The most complete Holocene peat record from Central Europe: multi-proxy reconstruction of postglacial wetness changes and climate events from Linje peatland, Poland

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Abstract. This study investigates the vegetation and hydrological dynamics of Linje peatland in northern Poland during the past 11,500 years by integrating testate amoeba and plant macrofossil analyses. The Linje profile is currently the only complete Holocene peat record in Central Europe and offers valuable insights into long-term climate variability and its ecological consequences for peatland ecosystems. The results reveal significant changes in peatland wetness and vegetation driven by autogenic processes, climatic fluctuations and anthropogenic influences. Major bryophyte species turnovers occurred around 11,200, 10,350, 8,200, 7,500, 5,500, 600, and 450 cal. BP often coinciding with declines in *Archerella flavum* and *Hyalosphenia papilio* abundances. Both proxies indicate a marked period of drier conditions between 7,600 and 6,800 cal. BP corresponding with the Holocene Thermal Maximum. Additionally, testate amoeba data suggest further disturbances at approximately 3,050, 2,000, and 200 cal. BP, and the latter, linked to a permanent shift in species composition, implies lasting changes to peatland conditions caused by intensified human activity. Around the end of the Early Holocene, most species turnovers and disturbances began to align with Holocene Rapid Climate Change (RCC) events.

1 Introduction

Peatlands serve as valuable archives of past environmental conditions, capturing a record of climatic, hydrological, and ecological changes over millennia (Chambers and Charman, 2004; Karpińska-Kołaczek et al., 2024; Margielewski et al., 2024; Piilo et al., 2025; Sim et al., 2023; Swindles et al., 2019, 2025). Research on peat deposits for paleoclimate reconstruction dates back to the late 19th century, and since then methodological advances have steadily improved the accuracy, resolution, and reliability of reconstructions, enabling robust comparisons of local and global events (Chambers et al., 2012, cf. Birks and Seppä, 2010). Recent innovations include trait-based paleoecology (Marcisz et al., 2020a), biomarker analyses (Pancost, 2024), and novel techniques for quantifying wildfire intensity in peatlands (Theurer et al., 2024).

Among the various vascular plants and bryophytes that contribute to peat formation, *Sphagnum* mosses stand out as particularly valuable in situ biological proxies in paleoecological research (Clymo, 1984; Lamentowicz et al., 2019b; Ronkainen et al., 2014; Rydin et al., 2006). This is due to their distinct ecological preferences, physiological limitations, slow vertical growth, and

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resistance to decay. Different *Sphagnum* species are confined to specific microhabitats that vary in pH, nutrient availability, and water table depth (Rydin et al., 2006). Species turnover is strongly linked to changes in peatland hydrology, as *Sphagnum* species differ in their sensitivity to moisture availability in the capitulum and cannot actively regulate water uptake or prevent water loss (Gong et al., 2020). Together, these traits make *Sphagnum* mosses reliable indicators of past environmental conditions, particularly fluctuations in water table levels. In the Northern Hemisphere, *Sphagnum* mosses are major contributors to peat accumulation, especially in ombrotrophic bogs and poor fens where they typically dominate (Granlund et al., 2022; Halsey et al., 2000; Kokkonen et al., 2019; Piilo et al., 2023). In contrast, peat formation in rich fens is primarily driven by brown mosses (mainly the Amblystegiaceae family), and by the roots and rhizomes of vascular plants (Jaszczuk et al., 2024). The unique morphological, physiological, and biochemical traits of *Sphagnum* mosses make them effective ecosystem engineers, capable of building peat from their dead tissue while creating acidic, nutrient-poor, and waterlogged conditions. In doing so, they suppress the growth of vascular plants, further reinforcing conditions that favor their own dominance and continued growth. (van Breemen, 1995; Turetsky et al., 2025). Sphagnum communities growing on sufficiently deep peat deposits are highly resilient, retaining their capacity to store carbon and recover growth after drought conditions (Lamentowicz et al., 2019b; Marcisz et al., 2020b; Moore et al., 2021).

Changes in bog surface wetness serve as one of the indicators of past climatic shifts (Charman et al., 2009). Two of the most used proxies for detecting wet and dry shifts in peatlands are the remains of plants and testate amoebae (Blackford, 2000; Charman et al., 2006; Davies et al., 2021; Kuuri-Riutta et al., 2022; Marcisz et al., 2014a; Rundgren et al., 2023; Sim et al., 2021b; Swindles et al., 2020; Väliranta et al., 2012). While testate amoebae and plants are ecologically interconnected, testate amoebae communities can adjust species composition over shorter timescales due to their short life cycles and high turnover rates, whereas mosses and perennial vascular plants tend to respond more gradually to hydrological changes (Marcisz et al., 2014ab; Väliranta et al., 2012). Consequently, a multi-proxy analysis of vegetation and testate amoebae assemblage dynamics provides a more comprehensive understanding of past surface wetness changes (Väliranta et al., 2012). Both proxies also offer insights into the trophic levels of peatlands, yielding valuable information about site development (Laine et al., 2018; Lamentowicz et al., 2010; Mauquoy and van Geel, 2007; Opravilová and Hájek, 2006).

Holocene climate variability offers an opportunity to study natural climate change before industrialization. Peat-based climatic reconstructions have mainly focused on the Northern Hemisphere spanning Middle to Late Holocene (Charman et al., 2006; Holmquist et al., 2016; Mauquoy et al., 2008; Sillasoo et al., 2007; Swindles et al., 2010). Peatland records have also been studied for specific climate events, such as the 8.2 ka (Daley et al., 2016; Hughes et al., 2006), 4.2 ka (Jordan et al., 2017) and 2.8 ka events (Słowiński et al., 2016). In rare cases, complete Holocene records from peatlands have been identified such as Walton Moss, England (Hughes et al., 2000). Full Holocene peat records from Europe are rare because of the temporal variation in peatland succession (Ruppel et al., 2013; Stivrins, 2025) as well as the extensive history of drainage-driven land use for economic purposes (Finlayson and Spiers, 1999; United Nations Environment Programme, 2022; Verhoeven, 2014). While there are examples of full postglacial records from Polish lakes (Bonk et al., 2021; Gałka et al., 2014; Ralska-Jasiewiczowa, 1998), the longest continuous peat records reported until now came from Stążki and Głęboczek peatlands, which span 7,500 and 6,500 years, respectively (Gałka et al., 2013a; Lamentowicz et al., 2019a). The present study extends this record further, providing the longest continuous peat sequence documented from Poland to date. Linje in northern Poland is notable as the only known peatland in Poland with a nearly 12-meter-thick uninterrupted peat layer that covers the past ca 11,500 years of its development history. Various research projects have been conducted on the site exploring its history, current biotic and abiotic environment. Open-top chambers on the site have been used to model climate change effects on local vegetation, plant-fungal interactions, microbial activity and peatland respiration processes (Buttler et al., 2023; Jassey et al., 2018; Reczuga et al., 2018; Samson et al., 2018). Additional research papers have explored the hydrological functioning and microclimatic properties of Linje (Słowińska et al., 2010, 2022) and testate amoebae

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In this study, we investigate a nearly 12 m long undisturbed peat core from Linje peatland. To our knowledge, it is the only continuous peat core in Central Europe that reflects the environmental dynamics of the entire Holocene (11,500 years). Our analysis centres on plant macrofossil and testate amoebae analysis, particularly emphasising changes in the species communities of bryophytes and testate amoebae. We aim to reconstruct local vegetation and wetness changes while exploring their connections with Holocene climatic fluctuations to better understand past ecosystem responses to climate change.

2 Study area

The studied core was extracted in 2019 from Linje (53°11'14.6"N, 18°18'35.4"E), a 5.95-hectare peatland located near Bydgoszcz in northern Poland (Fig. 1). Situated within the nemoral-continental vegetation zone (Preislerová et al., 2024) Linje peatland forms part of the 12.7 hectare Linje Nature Reserve, established in 1956 (Kucharski and Kloss, 2005). The surrounding landscape is a legacy of the last glacial and the peatland formed in a ~12 m deep depression (Żurek, 2005).

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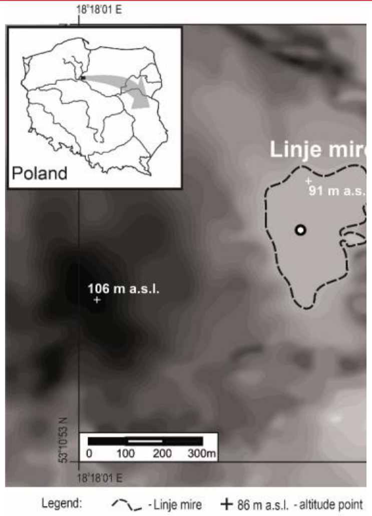

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Figure 1: Location of the Linje peatland study site. Basemaps (top left) are from ArcGIS Online, photographs (right and bottom left) by Michal Słowiński.

The peatland is surrounded by a mosaic of mixed forests (*Betula pendula*, *Quercus robur*, *Pinus sylvestris*, *Picea abies)*, arable land and villages (Kucharski and Kloss, 2005). Recognized as a microrefugium for protected dwarf birch (*Betula nana*), the site is protected under the Natura 2000 network (Marcisz et al., 2015; Noryśkiewicz, 2005).

The site features a gradient of vegetation types, ranging from poor fen at the periphery to ombrotrophic conditions in the centre reflecting its hydrological functioning (Noryśkiewicz, 2005; Słowińska et al., 2010). Since Linje is a small, forest-surrounded peatland in a depression, it has a cooler microclimate than a nearby open-air reference site (Słowińska et al., 2022). The authors point out that 19th-century drainage efforts have made the peatland surface highly responsive to meteorological changes, contributing to hydrological instability. This instability has also been observed in a testate amoeba-based water table reconstruction (Marcisz et al., 2015).

MATERIALS AND METHODS

3.1 Coring and radiocarbon dating

In 2019 two parallel peat profiles with a distance of 0.5 m were cored from the centre of Linje peatland with Russian style corer (chamber dimension: 10×100 cm), from vegetation area characteristic of the ombrotrophic section of the site. The longer profile, with the total length of 12.3 m was chosen for analyses of this study and it was cut into 2.5 cm thick sections.

Radiocarbon dating was performed on selected plant macrofossils (Table 1) at the Poznań Radiocarbon Laboratory (Poland) using their standard pre-treatment protocols. The chronology of the peat profile is based on a Bayesian age-depth model generated from 12 out of 14 ^{14}C AMS dates (Table 1). The model was constructed using OxCal. 4.4.4 software (Bronk Ramsey, 1995; 2006), by applying the *P_Sequence* function with the following parameters: k_0=0.75, log10(k/k_0)=1 and interpolation=0.5 cm (Bronk Ramsey, 2008; Bronk Ramsey and Lee, 2013). The IntCal20 (Reimer et al., 2020) ^{14}C atmospheric curve was used as the calibration set. Dates Poz-128079 and Poz-128073 were distinctly younger than the neighbouring dates. Preliminary model runs, both with the full set of dates included, and with only one problematic date excluded, showed that these two ages had very poor agreement with the model. Therefore, both were excluded from the final age–depth model. The sections of the profile in which peat properties point to potential changes in peat accumulation rate (AR$_{peat}$) were introduced to the model as boundaries (*Boundary* command). These were placed at depths: (i) 1230 cm – the base of the model, (ii) 1130 cm – transition from higher water tables towards *Sphagnum* peat, retrieved from low-resolution palynological data (data not published) and plant macrofossils (iii) 0 cm – top of the profile.

In the following sections of this article, μ (mean) values retrieved from the age-depth model were rounded to the nearest 50 years. The age was expressed as cal. BP (before present).

Table 1. AMS radiocarbon dates from the Linje 2019 profile. Poz= Poznań Radiocarbon Laboratory.

Laboratory code-number	Depth [cm b.g.l.]	^{14}C date [^{14}C BP]	Calibrated date (95.4% probability) [cal. BP]	Material dated; remarks
Poz-128072	50-51	275±30	441-357 (49.3%) 333-283 (41.9%)	*Sphagnum* stems

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Poz-127850	150-151	1365±30	1345-1322 (6.2 %) 1315-1262 (78.0 %) 1209-1177 (11.3 %)	*Sphagnum* stems
Poz-127851	250-251	2395±30	2676-2650 (4.3 %) 2613-2600 (2.5 %) 2495-2345 (88.7 %)	*Sphagnum* stems
Poz-127853	350-351	3045±30	3350-3169 (95.4 %)	*Sphagnum* stems
Poz-128077	450-451	3965±35	4523-4348 (86.3 %) 4333-4295 (9.2 %)	*Sphagnum* stems
Poz-127854	550-551	4395±35	5260-5248 (0.8 %) 5234-5222 (0.8 %) 5217-5191 (2.8 %) 5053-4857 (91 %)	*Sphagnum* stems
Poz-127855	650-651	5070±40	5916-5720 (95.4 %)	*Sphagnum* stems
Poz-128075	750-751	5970±30	6894-6730 (93.2 %) 6699-6679 (2.2 %)	*Sphagnum* stems
Poz-128176	850-851	6650±40	7583-7431 (95.4 %)	
Poz-128074	950-951	8220±50	9401-9363 (5 %) 9312-9021 (90.5 %)	*Sphagnum* stems
Poz-128073	1050-1051	8100±50	9266-9216 (3.9 %) 9209-9175 (3.2 %) 9142-8975 (76.4 %) 8956-8940 (0.9 %) 8919-8860 (5.3 %) 8833-8779 (5.8 %)	*Sphagnum* stems; outlier
Poz-128078	1150-1151	9970±50	11,690-11,670 (2.3 %) 11,641-11,252 (93.2 %)	Brown moss stems
Poz-128079	1217-1218	9250±50	10,565-10,530 (6.7 %) 10,521-10,256 (88.7 %)	Epidermis, branches; outlier
Poz-128080	1223-1224	10080±50	11,825-11,396 (94.1 %) 11,371-11,352 (1.4 %)	Brown moss stems

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3.2 Plant macrofossil analysis

Plant macrofossils were analysed in subsamples (volume: 2.5–39 cm^3) with a 5 to 10 cm resolution from depths 2.5–1187.5 cm. The analysed volume depended on the available sediment. The section 1230–1187.5 cm was not analysed to keep these data

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consistent with testate amoebae as below 1187.5 cm testate amoebae were not present in significant numbers. Samples were sieved through a 125 µm mesh and disaggregated using tap water without chemical pre-treatment. The residue on the sieve was observed under a stereomicroscope (Olympus SZX9) and a light microscope (Nikon Eclipse 90i). Quadrat and Leaf Count protocols (Barber et al., 1994; Mauquoy et al., 2010) were used to estimate the peat components and *Sphagnum* species compositions in percentages. When total *Sphagnum* was ≤5% of the sample then the *Sphagnum* species were not identified. Seeds, bud scales, catkin scales etc. were counted as absolute numbers and calculated as concentrations for 5 cm^3. During *Sphagnum* identification the branch leaves having most similarity to *S. angustifolium*, *S. balticum* and *S. fallax* were marked down as "*Sphagnum recurvum* complex" (Duffy et al., 2020). Stem leaves of all these species were found and counted separately. Other species that are difficult to identify in the fossil form include *S. divinum/medium* and *S. rubellum/fuscum,* thus they are combined in the macrofossil diagram. The presence of *S. fuscum* in *Sphagnum* section *Acutifolia*-dominated samples was confirmed with stem leaves and dark stem colour. *Sphagnum* identification followed (Laine et al., 2018) and a reference collection. Brown mosses and vascular plant remains were identified using several keys (Cappers et al., 2012; Grosse-Brauckmann, 1972; Katz et al., 1977; Mauquoy and van Geel, 2007; Tomlinson, 1985) and a reference collection. Vascular plant and bryophyte nomenclature follows GBIF Backbone Taxonomy (GBIF Secretariat, 2023).

In addition to botanical remains, the percentages of unidentified organic matter (UOM) and macrocharcoal (≥1 mm) were estimated in the samples as a part of the Quadrat method.

3.3 Testate amoebae analysis

Testate amoebae were analysed in ca. 5 cm^3 subsamples with a 5 cm resolution from depths 0–1187.5 cm. Samples were washed under a 300 µm mesh following the method described by Booth et al. (2010). Testate amoebae were analysed under a light microscope with ×200 and ×400 magnifications until a sum of 150 tests per sample was reached (Payne and Mitchell, 2009). In a few layers where the concentration of individuals was lower, testate amoebae were counted until a sum of 100 or 50 was reached; these were still suitable for performing further statistical analyses (Payne and Mitchell, 2009). To achieve the highest taxonomic resolution, species identifications were supported by several taxonomic keys and monographs (Clarke, 2003; Mazei and Tsyganov, 2006; Meisterfeld, 2000; Meisterfeld, 2001; Ogden and Hedley, 1980), and online resources (Siemensma, 2024). The results were used to reconstruct palaeohydrological conditions at the site.

3.4 Statistical analyses and data presentation

The stratigraphical diagrams were created in Tilia v. 3.0.1 (Grimm, 2004) or C2 v. 1.8.0. (Juggins, 2003) and edited in Adobe Illustrator (Adobe Inc., 2019). Subfossil bryophytes were used as a main proxy of this article, thus the changes on the peatland are based on the changes in bryophyte assemblages. *Sphagnum* leaf count data and the abundance of other mosses were extracted from the general plant macrofossil data, and the percentages were re-calculated considering the taxonomic proportions of bryophytes only. This bryophyte data was analysed in RStudio (R Core Team 2024) to create a stratigraphic zonation. The "vegdist" function from the vegan package (Oksanen et al., 2001) was used to compute a Bray-Curtis dissimilarity matrix from the bryophyte data, then hierarchical clustering was performed on the dissimilarity matrix using the constrained incremental sum of squares (CONISS) from the rioja package (Grimm, 1987; Juggins, 2009). The broken-stick method was used to determine the number of meaningful clusters (Bennett, 1996). Initially 11 clusters were identified. However, cluster 8 fell below the reference line (Fig. A1). Thus, cluster 8 was merged with cluster 7, resulting in a final solution of 10 clusters. In addition, bryophytes were grouped according to

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4 Results and interpretation

4.1 Chronology

The age-depth model (Fig. 2) recorded a model agreement (A_{model}) = 66.7 %, which is above the recommended minimum of 60 % (Bronk Ramsey, 2008). The profile spans the time period between ca. -69 cal. BP (2019 CE) and 11,710±139 (1σ error) cal. BP. The mean1σ error was ca. 65 cal. years. For the topmost 100 cm we lack the chronological control to detect short-term differences in accumulation rates. This section should thus be interpreted with caution due to this limitation as it is based on one date and it does not reflect an exponential depth-age relationship as it should with well-developed acrotelm and catotelm layers (Marcisz et al., 2015).

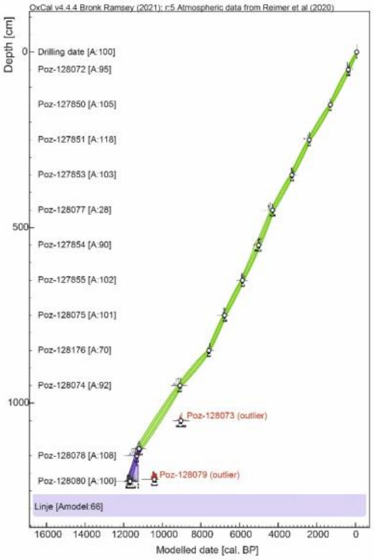

Figure 2: Bayesian age-depth model of the Linje core based on 20 radiocarbon dates (Table 1). The model was constructed using OxCal. 4.4.4 software (Bronk Ramsey, 1995; 2006).

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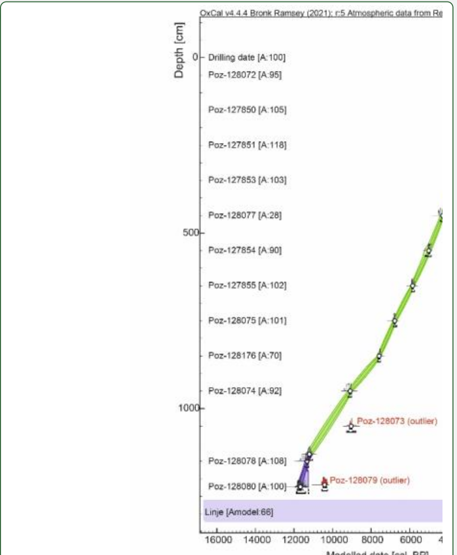

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4.2 Environmental changes

Ten zones were identified based on statistically significant changes in the bryological assemblages (Fig. 3). These zones, along with general plant macrofossil dynamics and testate amoebae assemblages (Figs. 4, 5), are discussed in detail below. Depth to water table (DWT) reconstructions are derived from testate amoebae analyses.

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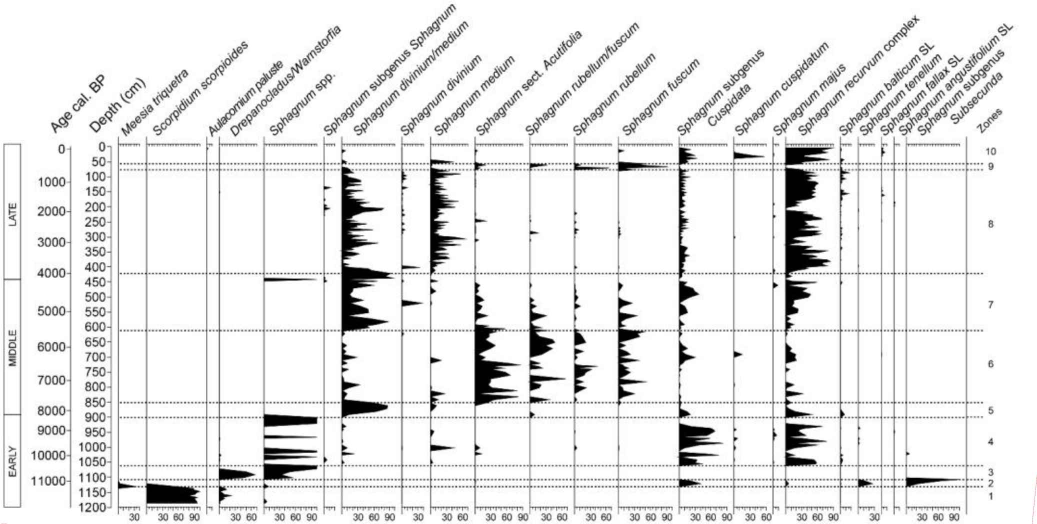

Figure 3: Bryophyte stratigraphy (%) from the Linje peatland core throughout Holocene. Percentages (black) were recalculated from the general plant macrofossil dataset based on bryophyte taxonomic proportions to establish core zonation. SL=stem leaves.

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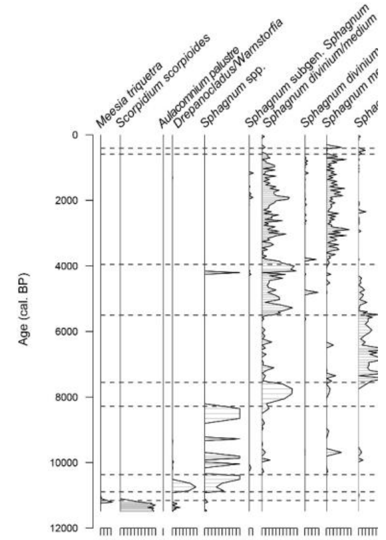

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Linje peatland macrofossil record (Fig. 4) is abundant in bryophytes, which constitute the largest proportion of peat-forming components. At the beginning of the study's timeline, moss assemblage (Fig. 3) reflected high water levels, nutrient availability, and elevated pH. After ~11,200 cal. BP, brown mosses were gradually replaced by *Sphagnum* species, coinciding with the first appearances of typical oligotrophic mire plants such as *Andromeda polifolia*, *Oxycoccus sp*., and *Drosera* spp. Around 10,350 cal. BP, a decline in pH and nutrient levels is evident as species from the *Sphagnum recurvum* complex established dominance, which persisted until ~8,200 cal. BP, when *Sphagnum divinum/medium* became the prevailing taxa. Approximately 400 years later (~7,500 cal. BP), *Sphagnum* sect. *Acutifolia* began to dominate until ~5,500 cal. BP, when the interplay between *S. divinum/medium* and *Sphagnum recurvum* complex species began. *Sphagnum* sect. *Acutifolia* experienced only a brief resurgence between ~600–450 cal. BP before being replaced by *Sphagnum* subgen. *Cuspidata* species, which have remained dominant to the present.

From the plant macrofossil record it is evident that birch (*Betula pubescens/pendula*) was already growing near Linje peatland ~11,500 cal. BP. *Pinus sylvestris* macrofossils were found in the record first ~11,200 cal. BP. Wetter periods are marked by increased abundances of *Equisetum fluviatile*, *Carex* spp. and *Scheuchzeria palustris* macrofossils, whereas drier intervals are sometimes characterized by a higher proportion of ericaceous remains.

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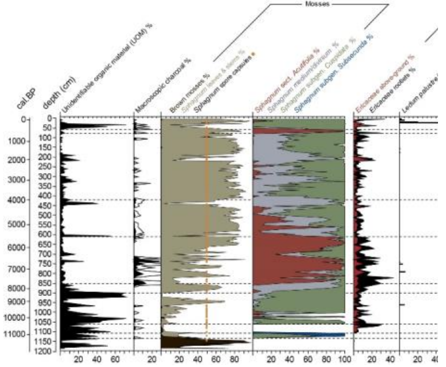

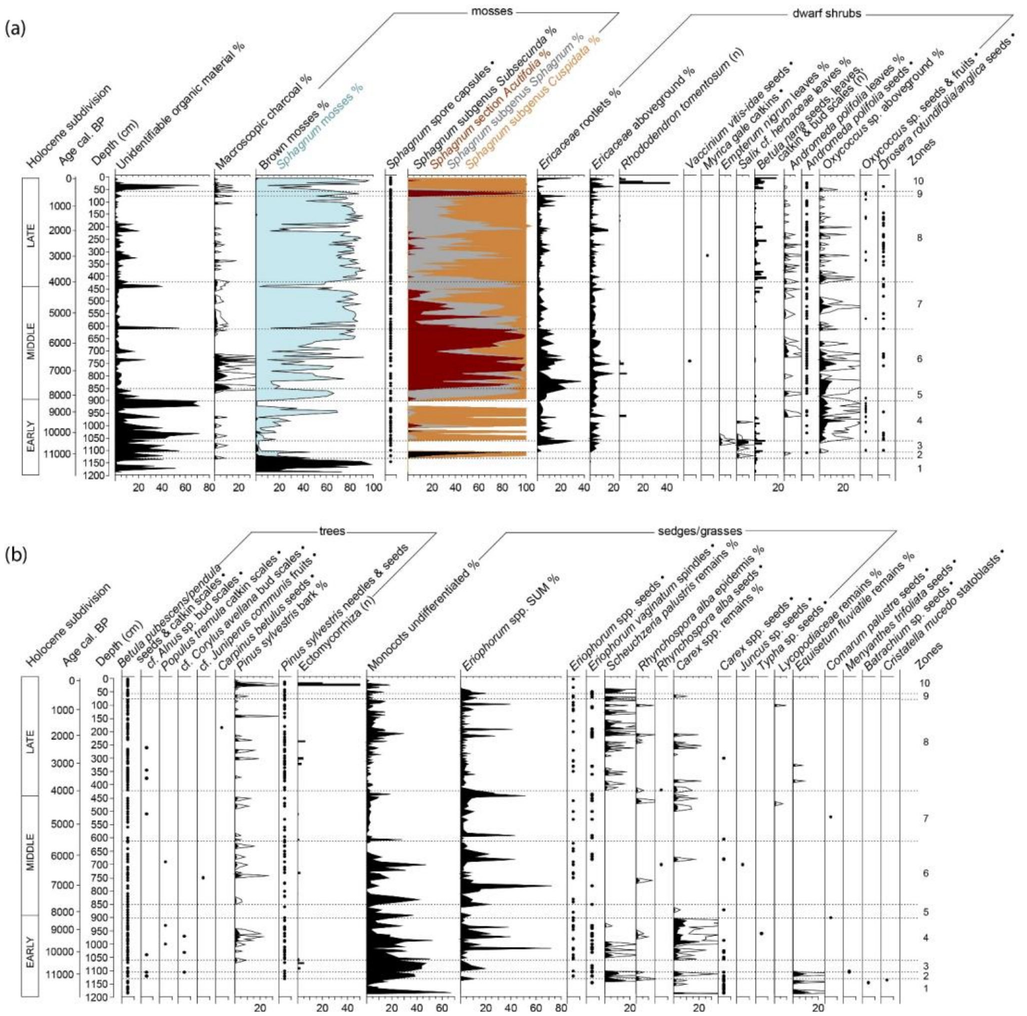

Figure 4: (a) and (b) Plant macrofossil stratigraphy from the Linje peatland core throughout Holocene. Histograms (black or coloured) represent taxon percentages with ×5 exaggeration (when needed). Abundance of countable macrofossils (n) is shown in bars, and presence is indicated by dots (•). Zonation (dashed line) follows bryophyte assemblages (see Fig. 3). (a) includes *Sphagnum* moss proportions, grouped by subtaxa and differentiated by colour.

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Testate amoeba-based water table reconstruction indicates that over the past 11,300 years, the average depth to the water table was 7.6 cm, increasing to a maximum of 15 cm during the Middle Holocene (Fig. 5). Depths exceeding 16 cm occurred only in the past ~200 years. Since the beginning of the record, the dominant testate amoebae species at the site have been *Archerella flavum* and *Hyalosphenia papilio*. After ~7,500 cal. BP declines in the abundance of *A. flavum* and *H. papilio* closely correspond with decreases in *Sphagnum* abundance. The two proxies exhibit strong general agreement in hydrological interpretation, with the exception of the last 600 years.

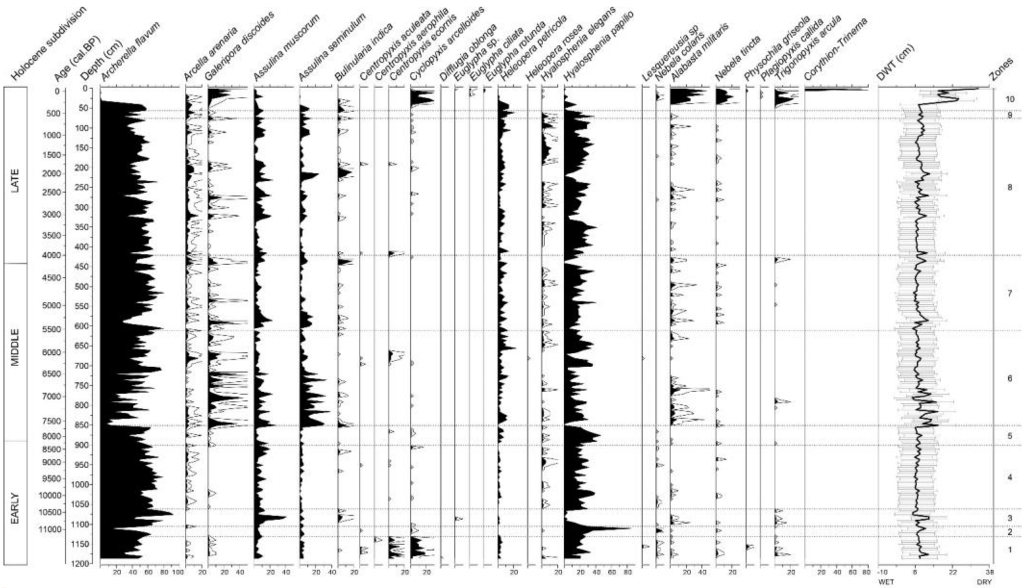

Figure 5: Testate amoebae stratigraphy (%) from the Linje peatland core throughout the Holocene. Where necessary, curves are exaggerated 5x for better visibility. The depth-to-water table (DWT, cm) curve illustrates the reconstruction derived from testate amoebae. Zonation (dashed line) follows bryophyte assemblages (see Fig. 3).

In this study, "disturbance" refers to phases of hydrological instability. At Linje, these are marked by elevated proportions of unidentified organic material (UOM), reduced test counts, and declines in dominant testate amoebae taxa (*A. flavum*, *H. papilio*), as well as reductions in *Sphagnum* abundance once the peatland became *Sphagnum*-dominated after ~9,050 cal. BP. Sudden peaks in UOM are interpreted as reflecting periods of increased peat decomposition, which are associated with peat surface drying in otherwise stable peatland systems (Loisel et al., 2017; Sim et al., 2021a). Disturbance episodes are also associated with higher abundances of testate amoebae species such as *Galeripora discoides*, *Assulina muscorum*, and *Assulina seminulum*, which are linked to either drier conditions (*Assulina* spp.) or fluctuating water tables (*G. discoides*) (Lamentowicz et al., 2008). Despite multiple disturbance episodes, major testate amoebae species turnover is absent until a shift ~200 years ago. Importantly, these disturbances were relatively short-lived, and peat accumulation resumed quickly, resulting in a stable and continuous age–depth model.

Zone 1: 11,500–11,200 cal. BP (1187.5–1130 cm) – waterlogged, rich fen

Bryophytes are dominated by *Scorpidium scorpioides* and some *Drepanocladus/Warnstorfia*-type mosses are also present. In samples dated to ~11,200 and ~11,100 cal. BP macrofossils of *Meesia triquetra* were also found. *S. scorpioides* and *M. triquetra*, considered characteristic boreal fen species (Hájková et al., 2015), are found in many Late glacial and Early Holocene sediments in northern Poland, but their present status in Central Europe is rare and endangered (Drzymulska, 2024; Hájková et al., 2015; Słowiński et al., 2015, 2017). *Betula* sect. *Albae* seeds are present from the beginning of the record, as well as *Betula nana* leaves, bud scales and seeds indicating that dwarf birch was growing on the site and tree-birches were already present in the region. Around 11,300 cal. BP, the presence of *Eriophorum vaginatum* is indicated by a spindle, although epidermis of this species was not found. *Carex* spp. remains and nutlets are found in this zone, as well as *E. fluviatile* remains. Around the end of zone 1 (~11,300 cal. BP)

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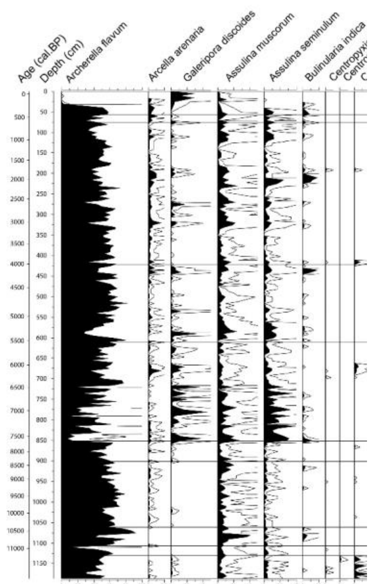

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a seed of water-crowfoot (*Batrachium sp.*) was found, followed by a statoblast of *Cristatella mucedo* (freshwater sponge) around 11,250 cal. BP which indicate inundated conditions or a shallow water habitat (Lumbreras et al., 2011; Økland and Økland, 2000). *S. palustris* remains also appear at the end of the zone, strengthening the interpretation of high water tables or the presence of a standing water pool (Tallis and Birks, 1965).

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The testate amoebae assemblage in this zone is dominated by *A. flavum* and *H. papilio*, which are associated with wetter microhabitats (Lamentowicz and Mitchell, 2005; Marcisz et al., 2014). *Centropyxis ecornis* is present throughout this zone and disappears at the end of this phase. According to a Polish training set, this species indicates wet and nutrient-rich conditions (Lamentowicz et al., 2008). Another distinctive feature of this zone is the presence of *Cyclopyxis arcelloides,* which is usually found in wet habitats in Poland (Lamentowicz and Mitchell, 2005). Both *C. ecornis* and *C. arcelloides*, as well as *Trigonopyxis arcula* that were present in this phase, incorporate mineral material in their tests which can indicate a source of mineral inputs into the peatland (Marcisz et al., 2020b). The abundance of species indicating drier and more acidic conditions such as *A. seminulum* and *A. muscorum* (Lamentowicz et al., 2008) remains under 20%. Reconstructed water table depths average at 8.3 cm.

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Zone 2: 11,200–10,900 cal. BP (1130–1105 cm) – wet, rich fen

Although not dominant, the *Sphagnum* assemblage indicates rich fen conditions with *S. cuspidatum*, *S. tenellum* and *Sphagnum* from subgenus *Subsecunda* (mainly *S. contorum*) (Gałka and Lamentowicz, 2014; Laine et al., 2018; Mauquoy and van Geel, 2007). In this zone, the first macrofossils (needles, bud scales and seeds) of *Pinus sylvestris* and a bud scale of cf. *Alnus* sp. were found, indicating their presence in the wider landscape. *E. vaginatum* epidermis and seeds were also found for the first time at the beginning of this zone. Vascular plants indicate persistently wet conditions with abundant *Carex* spp., *E. fluviatile* and *S. palustris* remains. Moreover, seeds of *Menyanthes trifoliata* were identified in samples dated to ~10,900 and ~10,850 cal. BP. In a sample dated to ~10,900 cal. BP a bud scale of cf. *Corylus avellana* was found. *Sphagnum* mosses increase in abundance between ~11,100 and ~11,000 cal. BP with ombrotrophic to weakly minerotrophic *Sphagnum tenellum* (Laine et al., 2018) and *Sphagnum* subgen. *Cuspidata*.

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The dominant testate amoebae species are still *A. flavum* and *H. papilio.* Both species increase become more numerous in this zone. *C. ecornis* and *Heleopera petricola* disappear during this phase and the abundance of *C. arcelloides* decreases. *Nebela collaris* is relatively abundant at this stage. *Assulina* species occurrence does not change significantly compared to the previous zone. Reconstructed water table depths are similar to the previous phase, pointing to wet conditions.

Zone 3: 10,900–10,400 cal. BP (1105–1060 cm) – a shift towards drier and nutrient poor conditions

Although not abundant, typical oligotrophic species such as *Oxycoccus palustris* and *Drosera rotundifolia/anglica* are found for the first time at this stage. Differentiating between the seeds of the two *Drosera* species is difficult. *D. rotundifolia* tends to indicate lower pH and exhibits a broad ecological tolerance, whereas *D. anglica* is typically associated with wetter conditions and slightly higher pH levels (Banaś et al., 2023). Nonetheless, the presence of either insectivorous species implies increasing nutrient limitation in the peatland environment (Mauquoy and van Geel, 2007). After ~10,900 cal. BP, when *Sphagnum* subgen. *Subsecunda* was relatively abundant, *Sphagnum* mosses decline. Since they occupied less than 5% of the peat components, species were not identified. A very small proportion of *Drepanocladus/Warnstorfia*-type brown moss is present. The main peat components are UOM, ericaceous rootlets and undifferentiated monocots. The shift towards drier conditions is seen in plant macrofossils since ericaceous remains appear in this stage, including arctic/boreal shrubs *Salix herbacea* and *Empetrum nigrum,* that are more abundant during the end of this phase.

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The conditions on the peatland remain wet, as the testate amoebae-inferred water table averages 7.6 cm, however slightly drier conditions occur between ~10,700 and ~10,650 cal. BP when the water table depth is around 12 cm. This is coupled with significant changes in the species composition: a reduction in the abundance of *H. papilio* is followed by a slight increase of *A. muscorum* and *Bullinularia indica*, the latter two species being associated with drier conditions (Lamentowicz et al., 2008).

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Zone 4: 10,400–8,350 cal. BP (1060–900 cm) – moderately wet phase, poor fen

The plant macrofossil record indicates wet conditions with abundant *S. palustris,* and *Carex* spp. remains (including nutlets) as well as some fragments of *Rhynchospora alba* stem. From ~10,200 cal. BP onwards *E. nigrum* does not appear in the plant macrofossil record. *S. herbacea* remains occur occasionally during this period, lastly in a sample dated to ~9,500 cal. BP. *Sphagnum* mosses start to be more present again after ~10,350 cal. BP. In the following samples, wet habitat species: *S. majus, S. cuspidatum* and especially species from the *Sphagnum recurvum* complex (stem leaves of *S. balticum* and *S. angustifolium* were present) were found. The *Sphagnum* stratigraphy is interrupted by a disturbance ~8,500–8,350 cal. BP characterized by a large proportion of UOM. At ~9700 cal. BP the presence of *Populus tremula* is indicated with a catkin scale.

The testate amoebae community shows this period as stable and wet. Compared to the previous phase, the abundance of wet indicator species, *H. papilio* and *A. flavum* increase and remain abundant until a slight drop around 8,500 cal. BP.

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Zone 5: 8,350–7,600 cal. BP (900–850 cm) – a shift to drier conditions, poor fen

After a disturbance in the previous phase, this phase is characterized by a shift in *Sphagnum* composition towards drier conditions. Previously dominating wet-habitat *Sphagnum* subgen. *Cuspidata* is replaced by *S. divinum/medium*, which might suggest development of a drier microform (Blackford, 2000; Hassel et al., 2018).

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The testate amoebae community composition does not show significant changes during this time. The abundance of *H. petricola* and *H. papilio* increases slightly, while *A. muscorum* abundance values drop.

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Zone 6: 7,600-5,550 cal. BP (850–610 cm) – dry phase, poor fen

Around 7,600 cal. BP, a notable decrease in the general abundance of *Sphagnum* is observed, coinciding with the first appearance of *Sphagnum* sect. *Acutifolia* species, primarily *S. rubellum* and *S. fuscum*, in the samples. By approximately 7,500 cal. BP, *Sphagnum* sect. *Acutifolia* begins to dominate over *S. divinum/medium.* Both *S. rubellum* and *S. fuscum* typically inhabit hummocks, which are more drought-resistant than hollows (Mauquoy and van Geel, 2007; Nungesser, 2003).

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During this period, the samples are notably rich in macroscopic charcoal (≥ 1 mm), which constitutes 10–13.5% of the peat at the onset of this zone (7,600–7,500 cal. BP). Similar levels of macrocharcoal abundance are detected at approximately 7,200 and 6,800 cal. BP. By around 6,650 cal. BP, macro-charcoal pieces account for more than a quarter of the sample (27.6%), which is accompanied by a decrease in *Sphagnum* (9.7%) and an increase in the percentage of UOM (25.8%). Macrocharcoal-rich samples, with minor interruptions, persist until about 6,500 cal. BP, correlating with an increase in aboveground ericaceous remains and the presence of drier habitat *Sphagnum* species. Given the limited transport distance of macrocharcoal (Clark, 1988; Peters and Higuera, 2007; Pisaric, 2002; Tinner et al., 2006), these phases likely reflect local fire activity.

The second half of this zone, beginning around 6,400 cal. BP reveals a transition toward moderately wet conditions, evidenced by the increased occurrence of *Sphagnum* subgen. *Cuspidata* and remains (including seeds) of *R. alba* and *Carex* spp. These changes indicate increased peatland surface wetness between 6,300 and 6,150 cal. BP. *B. nana* remains were not present in the entire zone, possibly because the drier microform conditions were not optimal for preserving the remains.

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Testate amoeba-based water table reconstructions indicate that the water table was significantly lower at the start of this period with an average of 10 cm between 7,600 and 6,800 cal. BP. The abundance of dominating species *A. flavum* and *H. papilio* declines sharply around 7,600 cal. BP but quickly recovers to previous high levels. This drop and generally low counts of testate amoebae may be linked to a local fire event, as the sample was also rich in macro-charcoal. A similarly low count of testate amoebae is observed in a sample dated to ~7,050 cal. BP, which is low in *Sphagnum* and particularly rich in *E. vaginatum* remains. In the initial phase, *Assulina* spp. and *A. militaris* are abundant, while the highly fluctuating abundance of *G. discoides* is characteristic of the entire zone. Lamentowicz et al. (2008) note that this species can indicate fluctuating water tables, sometimes linked to disturbance. The DWT reconstruction shows a transition to wetter and more stable conditions starting from ca 6,800 cal. BP.

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Zone 7: 5,550-4,000 cal. BP (610–420 cm) – a shift to wetter conditions, poor fen

This phase is wetter than the previous one, as indicated by a more heterogeneous *Sphagnum* composition: *S. divinum/medium* and the *S. recurvum* complex occur in large proportions, while *Sphagnum* sect. *Acutifolia* species are still present at the beginning of the phase but gradually decline thereafter. A peak of *Sphagnum* subgen. *Cuspidata* occurred around 4,600 cal. BP. This is followed by the occurrence of *Carex* spp. and *R. alba* in the plant macrofossil record, indicating that the second half of the phase is wetter. *B. nana*, which was absent from the record for approximately 1000 years, is present again from ~5,450 cal. BP onwards. The UOM that mainly remained less than 5% of the sample since ~6,250 cal. BP, reaches 55% around 5,500 cal. BP and 36-40% around 4,200–4,150 cal. BP. In these samples, *Sphagnum* abundance drops. The sample dated to ~4,200 cal. BP also has a very high count (>100) of *E. vaginatum* spindles and a high percentage of *E. vaginatum* roots. The following younger samples also contain aboveground epidermis of *E. vaginatum*, which could suggest a period of hydrological instability (Barber et al., 2004; Gałka et al., 2017; Łuców et al., 2022).

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The testate amoebae species composition is similar to the previous zone. Both disturbance events are also shown in the testate amoebae assemblage – test count is low around ~5500 and ~4200–4100 cal. BP. During the ~5500 cal. BP disturbance the abundance of *H. papilio* decreases abruptly, while the abundances of *A. flavum* decrease slightly resulting in a DWT of 5 cm. During the disturbance ~4210–4110 cal. BP, abundances of both species decrease abruptly and recover quickly acting similarly to *Sphagnum* mosses. DWT remains 7.8 cm during 4200 cal. BP, but averages to 10 cm by 4100 cal. BP.

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Zone 8: 4,000-600 cal. BP (420–75 cm) – wet phase, poor fen

Sphagnum mosses indicate wet conditions with a general dominance of *Sphagnum* subgen. *Cuspidata*. Numerous *S. balticum* stem leaves were found, although *S. fallax* and *S. angustifolium* stem leaves were also present. *S. divinum/medium* is also present throughout this zone, with a peak abundance around 3,050 and 1,950–1,900 cal. BP. *Sphagnum* sect. *Acutifolia* remains between 0–23% throughout this phase, being the highest around 2,350 and 2,700 cal. BP. This zone shows a strong presence of *S. palustris* and the occasional presence of *Carex* spp., *R. alba* and *E. fluviatile* – all plants that grow in wet conditions. These vascular plants show especially wet conditions around 3,750–3,650, 2,500–2,300 and 1,950 cal. BP. The *Sphagnum* percentage drops to 12% around ~2,000 cal. BP and remains low until ~1,900 cal. BP. In a sample dated to ~1,700 cal. BP a *Carpinus betulus* seed was present.

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The testate amoebae record indicates that this period was moderately wet. The abundance of *Hyalosphenia elegans* increases in the samples during the whole zone, which confirms wet conditions (Lamentowicz and Mitchell, 2005). Disturbance on the peatland occurs at ~3,050 cal. BP indicated by decrease in abundance of *A. flavum* and *H. papilio*. Around 2,000 cal. BP, drier conditions are inferred from an increase in *B. indica* and *A. seminulum* abundances, accompanied by a decline in *H. papilio*. This shift

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corresponds to a reconstructed depth to water table drop to approximately 12 cm. This period also coincides with low *Sphagnum* percentages and an increase in decomposed organic matter, collectively indicating increased hydrological instability.

Zone 9: 600-450 cal. BP (75–55 cm) – dry phase, poor fen

This ~200-year-period is characterized by a sudden peak in *Sphagnum* sect. *Acutifolia* (mostly *S. fuscum*) which replaces moderately wet habitat species from the previous phase. The testate amoebae and vascular plant record do not show any changes compared to the previous phase.

Zone 10: 450 cal. BP- 2019 AD (55–0 cm) – water table fluctuations

The Sphagnum composition switches from *S. fuscum* (sect. *Acutifolia*) to wet habitat *Sphagnu*m species – *S. cuspidatum* and *Sphagnum recurvum* complex species (*S. balticum* and later *S. fallax* stem leaves were found). *S. cuspidatum*, which can grow in submerged conditions, occurs most abundantly around 250–150 cal. BP – falling at the end of the 18th and first half of the 19th century. This very wet phase is preceded by a high peak (25–70%) of UOM around 300–250 cal. BP (1740-1650 CE), suggesting a disturbance around the second half of the 17th century and the first half of the 18th century. *S. fallax*, the dominant moss on the peatland today, has a confirmed continuous presence (stem leaves) since ~190 cal. BP (1750 CE) however, the exact proportion of this species among the identified *recurvum* complex species is uncertain. *Rhododendron tomentosum* macroremains (including seeds) are especially abundant in the samples dated to the early 19th century (depths 17.5 and 22.5 cm).

The phase is overall characterized by very rapid shifts in the testate amoeba-based water table fluctuations, although *Sphagnum* mosses show a stable wet period. Since the beginning of the phase, the abundance of *H. papilio* and *A. flavum* drops. In the samples with a high decomposition dated to ~300–400 cal. BP (1650–1570 CE) the count of tests is low. Around 200 cal. BP (1740 CE) rapid fluctuations on the drier side begin. *Nebela tincta*, *Alabasta militaris* and *G. discoides* are abundant, referring to fluctuating water tables with dry periods (Lamentowicz et al., 2008a; Lamentowicz and Mitchell, 2005; Marcisz et al., 2015). *Trigonopyxis arcula* which appears abundantly in this zone is considered a drought-resistant species (Charman et al., 2007; Turner et al., 2014). The topmost analyzed sample (1.25 cm) is dominated by *Corythion-Trinema* type, which does not occur in deeper layers and results in a DWT of 33.3 cm. Other species that occur only in the uppermost peat samples include *Aulacomnium palustre* and *Euglypha* species (Figures Z, TA). The average DWT is 17.5 cm in this zone with a minimum of 7 and a maximum of 33.3 cm.

Multivariate analysis

NMDS ordination results (stress value: 0.1891065) (Fig. 6) illustrate four stages in Linje peatland development: I) waterlogged rich fen (zones 1–2), II) transitional phase from rich fen to poor fen (zones 3–4) III) natural *Sphagnum*-dominated mire with various microforms (zones 5–9) and IV) disturbed peat layer (zone 10).

Species clustering on the positive side of NMDS1 and the negative end of NMDS2 (zones 1–2), represent the earliest stages of Linje peatland development, reflecting taxa preferring varying degrees of minerotrophic conditions (Gałka et al., 2013b; Hedenäs, 2003; Kalvaitienė and Jukonienė, 2025; Laine et al., 2018; Lamentowicz et al., 2007; Marcisz et al., 2020a; Stastney and Black, 2020). Among testate amoebae, these include *C. ecornis, Centropyxis aculeata*, *Centropyxis aerophile*, *Difflugia oblonga*, *Lesquereusia* sp. and *C. arcelloides*. Characteristic mosses are *S. scorpioides*, *M. triquetra*, *Drepanocladus/Warnstorfia*, *Sphagnum* subgenus *Subsecunda* and *S. tenellum*.

The following transitional period (zones 3–4) lacks clearly distinct species but overlaps with both the rich fen and *Sphagnum*-dominated assemblages, reflecting gradual ecological change.

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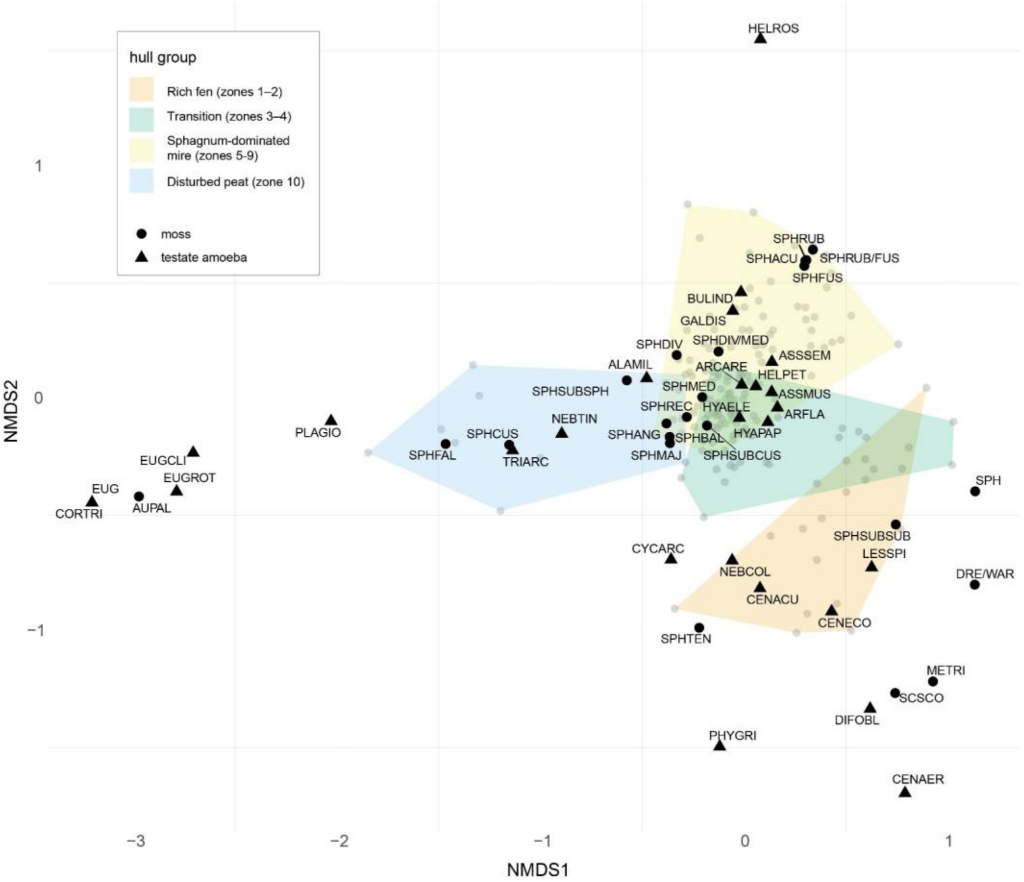
The central cluster (around 0,0) comprises zones 5–9 and most species encountered in the Linje core. It corresponds to the resilient *Sphagnum*-dominated mire. Species here include the most common testate amoebae such as *H. papilio*, *A. flavum* and *Assulina* spp. and mosses *S. divinium/medium* and *Sphagnum recurvum* complex among others. Species characteristic of hummock microforms, such as *Sphagnum* mosses in the *Acutifolia* section, together with disturbance indicators (*G. discoides*) and hummock specialists (*Bullinularia indica*) (Lamentowicz et al., 2008) occupy positions slightly toward the positive side of NMDS2.

Species found in the uppermost disturbed peat layer (zone 10) occupy the negative side of both axes. The testate amoebae in this side of the ordination are indicative of disturbances and suggest lower water tables. Mosses in this cluster include *S. fallax*, often linked to increased nutrient availability (Gąbka and Lamentowicz, 2008; Gałka and Lamentowicz, 2014; Limpens et al., 2003), and *S. cuspidatum*, a species of waterlogged conditions (De Vleeschouwer et al., 2012; Gałka et al., 2017). This contradiction may reflect a seasonal disagreement between the proxies, caused by low-resolution sampling, that does not capture rapid changes. *A. palustre* and testate amoebae of *Corythion-Trinema* type and *Euglypha* species that occur only in the uppermost peat samples, form a separate group on the ordination plot.



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Deleted: suggest that the DWT gradient weakly influences the species composition of testate amoeba and bryophytes (r^2= 0.04888747049). The DWT arrow vector points negatively along the first axis and the relation is significant (p= 0.015). Macrocharcoal percentage is moderately correlated with species composition (r^2= 0.16482738165) with its arrow vector aligned along the second NMDS axis (p= 0.001).

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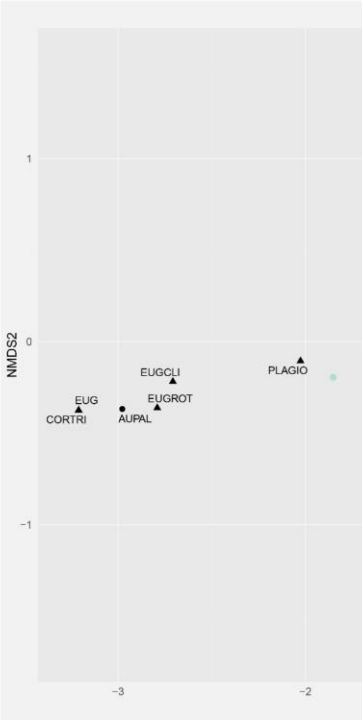

Figure 6: Non-Metric Multidimensional Scaling (NMDS) ordination plot visualizing relationships between testate amoebae (black triangles) and bryophyte (black circles) species composition. Manually defined colored hulls represent different stages (samples in gray dots) in Linje mire development. Stress value: 0.1891065. Taxa abbreviations, Mosses: METRI = *Meesia triquetra*, SCSCO = *Scorpidium scorpioides*, AUPAL= *Aulacomnium palustre*, DRE/WAR= *Drepanocladus/Warnstorfia*-type, SPH= *Sphagnum* spp. (unspecified), SPHSUBSPH= *Sphagnum subgenus Sphagnum*, SPHDIV/MED = *Sphagnum divinium/medium*, SPHDIV= *Sphagnum divinum*, SPHMED= *Sphagnum medium*, SPHSECTACU = *Sphagnum* section *Acutifolia*, SPHRUB/FUS= *Sphagnum rubellum/fuscum*, SPHRUB= *Sphagnum rubellum*, SPHFUS =*Sphagnum fuscum*, SPHSUBCUS= *Sphagnum* subgenus *Cuspidata*, SPHCUS = *Sphagnum cuspidatum*, SPHMAJ= *Sphagnum majus*, SPHREC= *Sphagnum recurvum* complex, SPHBAL= Sphagnum balticum (stem leaves), SPHTEN= Sphagnum tenellum, SPHFAL= *Sphagnum fallax* (stem leaves), SPHANG= *Sphagnum angustifolium* (stem leaves), SPHSUBSUB= *Sphagnum* subgenus *Subsecunda*. Testate amoebae: ARFLA= *Archerella flavum*, ARCARE= *Arcella arenaria*, GALDIS= *Galeripora discoides*, ASSMUS= *Assulina muscorum*, ASSSEM= *Assulina seminulum*, BULIND= Bulinularia indica, CENACU= Centropyxis aculeata, CENAER= *Centropyxis aerophile*, CENECO= *Centropyxis ecornis*, CYCARC= *Cyclopyxis arcelloides*, DIFOBL= *Difflugia oblonga*, EUG= *Euglypha* sp., EUGCLI= *Euglypha ciliata*, EUGROT= *Euglypha rotunda*, HELPET= *Heleopera petricola*, HELROS= *Heleopera rosea*, HYAELE= *Hyalosphenia elegans*, HYAPAP= *Hyalosphenia papilio*, LESSPI= *Lesquereusia* sp., NEBCOL= *Nebela colaris*, ALAMIL= *Alabasta militaris*, NEBTIN= *Nebela tincta*, PHYGRI= *Physochila griseola*, PLAGIO= *Plagiopyxis callida*, TRIARC= *Trigonopyxis arcula*, CORTRI= *Corythion-Trinema*

5 Discussion

Major shifts in the bryological assemblage correspond with established Holocene subdivisions, indicating wetter conditions during the Early and Late Holocene and drier conditions in the Middle Holocene (Wanner et al., 2011, 2015) (Figs. 3–5). Thus, the changes observed in these zones and their relationship to climatic and autogenic processes are analysed within the framework of the Early, Middle, and Late Holocene. Disturbance phases and shifts in bryological assemblages are considered in relation to the periods of Rapid Climate Change (RCC) (Mayewski et al., 2004) (Fig. 7). However, because RCC intervals span several centuries to millennia and are characterized by fluctuating rather than uniform climate conditions, they cannot be directly equated with the hydrological changes and disturbances observed at Linje. Thus, RCC periods (and other global climatic events) are used here as a broader climatic framework within which to interpret the proxy-related changes at Linje.

5.1 Early Holocene (Zones 1–5)

Peat formation in Linje mire began in the Early Holocene resulting from the short-term terrestrialization of a depression left by a dead ice block (Kloss, 2005; Kloss and Żurek, 2005). As the accumulation of peat started with brown mosses, there is possibility that they initially grew on deposits overlying the buried ice block (Słowiński et al., 2015). Considering, that some dead ice blocks in northern Poland persisted until the Early Holocene if meltwater drainage was sufficient (Błaszkiewicz et al., 2015; Słowiński, 2010) it is also possible that Linje depression was able to actively accumulate peat since the beginning of Holocene. In Linje, the sediments beneath the peat deposits consist of sand and gravel (Kloss and Żurek, 2005), suggesting that conditions for delayed melting may have been present. The dead ice should be marked by the presence of basal peat overlain by lacustrine sediments. These were not detected in the Linje profile. The layer of brown mosses suggests the development of a wet rich fen (with phases of short-term standing water) on the bottom of the site (Figs. 3–5). Therefore, this is not a typical situation as seen in other kettle-hole peatlands in Pomerania. Most kettle hole peatlands, in e.g. Tuchola Forest, possess brown moss peat under gyttja (Kowalewski, 2014; Lamentowicz, 2005). To sum up there are many pathways of so-called kettle-hole peatlands development (Brande et al., 1990; Succow and Joonsten, 2012; Timmermann, 1998, 2003, 2010; Timmermann and Succow, 2001) and there is a high uncertainty that dead ice played a role in the Linje basin formation. According to Żurek (2005) the dead ice block at Linje mire melted during the Allerød, as evidenced by basal brown moss peat dating. However, AMS 14C dates from our study (Fig 2., Table 1), suggest that the onset of peat accumulation during the Allerød is questionable, as these previous dates (Kloss, 2005; Kloss and Żurek, 2005) were carried out from bulk peat so they might have been affected by reservoir effect i.e. revealing much older age, as brown mosses such as *Drepanocladus* sp. may also absorb old HCO_3^- anions (Madeja and Latowski, 2008).

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Species inhabiting the hummock microform are positioned on the positive side of NMDS2 and show the strongest association with macroscopic charcoal abundance. Hummock-forming *Sphagnum* sect. *Acutifolia* species grow closely together, which means they retain moisture better than hollow species (Nungesser, 2003; Väliranta et al., 2012). Moreover, it is observed that hummocks are often left unburnt in peatland fires (Prat-Guitart et al., 2016), explaining the macrocharcoal-hummock species relationship on the NMDS ordination (Fig. 6). ¶

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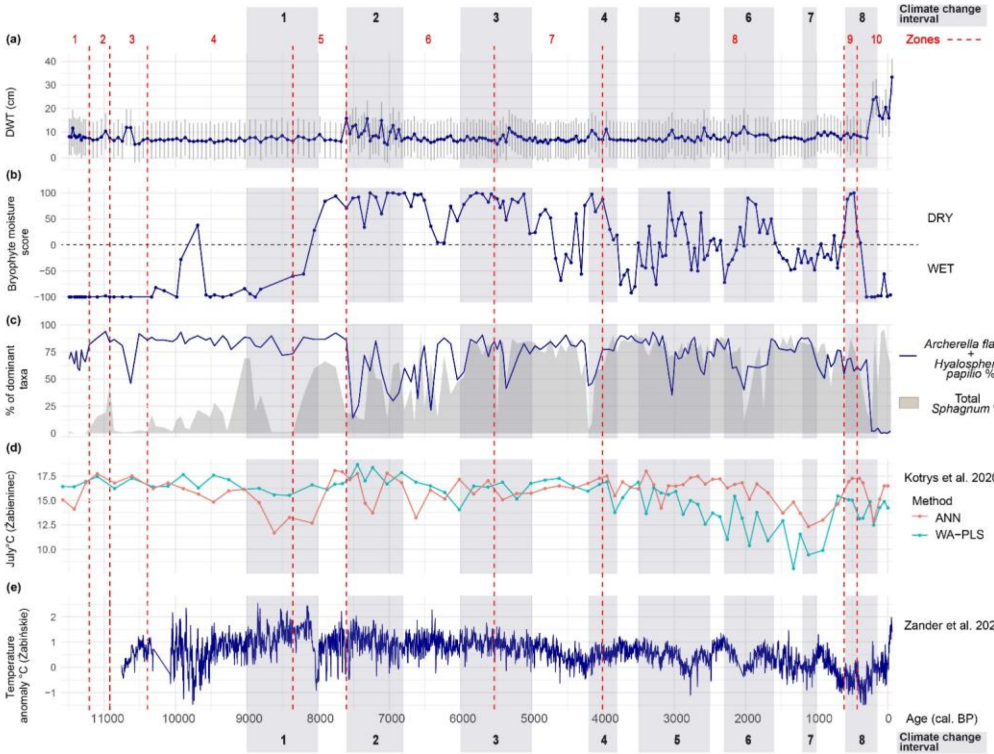

Figure 7: Diagram showing local wetness changes and disturbance phases (climatic and anthropogenic) in Linje, and temperature variability in Poland during the Holocene (a) Testate-amoebae based depth to water table reconstruction (b) Bryophyte moisture indices (see method in chapter 3.4; Table A1) (c) Disturbances indicated by declines in *Sphagnum* or in dominant wet-indicator testate amoebae species (sum of *A. flavum* and *H. papilio*) (d) Reconstructed mean July air temperature (°C) from lake Żabieniec (central Poland) based on the chironomid training set using weighted averaging-partial least squares regression (WA-PLS) or an artificial neural network (ANN) transfer function (Kotrys et al., 2020) (e) Holocene spring-summer temperature anomaly reconstruction from lake Żabińskie (northern Poland) based on Ca/Ti ratios in varves (Zander et al. 2024). Grey bars represent important climate change intervals recorded in Linje, RCC= period of rapid climate change (Mayewski et al., 2004): 1. RCC 9000-8000 cal. BP, 2. Holocene Thermal Maximum in Linje (7600-6800 cal. BP) 3. RCC 6000-5000 cal. BP, 4. RCC 4200–3800 cal. BP, 5. RCC 3500–2500 cal. BP, 6. Roman Warm Period (2300-1600 cal. BP) (Gauld et al., 2024), 7. RCC 1200–1000 cal. BP (not recorded in Linje) 8. RCC 600–150 cal. BP. Red dashed lines mark the bryophyte zones.

The transition from rich fen to poor fen in the centre of the peatland began around 10,900 cal. BP, as *E. vaginatum* began to form a suitable base for *Sphagnum* mosses to establish (Hughes and Dumayne-Peaty, 2002). A prerequisite for this process was the lowering/fluctuations of the water table during zone 3. The vegetation between ~10,900 and 8,350 cal. BP is already suggesting a decrease in nutrients and increase in acidity. Peatland water table fluctuations in these early successional stages can most likely be attributed to autogenic peatland processes (Hughes et al., 2000).

The period between 9,000–8,000 cal. BP is recognized as one of the periods of RCC and it is expressed as a cooling in the Northen Hemisphere (Mayewski et al., 2004). During this period pioneering oligotrophic *Sphagnum* communities became established in Linje, making the record more sensitive to climate fluctuations (Hughes and Barber, 2003). Between ~8,500–8,350 cal. BP samples

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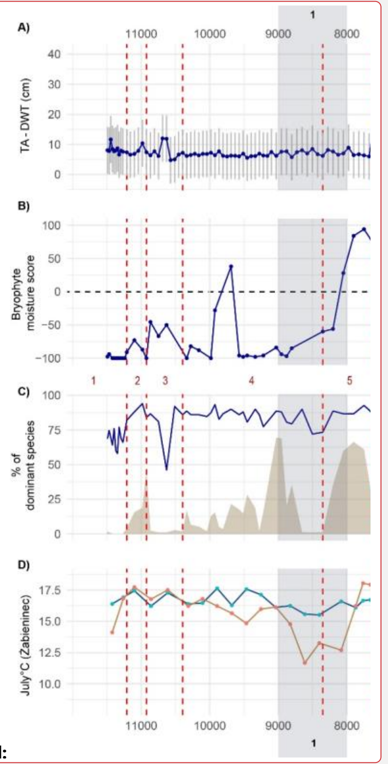

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Deleted: 5.1 Early Holocene (Zones 1–5)¶
Peat formation in Linje mire began in the Early Holocene resulting from the short-term terrestrialization of a depression left by a dead ice block (Kloss, 2005; Kloss and Żurek, 2005). As the accumulation of peat started with brown mosses, there is possibility that they initially grew on deposits overlying the buried ice block (Słowiński et al., 2015). Considering, that some dead ice blocks in northern Poland persisted until the Early Holocene if meltwater drainage was sufficient (Błaszkiewicz et al., 2015;

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from Linje show high decomposition, with a large proportion of UOM and an absence of *Sphagnum*. This suggests water table lowering, which aerated the acrotelm and accelerated decomposition. Concurrently, testate amoebae indicative of stable wet conditions show a decrease in abundance (Fig. 7c). This disturbance may be linked to the Early Holocene Thermal Maximum (Väliranta et al., 2015), that Zander et al. (2024) have described as a period of maximum summer warmth in NE Poland between 8500 and 8100 cal. BP (Fig. 7e). However, chironomid-based summer temperature reconstructions from Central Poland (170 km southeast of Linje) suggest slight cooling during this period (Kotrys et al., 2020) (Fig. 7d). Linje record does not resolve this apparent contradiction, owing to poor sample preservation during this period.

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When *Sphagnum* recolonized after the disturbance (~8,200 cal. BP), the species composition in Linje shifted from wetter microform species to those indicative of slightly drier conditions. This timing aligns with the well-documented 8.2 ka event, with strong evidence from multiple independent proxies across the Northern Hemisphere, including pollen-based reconstructions (Seppä et al., 2007; Veski et al., 2004), stable isotopes and geochemical analyses from lake sediments, including varves (Hammarlund, 2003; Filoc et al., 2017; Zander et al., 2024), peat-based archives using testate amoebae and plant macrofossils (Gałka et al., 2014; Fletcher et al., 2024a), and stable peat isotopes (Daley et al., 2016). The hydrological response at the latitude of Linje and in Northern Europe is often associated with a drier climate during the 8.2 ka event (Magny et al., 2003, 2007), agreeing with the Linje record. At the same time the multi-proxy paleorecord of lake Suminko (NE Poland) shows a major lake-level rise between 8,300–8,100 cal. BP (Pędziszewska et al., 2015). Overall, the period between 9,000 and 8,000 cal. BP seems to be a time of hydrological instability in Linje peatland but the exact interpretation in relation to temperature, humidity or specific climate events remains uncertain because of the high degree of peat decomposition.

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5.2 Middle Holocene (Zones 6–7)

The Holocene Thermal Maximum (HTM) was a period of elevated temperatures in the Northern Hemisphere, with noticeable effects in Northern Europe, including high-altitude tree migration, glacier retreat, and increased evapotranspiration (Davis et al., 2003 and references therein; Fletcher et al., 2024b; Kaufman et al., 2020; Wanner et al., 2015). Temperature reconstructions from Lake Żabińskie indicate the HTM in Poland began and peaked around 8,500 cal. BP, with stable warm conditions lasting until 4,700 cal. BP (Zander et al., 2024). However, in Linje, bryophyte and testate amoebae records indicate the driest conditions between ~7,600 and 6,800 cal. BP (Figs. 3–5, 7AB). Around 7,600 cal. BP, high macrocharcoal percentages suggest increased local fire activity, while dominant testate amoebae and *Sphagnum* mosses experienced a simultaneous dramatic decline between 7,600 and 7,350 cal. BP (Figs. 4, 7C).

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Pollen records from northern Finland also indicate the warmest summer temperatures and lowest precipitation between 7.900 and 5,700 cal. BP (Seppä and Birks, 2001). Similarly, evidence of increased dryness appears in reduced peat formation rates in southern Finland (Korhola, 1995) and lowered water tables in southern Sweden around 7,500–7,300 cal. BP (Digerfeldt, 1988). Plant macrofossil and pollen records from a Polish lake (~320 km northeast of Linje) suggest a corresponding temperature peak around ~7,750 cal. BP (Gałka et al., 2014). Chironomid-based summer temperature reconstructions from Lake Zabieniec further confirm a temperature peak between either ~7760–7450 or ~7,450–7,230 cal. BP, depending on the method used (Kotrys et al., 2020), aligning with Linje's testate amoebae and bryophyte records (Fig. 7d).

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The onset of drier conditions in Linje aligns with several paleoclimate records that indicate Holocene temperature peaks following the 8.2 ka cooling event (Fletcher et al., 2024b; Wanner et al., 2015). However, this dry phase does not correspond with multiple regional climate reconstructions. For example, the period 7,600–7,250 cal. BP has been identified as a cold phase based on pollen and aquatic invertebrate data from lakes in northeastern Poland (Fiłoc et al., 2017). The time interval between ca 8,000–6,800 cal. BP is described to be favourable for peat initiation in Walton moss in England (Hughes et al., 2000) and in southern Finland (Korhola, 1995), indicating increased effective precipitation. These inconsistencies highlight how atmospheric and oceanic circulation shifts during this period caused regional climate anomalies and variations in the timing of the HTM (Fletcher et al., 2024b). Cartapanis et al. (2022), further note that the Northern Hemisphere HTM, as inferred from terrestrial proxies, lasted approximately 4000 years (8–4 ka), making precise synchronization across regions difficult. Additionally, it cannot be ruled out that the dry shift observed in Linje reflects a localized autogenic succession.

Drier conditions persisted in Linje until ~5,500 cal. BP, when a sudden peak in UOM occurs, followed by a gradual wet shift indicated by the bryophytes (Figs. 3–4, 7BC). This coincides with “Mid-Holocene Cooling”, characterized by glacier advances and North-Atlantic ice-rafting events in many regions between 6,000–5,000 cal. BP (Fletcher et al., 2024b; Kobashi et al., 2017; Mayewski et al., 2004; Wanner et al., 2015). A strong cooling signal has been recorded in varved lake sediments in eastern Poland around 5,500–5,200 cal. BP (Pędziszewska et al., 2015). Lake Gościąż (central Poland) also shows a higher water table between 6,000 and 5,200 cal. BP (Pazdur et al., 1995). Similarly, in Gązwa bog, a period of increased humidity begins around 5,750 cal. BP (Gałka and Lamentowicz, 2014). Multiple paleorecords across Europe also indicate a shift to wetter conditions during this time (see table 4 in Hughes et al., 2000). Additionally, a wet shift (ca 5,800 to 4,800 cal. BP) has been recognised from subfossil *Sphagnum* lipid biomarkers in Ireland (Jordan et al., 2017). However, not all records show a uniform pattern of increased moisture. In contrast, Stążki peatland experienced a period of hydrological instability and drier conditions ~5,400 cal. BP (Gałka et al., 2013) and around 5,600 cal. BP, lake-level lowering is observed in lake Linówek (northeastern Poland) (Gałka et al., 2014).

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5.3 Late Holocene (Zones 8–10)

Between ~4,200 and 4,150 cal. BP, Linje experienced a brief disturbance marked by hydrological instability (Fig. 7a–c). This event likely corresponds to the 4.2 ka climatic event, which is often underrepresented in peat (Roland et al., 2014) but displays broad temporal variability in other paleo-proxies (Geirsdóttir et al., 2019; McKay et al., 2024). The 4.2 ka event is generally expressed as cooling or drought in the Northern Hemisphere (Yan and Liu, 2019). Hydrological instability or drought has also been recorded in other Polish peatlands coinciding with the 4.2 ka event (Gałka et al., 2013; Lamentowicz et al., 2019a). A lake water decrease that resulted in a terrestrialization was also recorded ~4,150 cal. BP in Rąbień mire (Central Poland) (Słowiński et al., 2016).

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Between ~3,500 and 2,500 cal. BP *Sphagnum* and testate amoebae assemblages indicate a period of rapid hydrological fluctuations in Linje, agreeing with a RCC interval identified by Mayewski et al. (2004). Following this disturbance of the 4.2 ka event, the *Sphagnum* composition in Linje shifted to low-lawn and hollow species. Wetter conditions prevailed until ~3,250 cal. BP, followed by a drier phase ~3,050 cal. BP, when *A. flavum* and *H. papilio* abundance drops drastically (Fig. 7c). Moisture levels increased again towards the end of this period but remained variable. These fluctuations likely reflect the complex climatic dynamics between the Bronze Age Cold Epoch, the Bronze Age Optimum (characterized by drought and disturbance around 3,050 cal. BP), and the Iron Age Cold Epoch, or the 2.8 ka event (Gauld et al., 2024; Geirsdóttir et al., 2019; Hammarlund, 2003; Kobashi et al., 2017). The latter is a widely documented wet shift in Europe (Barber et al., 2004; Mauquoy et al., 2008; Swindles et al., 2020), including in Polish peat archives: in Kusowskie Bagno ~2,700 cal. BP (Lamentowicz et al., 2015) and in Głęboczek ~2,800–2,600 cal. BP (Lamentowicz et al., 2019a). However, this pattern contrasts with the findings of Słowiński et al. (2016), who suggest that the 2.8 ka event in Europe followed a wet-to-dry gradient from west to east, with some Polish sites experiencing drier conditions. The hydrological response in Linje follows the pattern observed in Western Europe.

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Another notable disturbance appears around 2,000 cal. BP in plant and testate amoebae records (Fig. 7c), coinciding with the Roman Warm Period (Gauld et al., 2024), which is reflected in two Northern Ireland peatlands as drought episodes over an extended interval (Swindles et al., 2010). Similarly, lake sediment records from Northern Europe suggest an increase in dry conditions around 2,000 cal. BP (Seppä et al., 2009). Pollen records shows that human impact in the vicinity of Linje during ~2,000 cal. BP was low (Marcisz et al., 2015). However, human impact to the forest surrounding Linje is clearly visible in the pollen record between ~3,000 and ~2,500 cal. BP (Szambelan et al., 2025 accepted), thus it is difficult to disentangle whether the observed disturbance is climate-driven or caused by human activity.

The period between 1,200–1,000 cal. BP is marked as a global RCC interval (Mayewski et al., 2004). Marcisz et al. (2015) have recorded a strong wet shift coinciding with this period, however in this work conditions are wet according to all proxies, but no major shifts or events are visible (Fig. 7a–c).

A relatively brief (around 200 years) dry period occurred in Linje between ~600–450 cal. BP characterised by changes in the *Sphagnum* composition in this section of the record. This shift can be associated with the climate fluctuations of the Little Ice Age (LIA) (Gauld et al., 2024; Marcisz et al., 2015, 2020a; Mauquoy et al., 2002). From a nearby coring location in Linje, a rapid shift to dry conditions (water table drop from 0 to 25 cm) in the testate amoebae record was found especially around 550 cal. BP (1390–1425 CE) (Marcisz et al., 2015), agreeing with the dry shift found in mosses in this work. Contradictory wet indicators, such as green algae, were also reported by Marcisz et al. (2015) and attributed to reduced evapotranspiration due to decreased forest cover and rapid climatic oscillations, causing temporary snowmelt excess. The dry phase in Linje coincides with hydrological instability recorded in peatlands from northern Poland, such as Słowińskie Błota (~ 600 cal. BP) (Lamentowicz et al., 2009a), around 170 km northwest from Linje, Stążki (~850–450 cal. BP) (Lamentowicz et al., 2008c), located around 140 km north from Linje and in Kusowskie Bagno (~710–400 cal. BP), a peatland ~130 km northwest from Linje. These sites display high water table fluctuations, growth of *Eriophorum vaginatum*, and the disappearance of *S. fuscum*. In contrast, Linje exhibited persistent *S. fuscum* and *S. rubellum* growth, suggesting uninterrupted peat accumulation. Peatlands in central Poland might have had a different response as a multiproxy study from Żabieniec kettle hole contrastingly demonstrates a rapid wet shift at ~600 cal. BP (Lamentowicz et al., 2009b). In Saxnäs Mosse bog in Southern Sweden, the period of ~675–360 cal. BP records a cooling signal in the palynological data while the shifts in moss composition might indicate either a dry shift or an eutrophication signal (van der Linden and van Geel, 2006).

The drier period in Linje is interrupted around 450 cal. BP (1510 CE) when *Sphagnum* mosses indicate a sudden switch to wetter conditions. This coincides with the beginning of a prominent cooling during the LIA in Europe. The wet shift around 450 cal. BP is also observed in Stążki bog (Lamentowicz et al., 2008c), Żabieniec kettle hole (Lamentowicz et al., 2009b), Kusowskie Bagno (Lamentowicz et al., 2015), Finland (Väliranta et al., 2007) and Estonia (Sillasoo et al., 2007). However, the last 1000 years of climate records in Northern European peat show many alterations between dry and wet conditions that often do not align and are likely caused by differences in oceanic and continental climate (Marcisz et al., 2020a; Väliranta et al., 2007). The lack of spatial and temporal coherency during the LIA is also pointed out by Neukom et al. (2019) and possible climatic signals could be obscured by increasing human impact since early Medieval times resulting in deforestations and increasing openness affecting the hydrology of peatlands (Lamentowicz et al., 2009a). The early 16th-century wet phase may also reflect factors unrelated to climate. As Marcisz et al. (2015) point out, ~430 cal. BP (coinciding with the onset of the wet phase identified in this study) was marked by high fire activity in the Linje region, likely linked to military activities during the Polish-Teutonic war, suggesting that anthropogenic impact on the peatland was increasing.

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Testate amoebae and bryophytes show contradicting information in the top 30 cm peat layer, which starts around 250 cal. BP (1700 CE): testate amoebae show rapidly decreasing water tables and dry conditions whereas the *Sphagnum* taxa indicate wet, even waterlogged conditions (Figs. 3–6, 7A–C). During these shifts, human impact in the vicinity of Linje was increasing, culminating with drainage in the 19th century, resulting in destabilized hydrology (Marcisz et al., 2015). Marcisz et al. (2014) has found that the current testate amoebae communities in Linje differ significantly in spring and summer across all microforms. Thus, it is possible that the drought-resistant testate amoebae species recorded in the top layer reflect summer droughts that intensified after the drainage whereas plant macrofossils reflect the seasonal inundation and post-drainage peat subsidence. Current observations confirm that Linje's surface reacts sensitively to meteorological fluctuations due to drainage (Słowińska et al., 2022). The recent drying trend at Linje is consistent with patterns documented across many European peatlands (Swindles et al., 2019). The increased presence of *S. fallax* on the peatland might indicate a change in peatland chemistry, as *S. fallax* is more tolerant of nutrient inputs compared to the other *Sphagnum* mosses and the expansion of this species is connected to increased N deposition to nutrient-poor peatlands (Gąbka and Lamentowicz, 2008; Limpens et al., 2003). This change could be further investigated using geochemical analyses.

5.4 Site-specific considerations

Linje lies within a forest surrounded depression, that produces a distinctive microclimate compared to adjacent areas, with lower air temperatures and increased ground frost days (Słowińska et al., 2022). Although the forest cover in the surrounding of the peatland has been dynamic (Marcisz et al., 2015; Szambelan et al., 2025 accepted), it is likely that during the formation of the peat layer in the depression, the site experienced a unique microclimate as well. Consequently, the peat profile's hydrological signals likely reflect both broader climate trends and local microclimatic conditions.

In addition to microclimate, peatland type should be considered while talking about climate sensitivity. Although we found in this study that the centre of Linje has been *Sphagnum*-dominated since ca 9050 cal. BP, it should be considered that the peatland is not ombrotrophic as groundwater incursion influences its western side (Słowińska et al., 2010). This groundwater input cannot be overlooked, as it may have impacted the recorded hydrological shifts. However, other *Sphagnum*-dominated peatlands, beyond ombrotrophic bogs, have been recognized as valuable climate archives (Booth, 2010; Lamentowicz et al., 2008b). To know whether the shifts observed in Linje are climate-driven or products of internal peatland processes, it is essential to identify synchronous changes in other regional records (Hughes et al., 2000; Swindles et al., 2012), which is the case in Linje: after the peatland became *Sphagnum*-dominant, bryophyte species turnovers, the decreases in *Sphagnum* cover or dominant testate amoebae species closely coincide with major Holocene climatic events (Fig. 7).

5.5 Comparison to earlier work

One peat profile can provide detailed information on bog vegetation at a microform scale (Mauquoy and Yeloff, 2008). As observed by Słowińska et al. (2022), the microclimatic conditions within the microsites in Linje exhibit considerable variability. Ideally multiple cores from the same site could be used to reconstruct mesoscale ecohydrological changes through time (Barber et al., 1998; Mauquoy and Yeloff, 2008).

Among previous studies, the work by Marcisz et al. (2015), based on a nearby coring location within the same vegetation zone, is most directly comparable to this study. Covering the last 2,000 years, their reconstruction of the upper 2 m of peat shows strong

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Deleted: *R. tomentosum*, which is a very common plant on the site in the present dayis very common plant on the peatland today, also became abundant in the paleorecord in the topmost 30 cm. Experimental field experiments in Linje and elsewhere have shown that ericoid shrub encroachment is connected to lower water tables (Buttler et al., 2023). During these shifts, human impact in the vicinity of Linje was increasing, culminating with drainage in the 19th century, resulting in destabilized hydrology (Marcisz et al., 2015). to which testate amoeba react faster than mosses. Marcisz et al. (2014) has found that the current testate amoebae communities in Linje differ significantly in spring and summer across all microforms. Thus, it is possible that the drought-resistant testate amoebae species recorded in the top layer reflect summer droughts that intensified after the drainage whereas plant macrofossils reflect the seasonal inundation and post-drainage peat subsidence. Current observations confirm that Linje's surface reacts sensitively to meteorological fluctuations due to drainage (Słowińska et al., 2022). Recent drying trend on Linje peatland follows the changes documented on many peatlands in Europe (Swindles et al., 2019).

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agreement with our results: showing a progression from wet to waterlogged conditions, followed by a brief dry phase, and culminating with hydrologically unstable conditions in the uppermost layer.

Earlier paleoecological studies at Linje offer valuable points of comparison, despite differences in methodology and data resolution. The stratigraphy outlined by Kloss and Żurek (2005) broadly agrees with the succession in the vegetation described in this work. From the same core, Kloss (2005) further described hydrological transformations in Linje based on a phytocoenotic moisture index, which presents a moisture gradient ranging from moderately wet to heavily waterlogged. This hydrological interpretation agrees with water table changes captured by testate amoebae in this study as it shows rather wet conditions throughout the Holocene. Moreover, a decrease in moisture around 400 cal. BP was also recorded in the work of Kloss (2005). However, a distinctly drier episode around the Middle Holocene is not recorded in this earlier paleohydrological work. The discrepancy could be attributed to the different resolution and methods employed for plant macrofossil analysis in Kloss's work (2005). Additionally, the analysed core in the work of Kloss (2005) is closer to the margin of the peatland (Kucharski and Kloss, 2005) located about 50 m southward from the coring site of this study.

6 Conclusions

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A new full Holocene peat record from *Sphagnum*-dominated Linje peatland in northern Poland provides valuable insights into past wetness changes. Plant macrofossil and testate amoebae analysis reveal significant shifts in peatland hydrology and vegetation, driven by autogenic succession, climatic variability and later anthropogenic impacts. Bryological species turnovers are recorded at 11,200, 10,350, 8,200, 7,500, 5,500, 600, and 450 cal. BP. Early Holocene changes appear to result from autogenic succession. Toward the end of the Early Holocene, peatland changes increasingly align with known periods of rapid climate change. Both plant macrofossil and testate amoebae proxies indicate drier conditions between 7,600–6,800 cal. BP, coinciding with the Holocene Thermal Maximum. In the Late Holocene, the testate amoebae record indicates additional disturbances around 3,050, 2,000, and 200 cal. BP. While earlier episodes were short-lived, the most recent disturbance (~200 cal. BP) marks a permanent species turnover, reflecting a fundamental shift in peatland conditions driven by drainage.

For millennia, Linje peatland remained resilient to natural climate variability, maintaining peat accumulation despite repeated hydrological and vegetational shifts. However, following historical drainage, the system has not recovered, which highlights the limits of resilience once strong anthropogenic pressures are introduced. The Linje record confirms the complementary value of plant macrofossils, particularly bryophytes, and testate amoebae in reconstructing palaeohydrological conditions, and highlights the value of *Sphagnum*-dominated poor fens as climate archives.

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Data availability

Plant macrofossil and testate amoebae data will be made available via Mendeley Data repository.

Author contribution

EP prepared the manuscript, contributed to the statistical analysis, and visualization of the data, with help from KM and ML. EP also analysed plant macrofossils with guidance from LA and DM. ML organised the fieldwork plan and logistics. KM, LA, PK, MS, SV, and ML carried out the fieldwork. KM and PF analysed testate amoeba. KL and LA contributed to subsampling. KL and

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ML contributed to radiocarbon dating, for which KL aquired the funding. LA and ML aquired funding for the project. All authors contributed with their comments, and edits to the finalisation of the manuscript.

Competing interests

The authors declare that they have no conflict of interest.

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