity and ecological sustainability.

## Acknowledgements

We thank foresters of the Woziwoda Forest Unit for their help in the field and assistance throughout the project.

## Author contribution(s)

**Jay Tipton:** Data curation; Formal analysis; Investigation; Visualization; Writing – original draft.

**Katarzyna Marcisz:** Conceptualization; Data curation; Formal analysis; Funding acquisition; Investigation; Methodology;

Project administration; Supervision; Validation; Visualization; Writing– review & editing.

**Dominika Łuców:** Data curation; Investigation; Visualization; Writing– review & editing.

**Milena Obremska:** Data curation; Writing– review & editing.

**Mariusz Lamentowicz:** Conceptualization; Data curation; Formal analysis; Funding acquisition; Investigation; Methodology; Project administration; Resources; Supervision; Validation; Visualization; Writing– review & editing.

## Declaration of conflicting interests

The authors declared no potential conflicts of interest with respect to the research, authorship, and/or publication of this article.

## Funding

The authors disclosed receipt of the following financial support for the research, authorship, and/or publication of this article: This work is based on JT MSc thesis defended on the Faculty of Biology, Adam Mickiewicz University, Poznań in 2023. The study was funded by the National Science Centre, Poland, grants 2020/39/D/ST10/00641 (radiocarbon dating) and 2021/41/B/ST10/00060 (fieldwork). The fieldwork was done within the scope of the project “Protection of Valuable Ecosystems of Tuchola Forest” funded by the European Economic Area Financial Mechanism 2014–2021 within the framework of the Environment, Energy and Climate Change Programme MF EEA 2014–2021 “Implementation of Ecosystem Management Plans”.

## ORCID iDs

Katarzyna Marcisz  <https://orcid.org/0000-0003-2655-9729>

Dominika Łuców  <https://orcid.org/0000-0001-9966-7478>

Milena Obremska  <https://orcid.org/0000-0002-3465-1894>

## Data availability statement

The data generated for this study can be assessed in Supplemental 1.

## Supplemental material

Supplemental material for this article is available online.

## References

- Adolf C, Wunderle S, Colombaroli D et al. (2018) The sedimentary and remote-sensing reflection of biomass burning in Europe. *Global Ecology and Biogeography* 27: 199–212.
- Amesbury MJ, Swindles GT, Bobrov A et al. (2016) Development of a new pan-European testate amoeba transfer function for reconstructing peatland palaeohydrology. *Quaternary Science Reviews* 152: 132–151.
- Archibald S, Lehmann CE, Gómez-Dans JL et al. (2013) Defining pyromes and global syndromes of fire regimes. *Proceedings of the National Academy of Sciences of the United States of America* 110: 6442–6447.
- Bąk M, Lamentowicz M, Kołaczek P et al. (2024) Assessing the impact of forest management and climate on a peatland under Scots pine monoculture using a multidisciplinary approach. *Biogeosciences* 21: 5143–5172.
- Bąk M, Lamentowicz M, Kołaczek P et al. (2025) Twentieth-century ecological disasters in central European monoculture pine plantations led to critical transitions in peatlands. *Biogeosciences* 22: 3843–3866.
- Baltodano J (2000) *Monoculture Forestry: A Critique From an Ecological Perspective. Proceedings of the Tree Trouble: A Compilation of Testimonies on the Negative Impact of Large-Scale Monoculture Tree Plantations Prepared for the 6th COP of the FCCC*. Hague: Friends of the Earth International.
- Boiński M (1980) Charakterystyka geobotaniczna Tucholskiego Parku Krajobrazowego (eng. Geobotanical characteristics of the Tuchola Landscape Park). *MSR. Tucholski Park Krajobrazowy*.
- Boiński M and Boińska U (1993) Torfowiska Borów Tucholskich. *Chrońmy Przyrodę Ojczystą* 5: 51–57.
- Booth RK, Lamentowicz M and Charman DJ (2010) Preparation and analysis of testate amoebae in Peatland Palaeoenvironmental Studies. *Mires and Peat* 7(11): 1–7.
- Broda J (2000) *Historia leśnictwa w Polsce: Wydaw. Akademii Rolniczej im. Augusta Cieszkowskiego*, pp. 368.
- Broda J (2003) Gradacje strzygoni choinkowki w Lasach Państwowych Wielkopolski i Pomorza Gdanskiego w okresie międzywojennym (eng. Gradations of christmas tree cutters in the state forests of Greater Poland and Pomerania Gdańsk in the interwar period). *Studia i Materiały Ośrodka Kultury Leśnej* 5: 77–94.
- Bronk Ramsey C (1995) Radiocarbon calibration and analysis of stratigraphy: The OxCal program. *Radiocarbon* 37: 425–430.
- Chambers FM (2022) The use of paleoecological data in mire and moorland conservation. *Past Global Change Magazine* 30: 16–17.
- Chambers FM, Booth RK, De Vleeschouwer F et al. (2012) Development and refinement of proxy-climate indicators from peats. *Quaternary International* 268: 21–33.
- Charman DJ (2001) Biostratigraphic and palaeoenvironmental applications of testate amoebae. *Quaternary Science Reviews* 20: 1753–1764.
- Che Azmi NA, Mohd Apandi N and Rashid AS (2021) Carbon emissions from the peat fire problem—a review. *Environmental Science and Pollution Research* 28: 16948–16961.
- Climate Data (2026) Climate Data. Available at: [www.climate-data.org](http://www.climate-data.org) (accessed 16 February 2026).
- Connor SE, Colombaroli D, Confortini F et al. (2018) Long-term population dynamics: Theory and reality in a peatland ecosystem. *Journal of Ecology* 106: 333–346.
- Cyzman W and Oleksik-Tusińska A (2008) Jednolity Program Gospodarczo – Ochronny Dla Leśnego Kompleksu Promocyjnego “Bory Tucholskie” (eng. Unified economic and protective program for Promotional Forest Complex “Tuchola Pinewoods”). (Toruń), pp.233.
- FAO (2022) *Peatlands and Climate Planning – Part 1: Peatlands and Climate Commitments*. Rome: FAO.
- Frolking S, Talbot J, Jones MC et al. (2011) Peatlands in the Earth’s 21st century climate system. *Environmental Review* 19: 371–396.
- Giętkowski T (2009) Temporal change of forest area in Tuchola Pinewoods region between 1938 and 2000 (in Polish: Zmiany lesistości Borów Tucholskich w latach 1938 - 2000). *Promotio Geographica Bydgosiensis* : 1–12.
- Gillson L and Marchant R (2014) From myopia to clarity: Sharpening the focus of ecosystem management through the lens of palaeoecology. *Trends in Ecology & Evolution* 29: 317–325.
- Gorham E (1991) Northern peatlands: Role in the carbon cycle and probable responses to climate warming. *Ecological Applications* 1: 182–195.
- Harenda KM, Lamentowicz M, Samson M et al. (2018) The role of peatlands and their carbon storage function in the context of Climate Change. In: Zielinski T, Sagan I and Surosz W (eds) *Interdisciplinary Approaches for Sustainable Development Goals: Economic Growth, Social Inclusion and Environmental Protection*. Cham: Springer International Publishing, pp.169–187.
- Institute for Nature Conservation (2015) Monitoring of species and habitats.
- IPCC (2014) Climate Change 2014: Synthesis Report. Contribution of Working Groups I, II and III to the Fifth Assessment

- Report of the Intergovernmental Panel on Climate Change. In: Core Writing Team RKPALAME (ed). IPCC, Geneva, Switzerland, 151pp.
- IPCC (2021) Climate Change 2021: The Physical Science Basis. Contribution of Working Group I to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change. In: Masson-Delmotte V, Zhai P, Pirani A et al. (eds). Cambridge University Press.
- Jabłoński T (2015) Występowanie i zwalczanie leśnych foliofagów-trendy i prognozy (eng. Occurrence and control of forest foliophages - trends and forecasts). *Postępy Techniki w Leśnictwie* 132: 13–19.
- Jactel H, Nicoll BC, Branco M et al. (2009) The influences of forest stand management on biotic and abiotic risks of damage. *Annals of Forest Science* 66: 701–701.
- Jassey VEJ, Meyer C, Dupuy C et al. (2013) To what extent do food preferences explain the trophic position of heterotrophic and mixotrophic microbial consumers in a Sphagnum peatland? *Microbial Ecology* 66: 571–580.
- Jassey VEJ, Shimano S, Dupuy C et al. (2012) Characterizing the feeding habits of the testate amoebae *Hyalosphenia papilio* and *Nebela tincta* along a narrow “Fen-Bog” gradient using digestive vacuole content and  $^{13}\text{C}$  and  $^{15}\text{N}$  isotopic analyses. *Protist* 163: 451–464.
- Jazdzewski K (2008) Administracja lasami państwowymi na obszarze RDLP w Gdańsku w latach 1815–1867. *Sylvan* 152: 56–61.
- Juggins S (2007) *C2 Version 1.5 User Guide. Software for Ecological and Palaeoecological Data Analysis and Visualisation*. Newcastle upon Tyne: Newcastle University, p.73.
- Juggins S (2015) Rioja: Analysis of Quaternary Science Data. R Package Version 0.9-5. Available at: <https://cran.r-project.org/web/packages/rioja/index.html>
- Juggins S, Birks HJB et al. (2012) Quantitative environmental reconstructions from biological data. In: Birks HJB, Lotter AF and Juggins S (eds) *Tracking Environmental Change Using Lake Sediments: Data Handling and Statistical Techniques*. Dordrecht: Springer, pp.431–494.
- Kannenberga K and Szramki H (2008) Management of Nature Conservation in Forests [Polish: Zarządzanie Ochroną Przyrody W Lasach]. *WSZS w Tucholi*, pp. 278.
- Kiełczewski B (1947) Klęska sówki chojnówki jako zagadnienie biocenotyczne. *Stepowienie Wielkopolski*. Prace Komisji Matematyczno-Przyrodniczej Poznańskie Towarzystwo Przyjaciół Nauk, Poznań, ser. B, 167–171.
- Kirschenstein M (2005) Wieloletnie zmiany sum opadów atmosferycznych na wybranych stacjach północno-zachodniej Polski. *Słupskie Prace Geograficzne* 2: 199–214.
- Konczal S, Lamentowicz M, Bąk M et al. (2024) Rekomendacje dla ochrony mokradł w lasach (Recommendations for wetland protection in forests [in Polish]. In: Lamentowicz M and Konczal S (eds) *Jak chronić torfowiska w lasach? (How to Protect Peatlands in the Forest? [in Polish])*. Łódź: Archaeograph, pp.161–165.
- Kotowski W, Dembek W and Pawlikowski P (2017) Mires and peatlands in Europe: Status, distribution, and conservation – Poland. In: Joosten HT and Moen A (eds) *European Mires*. E. Schweizerbartsche Verlagsbuchhandlung, Stuttgart, Germany, pp.549–671.
- Kreyling J, Tanneberger F, Jansen F et al. (2021) Rewetting does not return drained fen peatlands to their old selves. *Nature Communications* 12: 5693.
- Kurz WA, Dymond CC, Stinson G et al. (2008) Mountain pine beetle and forest carbon feedback to climate change. *Nature* 452: 987–990.
- Lamentowicz M, Obremska M and Mitchell EAD (2008b) Auto-genic succession, land-use change, and climatic influences on the holocene development of a kettle-hole mire in northern Poland. *Review of Palaeobotany and Palynology* 151: 21–40.
- Lamentowicz M, Andrews L, Czerwiński S et al. (2025) Multi-proxy palaeoecological studies from peatlands: A comprehensive review of recent advances and future developments. *Earth-Science Reviews* 271: 105278.
- Lamentowicz M, Cedro A, Gafka M et al. (2008a) Last millennium palaeoenvironmental changes from a Baltic bog (Poland) inferred from stable isotopes, pollen, plant macrofossils and testate amoebae. *Palaeogeography Palaeoclimatology Palaeoecology* 265: 93–106.
- Lamentowicz M, Kołaczek P, Mauquoy D et al. (2019) Always on the tipping point – A search for signals of past societies and related peatland ecosystem critical transitions during the last 6500 years in N Poland. *Quaternary Science Reviews* 225: 105954.
- Lamentowicz M and Mitchell EA (2005) The ecology of testate amoebae (Protists) in Sphagnum in north-western Poland in relation to peatland ecology. *Microbial Ecology* 50: 48–63.
- Lamentowicz M, Tobolski K, Mitchell EAD (2007) Palaeoecological evidence for anthropogenic acidification of a kettle-hole peatland in northern Poland. *The Holocene* 17: 1185–1196.
- Lamentowicz M and Mitchell EAD (2007) Testate amoebae as ecological and palaeohydrological indicators in peatlands – The Polish experience. In: Okruszko ETM, Szatyłowicz J, Swiatek D, et al. (eds) *Proceedings of the international conference W3M “Wetlands: Monitoring, Modelling and Management”*, Wierzba, Poland, 22–25 September 2005, pp.85–90. Leiden: Taylor & Francis/Balkema.
- Lamentowicz M, Obremska M and Mitchell EAD (2006) Developmental history of two kettle-hole mires in Tuchola Pine-woods (N Poland). *Przegląd Geologiczny* 54: 76–80.
- Leuschner C and Ellenberg H (2017) *Ecology of Central European Non-forest Vegetation: Coastal to Alpine, Natural to Man-Made Habitats: Vegetation Ecology of Central Europe*. Berlin: Springer.
- Loisel J, Gallego-Sala AV, Amesbury MJ et al. (2021) Expert assessment of future vulnerability of the global peatland carbon sink. *Nature Climate Change* 11: 70–77.
- Longman J, Veres D, Haliuc A et al. (2021) Carbon accumulation rates of holocene peatlands in central-eastern Europe document the driving role of human impact over the past 4000 years. *Climate of the Past* 17: 2633–2652.
- Łuców D, Lamentowicz M, Kołaczek P et al. (2021) Pine Forest Management and disturbance in northern Poland: Combining high-resolution 100-year-old paleoecological and remote sensing data. *Frontiers in Ecology and Evolution* 9: 747976.
- Marcisz K, Bąk M, Lamentowicz M et al. (2025) Substantial changes in land and forest management led to critical transitions in peatland functioning over the last 700 years. *Scientific Reports* 15: 18211.
- Marcisz K, Czerwiński S, Lamentowicz M et al. (2022) How paleoecology can support peatland restoration. *Past Global Change Magazine* 30: 12–13.
- Marcisz K, Jassey VEJ, Kosakyan A et al. (2020) Testate Amoeba functional traits and their use in paleoecology. *Frontiers in Ecology and Evolution* 8: 340.
- Mauquoy D and Barber K (2002) Testing the sensitivity of the palaeoclimatic signal from ombrotrophic peat bogs in northern England and the Scottish Borders. *Review of Palaeobotany and Palynology* 119: 219–240.
- Mazei Y and Tsyganov AN (2006) *Freshwater testate amoebae*. Moscow: KMK.
- McGrath MJ, Luyssaert S, Meyfroidt P et al. (2015) Reconstructing European forest management from 1600 to 2010. *Biogeosciences* 12: 4291–4316.

- Meisterfeld R (2000) Testate amoebae with filopodia. In: *The Illustrated Guide to the Protozoa*, 2nd edn. Lawrence, Kan: Soc. of Protozoologists, pp.1054–1083.
- Milecka K, Kowalewski G, Fiałkiewicz-Kozieł B et al. (2017) Hydrological changes in the rzecin peatland (Puszcza Notecka, Poland) induced by anthropogenic factors: Implications for mire development and carbon sequestration. *Holocene* 27: 651–664.
- Miller JD, Anderson HA, Ferrier RC et al. (1990) Hydrochemical fluxes and their effects on stream acidity in two forested catchments in Central Scotland. *Forestry An International Journal of Forest Research* 63: 311–331.
- Mitchell EAD, Charman DJ and Warner BG (2008) Testate amoebae analysis in ecological and paleoecological studies of wetlands: Past, present and future. *Biodiversity and Conservation* 17: 2115–2137.
- Mokrzejki Z (1928) *Strzygonia Choinówka. Panolla Llammea Schiff. Monografia*. Warsaw, Poland.
- Obremska M (2006) *Dynamics of Sediments Accumulation in Area Influenced by Żur Dam Lake (Tuchola Pinewoods) (In Polish: Dynamika Akumulacji Biogenicznej w Obszarze Oddziaływania Zalewu Żur (Bory Tucholskie)*. PhD Thesis, Adam Mickiewicz University, Poznań.
- Ogden CG and Hedley RH (1980) *An Atlas of Freshwater Testate Amoebae*. London: Oxford University Press.
- Orłowicz M (1924) *Ilustrowany Przewodnik Po Województwie Pomorskiem*. Książnica Polska: Lwów-Warszawa.
- Ott F, Kramkowski M, Wulf S et al. (2018) Site-specific sediment responses to climate change during the last 140 years in three varved lakes in northern Poland. *Holocene* 28: 464–477.
- Payne RJ and Mitchell EAD (2009) How many is enough? Determining optimal count totals for ecological and palaeoecological studies of testate amoebae. *Journal of Paleolimnology* 42: 483–495.
- Ramsey CB (2008) Deposition models for chronological records. *Quaternary Science Reviews* 27: 42–60.
- Ramsey CB and Lee S (2013) Recent and planned developments of the program OxCal. *Radiocarbon* 55: 720–730.
- RDOŚ Bydgoszcz (2024) Nowe rezerваты w województwie kujawsko-pomorskim. Available at: <https://www.gov.pl/web/rdos-bydgoszcz/nowe-rezerваты-w-województwie-kujawsko-pomorskim> (accessed 15 September 2025).
- Reimer PJ, Austin WEN, Bard E et al. (2020) The IntCal20 Northern Hemisphere radiocarbon age calibration curve (0–55 cal kBP). *Radiocarbon* 62: 725–757.
- Rutkowska P (2019) *Przebieg Procesu Bielcowania w Cyklu Uprawy Monokultur Sosnowych w Wybranych Obszarach Piaszczystych Polski Północnej* (eng. *The Course of the Podzolic Process in the Cycle of Pine Monoculture Cultivation in Selected Sandy Areas of Northern Poland*). Torun: Uniwersytet Mikołaja Kopernika w Toruniu.
- Schütte R (1893) *Die Tucheler Haide Vornehmlich in Forstlicher Beziehung*. Gdańsk, Poland.
- Seidl R, Thom D, Kautz M et al. (2017) Forest disturbances under climate change. *Nature Climate Change* 7: 395–402.
- Siemensma FJ (2025) *Microworld, World of Amoeboid Organisms*. Kortenhoef: World-wide Electronic Publication. Available at: <https://www.arcella.nl> (accessed 15 September 2025).
- Sim TG, Swindles GT, Morris PJ et al. (2023) Regional variability in peatland burning at mid-to high-latitudes during the Holocene. *Quaternary Science Reviews* 305: 108020.
- Śliwa E (1989) Przebieg masowego pojawu brudnicy mniszki (*Lymantria monacha* L.) i jej zwalczania w Polsce w latach 1978–1985 oraz regeneracja aparatu asymilacyjnego w uszkodzonych drzewostanach (eng. The course of the mass outbreak of the nun moth (*Lymantria monacha* L.) and its control in Poland in 1978–1985 and the regeneration of the assimilation apparatus in damaged stands). *Prace Instytutu Badań Leśnictwa* 710: 3–120.
- Słowiński M, Lamentowicz M, Łuców D et al. (2019) Paleoecological and historical data as an important tool in ecosystem management. *Journal of Environmental Management* 236: 755–768.
- Soja AJ, Tchekakova NM, French NHF et al. (2007) Climate-induced boreal forest change: predictions versus current observations. *Global and Planetary Change* 56: 274–296.
- Steckel M, del Río M, Heym M et al. (2020) Species mixing reduces drought susceptibility of Scots pine (*Pinus sylvestris* L.) and oak (*Quercus robur* L., *Quercus petraea* (Matt.) Liebl.) – Site water supply and fertility modify the mixing effect. *Forest Ecology and Management* 461: 117908.
- Sujetovienė G and Dabašinskas G (2025) The impact of restoration of Lithuanian peatlands on the economic value of certain ecosystem services. *Ecological Engineering* 212: 107475.
- Swindles GT, Morris PJ, Mullan DJ et al. (2019) Widespread drying of European peatlands in recent centuries. *Nature Geoscience* 12: 922–928.
- Szneider B and Krysiak R (2024) *Nadleśnictwo Lubichowo*, Fundacja Oko-Lice Kultury, Zblewo, pp.48.
- Thurm EA, Uhl E and Pretzsch H (2016) Mixture reduces climate sensitivity of Douglas-fir stem growth. *Forest Ecology and Management* 376: 205–220.
- Turetsky MR, Bond-Lamberty B, Euskirchen E et al. (2012) The resilience and functional role of moss in boreal and arctic ecosystems. *New Phytologist* 196: 49–67.
- Wardenaar ECP (1987) A new hand tool for cutting peat profiles. *Canadian Journal of Botany* 65: 1772–1773.
- Warner BG (1990) Testate amoebae (Protozoa). Methods in Quaternary ecology no. 5. *Geoscience Canada* 5: 65–74.
- Westman CJ and Laiho R (2003) Nutrient dynamics of drained peatland forests. *Biogeochemistry* 63: 269–298.
- Whitlock C, Colombaroli D, Conedera M et al. (2018) Land-use history as a guide for forest conservation and management. *Conservation Biology* 32: 84–97.
- Wilkinson DM and Mitchell EAD (2010) Testate amoebae and nutrient cycling with particular reference to soils. *Geomicrobiology Journal* 27: 520–533.
- Wilson JK (2012) Reforestation as reform: Pomerelia and the Tuchel Heath. In: Wittmann R (ed.) *The German Forest. Nature, Identity, and the Contestation of a National Symbol, 1871–1914*. Toronto Buffalo London: University of Toronto Press, pp.132–174.
- Wochal D, Marcisz K, Barabach J et al. (2025) The fen that vanished: The untold story of drainage and peat extraction in Bagno Chlebowo peatland with implications for nature conservation. *Global Ecology and Conservation* 61: e03647.