Responses of vegetation and testate amoeba trait composition to fire disturbances in and around a bog in central European lowlands (northern Poland)

Katarzyna Marcisz*[1,2,3], Mariusz Lamentowicz[2,3], Mariusz Gałka[3,4], Daniele Colombaroli[1,5], Carole Adolf[1,6], Willy Tinner[1]

[1] Institute of Plant Sciences and Oeschger Centre for Climate Change Research, University of Bern, Altenbergrain 21, CH-3013 Bern, Switzerland

[2] Laboratory of Wetland Ecology and Monitoring, Adam Mickiewicz University in Poznań, Krygowskiego 10, 61-680 Poznań, Poland

[3] Department of Biogeography and Palaeoecology, Adam Mickiewicz University in Poznań, Krygowskiego 10, 61-680 Poznań, Poland

[4] Department of Geobotany and Plant Ecology, Faculty of Biology and Environmental Protection, University of Lodz, 12/16 Banacha Str., Lodz, Poland

[5] Department of Geography, Royal Holloway, University of London, UK

[6] Department of Zoology, Long-Term Ecology Laboratory, University of Oxford, UK

* Correspondence: Katarzyna Marcisz, Laboratory of Wetland Ecology and Monitoring, Adam Mickiewicz University in Poznań, Krygowskiego 10, 61-680 Poznań, Poland, e-mail: marcisz@amu.edu.pl

ABSTRACT

Compared to boreal or Mediterranean biomes, the influence of fire on peatlands in Central Europe is not well studied. We aim to provide first analysis of statistically significant charcoal-inferred fire events from a peatland from central European lowlands, spanning the period of the last 650 years, and define peatland vegetation and microbial trait-related responses to local fire events**.** Here, we reconstructed regional and local fire activity from Bagno Kusowo bog (Poland) using high-resolution microscopic charcoal and macroscopic charcoal and its morphotypes, inferring past fire regimes using numeric analyses. We compared fire data with extra-local (pollen) and local (plant macrofossils, testate amoebae (TA) and their trait composition) proxies. Our data show that within the chronological uncertainties, regional fires recorded in the peat core coincide with historically-documented fires. Macroscopic charcoal analysis suggests 3-8 local fire events, while fire frequency varied between 0-2 events/1000 years. Wood charcoal was dominant throughout the profile, pointing to forest fires in close proximity to the peatland. Local fire activity was the most intensive in the 17th century, when the water table was at its lowest. The abundance of *Sphagnum* spp. declined, whereas vascular plants, mixotrophs and TA with proteinaceous shells were significantly positively correlated to fire. Xenosomes were significantly negatively correlated to fires, and they responded to water table lowering. We show that the peatlands' vegetation recovered from low-intensity and short-lasting disturbances and, to some extent, maintained "pristine" local vegetation cover with *Sphagnum* as the dominant species. A substantial decrease of TA traits common before disturbances, mainly mixotrophs and TA with proteinaceous shells, temporarily re-appeared after fire. We conclude that TA communities in peatlands are good bioindicators of disturbances.

Keywords: Central Europe, charcoal, functional and morphological traits, high-resolution, macrofossils, palaeoecology, fire history, peatland

1. INTRODUCTION

Increased fire activity is anticipated by climatic models in the near future, and this alteration will strongly affect ecosystems (EEA Report, 2012). Peatlands are predicted to suffer from global changes and anthropogenic influence, their response to changing climate already being recorded in the boreal and temperate biomes (Dise, 2009). Peatlands located in temperate Central and Eastern Europe may become threatened, even though currently fire activity in this area is not as pronounced as in other latitudes (e.g. boreal or Mediterranean ecosystems; Marlon et al. (2013)). As this area of Europe is considered virtually fire-free, it received much less attention compared to areas classified as typical 'pyromes' (Archibald et al., 2013). Similarly to Western and Central Europe the use of fire by humans is recorded since at least the Mesolithic (ca. 11200 years back) or Neolithic (ca. 7500 years back; (Clark et al., 1989; Barber et al., 2004; Kuneš et al., 2008; Kothieringer et al., 2015; Vannière et al., 2016) and natural fires have been recorded especially in fire-prone *Pinus sylvestris*-dominated forests (Adámek et al., 2015). Drying or hydrological instability observed in peatlands in central European lowlands over the last 300 years, as an effect of human activity but also changing climate (Lamentowicz et al., 2015; Marcisz et al., 2015; Gałka et al., 2017b), may trigger an increase in fire activity in the future. During droughts fires can easily spread on dry peatland surfaces, causing carbon emissions (Kettridge et al., 2015; Turetsky et al., 2015). Severe fires are strong ecosystem disturbances that cause hydrological fluctuations and affect local vegetation composition (Kuhry, 1994), especially when smouldering combustion takes place over long periods (Benscoter et al., 2015). The influence of fire on the peatland surface is demonstrated by the change in the microtopography: a reduction of hummock microforms that are much drier than hollows and, therefore, burn first (Sillasoo et al., 2011; Benscoter et al., 2015). Even though ombrotrophic peatland vegetation is, in general, resilient to fire, burning can have an influence on mosses over decades (Magnan et al., 2012). Sillasoo et al. (2011) showed that severe fires can influence ombrotrophic bog vegetation composition typical for dry hummocks, mainly Ericaceae (Tuittila et al., 2007), and that recovery time after fire may take up to 350 years. Therefore, an important additional information for studying local environmental changes is the type of burnt material that can give an idea of the extent and the location of past fires. The importance of charcoal morphotypes for the interpretation of fire data have been shown in previous studies (Umbanhowar and McGrath, 1998; Colombaroli et al., 2014; Feurdean et al., 2017).

The change in the vegetation composition on the peatland surface and dust deposition have an influence on microbial communities, mainly testate amoebae (Fiałkiewicz-Kozieł et al., 2015; Payne et al., 2016); however, microbial response to fire is not well recognized. Out of different groups of microbes inhabiting peatlands, testate amoebae (TA) are especially important as they are top predators in the microbial food web indicating changes in lower food web levels (Jassey et al., 2013). So far, few studies focused on the relationship between TA and fire looking at a long-term response of TA communities to fire (Marcisz et al., 2015), TA functional and morphological traits response to fire (Marcisz et al., 2016), and a short-term TA response to wildfire (Qin et al., 2017). However, more studies are needed to recognize those relationships accurately.

Given the irrelevance of fire today, past fire activity in central European lowlands is under-investigated and, so far, only one study provided high-resolution, contiguous macroscopic charcoal record from peat sediments from Poland and neighbouring countries (Marcisz et al., 2015). Additionally, the analysis of charcoal morphotypes have only been performed on lake sediments (Feurdean et al., 2017). Moreover, there is no palaeoecological study from this area of Poland using numerical analyses to identify fire frequency and the background and peak components of a charcoal record (Higuera et al., 2010). Likewise, no studies so far have used the fire transfer functions based on the European-scale training set for palaeofire reconstructions (Adolf et al., 2018b). As the influence of fire on peatlands in this part of the world is still not well known (Gałka et al., 2013; Marcisz et al., 2015; Marcisz et al., 2016; Marcisz et al., 2017), these are crucial analyses that help to understand the nature and effects of fire-regimes in this and similar systems.

Here, we aim to investigate the effects of fire disturbance on wetland vegetation and testate amoebae diversity. To reach this goal we analysed microscopic and macroscopic charcoal and its morphotypes, and used previously analysed pollen, plant macrofossil and testate amoeba data from Gałka et al. (2014) to understand the impact of fire on the peatland ecosystem. We aimed to (1) provide first evidence of statistically significant fire events in Poland (over the last 650 years) by additionally applying novel fire transfer functions; and (2) define the response of local vegetation and testate amoebae (TA) to local fire events. We hypothesized, that fire on the peatland leads to (1) changes in surface vegetation cover favouring vascular vegetation, and (2) change in TA functional diversity – a loss of mixotrophs due to drying and lower light availability, and increase of xenosomes as those possess shells more resistant to mechanical damage.

2. MATERIALS AND METHODS

2.1. Study site and sediment sub-sampling

Bagno Kusowo is an ombrotrophic bog located in northern Poland, central European lowlands (53°48’59’’N, 16°35’20’’E, Fig. 1) (Gałka et al., 2014). Covering an area of 318.82 ha, it is one of the biggest peatlands in Poland. Environmental history of the bog was studied before, focusing on vegetation changes, hydrological dynamics, non-contiguous examination of microscopic charcoal, and investigation of volcanic tephra (Gałka et al., 2014; Lamentowicz et al., 2015; Gałka et al., 2017a; Marcisz et al., 2017; Watson et al., 2017).

A one meter-long peat monolith was collected from the northern part of the peat bog in 2010 and sub-sampled every two cm for pollen (sample volume: 1 cm^3), and contiguously every cm for testate amoebae (6 cm^3) and plant macrofossils (25 cm^3) analyses (Gałka et al., 2014). For this study, we sub-sampled contiguously every cm for microscopic charcoal (100 samples, 1 cm^3) and macroscopic charcoal (100 samples, 1 cm^3) analyses.

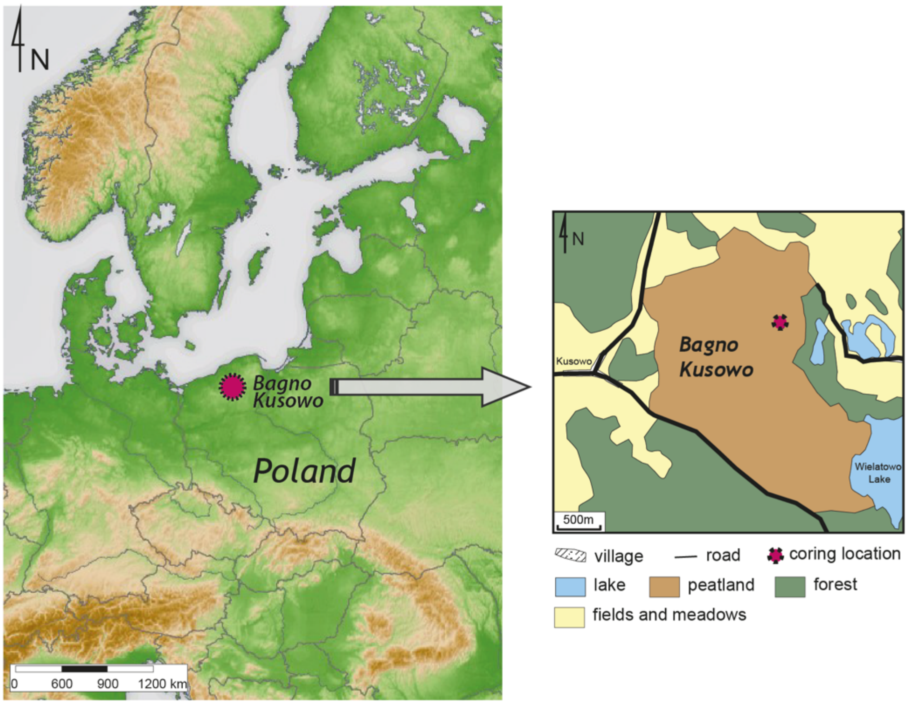

Figure 1. Location of Bagno Kusowo and coring spot. Map of Europe source: http://pl.wikipedia.org/w/index.php?title=Plik:Europe_topography_map.png&filetimestamp=20080612084157, Author: San Jose; modified.

2.2. Laboratory analyses of charcoal

Samples for microscopic charcoal were prepared following standard procedures for pollen slides preparation (Berglund and Ralska-Jasiewiczowa, 1986). One *Lycopodium* tablet (9,666 spores) was added to every sample for calculations of charcoal concentrations (Stockmarr, 1971). Microscopic charcoal (particles >10 µm) was analysed using a light microscope at 400× magnification until the sum of 200 was reached (Tinner and Hu, 2003; Finsinger and Tinner, 2005).

Samples for macroscopic charcoal were prepared following Whitlock and Larsen (2001). Macroscopic charcoal (particles >100 µm) was analysed under a stereoscopic microscope at 40× magnification; additionally, macroscopic charcoal morphotypes – wood, leaf, and grass – were determined following the approach by (Colombaroli et al., 2014) and available literature (Umbanhowar and McGrath, 1998; Jensen et al., 2007). We considered charcoal particles originating from grass as possessing a length to width ratio ≥4:1 and stomata within the rows of epidermal cells (Jensen et al., 2007; Colombaroli et al., 2014), whereas wood charcoal was identified as particles with a length to width ratio ≤4:1 and thicker structure (Umbanhowar and McGrath, 1998). The characteristics to classify particles into leaf charcoal were the visibility of leaf veins (Jensen et al., 2007) and the presence of a divergence of the branches from the node (Umbanhowar and McGrath, 1998).

2.3. Statistical analyses

We established a new chronology on the basis of eight AMS (Accelerator Mass Spectroscopy) radiocarbon dates (Gałka et al., 2014). The IntCal13 (Reimer et al., 2013) calibration curve was applied for calibration of radiocarbon dates and Bayesian approaches to establish an age-depth model (OxCal v.4.2, Bronk Ramsey (2008); Fig. 2). For the calculation of the age-depth model, the *P_Sequence* command with *k* parameter equal to 0.9 cm^{-1} was applied.

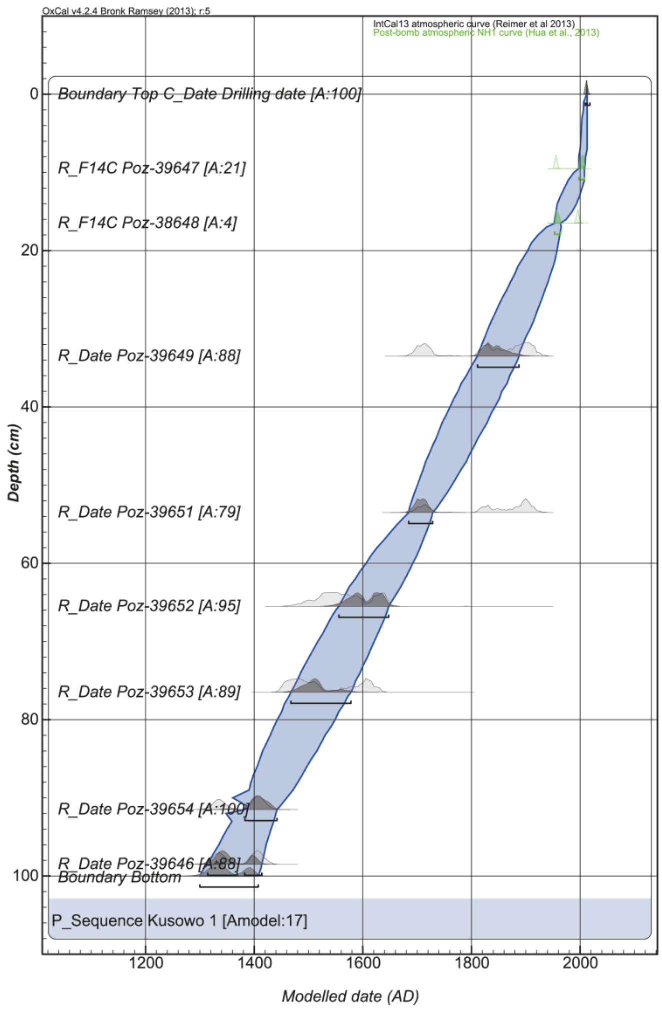

Figure 2. Age-depth model for KB1 core.

Microscopic and macroscopic charcoal influx or accumulation rates (MIC and MAC, particles/cm^2/yr) were calculated using charcoal concentrations (particles/cm^3) and the peat accumulation rate, which was inferred from the radiocarbon chronology. Microscopic charcoal is a proxy for regional fire activity (Tinner et al., 1998), while macroscopic charcoal is usually interpreted as a proxy for local fires (Clark et al., 1998; Conedera et al., 2009). The first continental-scale calibration study, however, suggests that microscopic and macroscopic charcoal have similar regional proveniences for particles <600 µm (Adolf et al., 2018b), while larger particles may indeed come from local fires. To bypass this issue, we applied a conservative peak recognition approach, assuming that the likelihood of identifying local fires increases with increasing MAC. The reconstruction of statistically significant fire peaks/episodes and fire frequency was done using MAC in CharAnalysis (Higuera et al., 2009; Higuera et al., 2010). Moreover, based on MAC we reconstructed fire number (FN), total fire radiative power (tFRP; MW) and burned area (BA; km^2) using fire transfer functions (Adolf et al., 2018a;

Adolf et al., 2018b) that reflect extra-local fires in a 40 km (180 km for burned area) radius from the study site. For better comparison, we standardised transfer function results to reflect FN, tFRP and BA within an area of 1000 km^2. Microscopic charcoal is mostly linked to regional fire activity up to 40 and more km from the coring location in Europe, specifically fire frequency and intensity and to lesser degree also burned area (Adolf et al., 2018b). Results of charcoal statistical analyses are presented in the Figs 3-5 and S1.1.

Relationships between local components (vegetation, testate amoebae, local fires) were explored using cross-correlations on contiguously analysed local proxies (Fig. 6, S1.2, one lag=7 years). We tested correlations between MAC and plant macrofossil data (*Sphagnum* species and sum of vascular plants) to assess if fire influenced vegetation cover, and testate amoeba-based depth-to-water table reconstruction (DWT) to assess if fires influenced local hydrology (Fig. 6, S1.2). Correlation between DWT and plant macrofossils was tested to investigate water-table effect on wetland vegetation (Fig. 6, S1.2). Moreover, we tested correlations between MAC and selected traits of testate amoebae (TA) to evaluate if fire had an impact on microbial communities, as an influence of fire on TA communities and trait composition has been shown before (Marcisz et al., 2015; Marcisz et al., 2016; Qin et al., 2017) (Fig. 6, S1.2). We looked at the sum of mixotrophic species (wet indicators), as they are related to *Sphagnum* photosynthesis and thus C assimilation in peatlands (Jassey et al., 2015; Marcisz et al., 2016), and shell types present in the communities as this trait may be important for TA survival during fire (Qin et al., 2017). Species were divided into four groups according to shell type, following Mitchell et al. (2008): idiosomes – shells made of secreted biosilica plates, idiosomes with thick organic coating, proteinaceous shells, and xenosomes – shells built from recycled organic or mineral particles (Table 1).

Table 1. Groups of testate amoebae based on their traits.

Trait	List of species included in a group
Mixotrophs	*Archerella flavum, Amphitrema wrightianum, Heleopera sphagni, Hyalosphenia papilio*
Shell types	
Idiosomes	*Corythion dubium, Euglypha ciliata, Euglypha rotunda, Euglypha compressa, Euglypha tuberculata, Euglypha strigosa, Euglypha* sp., *Trinema lineare*
Idiosomes with organic coating	*Assulina muscorum, Assulina scandinavica, Assulina seminulum*
Proteinaceous	*Archerella flavum, Arcella artocrea, Arcella catinus, Arcella discoides, Arcella* sp., *Hyalosphenia elegans, Hyalosphenia papilio, Hyalosphenia subflava*
Xenosomes	*Alabasta (Nebela) militaris, Amphitrema stenostoma, Amphitrema wrightianum, Bullinularia indica, Centropyxis aerophila, Cyclopyxis arcelloides,*

	Cryptodifflugia oviformis, *Difflugia leidyi*, *Difflugia* sp., *Heleopera petricola*, *Heleopera sphagni*, *Heleopera sylvatica*, *Nebela bohemica*, *Nebela collaris*, *Physochila griseola*, *Nebela parvula*, *Nebela tincta s.l.*, *Nebela* sp., *Trigonopyxis arcula*

To highlight the patterns between studied proxies, non-metric multidimensional scaling (NMDS) ordination was computed for all analysed proxies as well as separately for local (MAC, plant macrofossils, TA traits) and regional (MIC and pollen) proxies (S1.3). For regional analyses, anthropogenic and open land pollen-indicators were used (S1.5). We chose Bray–Curtis distance measure, six starting axes and 100 random starting configurations. Cross-correlations and ordinations were conducted with R 3.0.1 (R Development Core Team, 2011) using the *vegan* (Oksanen et al., 2017) and *astsa* (Stoffer, 2016) packages.

3. RESULTS

3.1. Microscopic and macroscopic charcoal

Microscopic charcoal (Fig. 5, S1.1) was abundant along the sequence, showing fluctuations with increases around ca. 1480 CE, 1630-1770 CE, 1835-1935 CE and ca. 2003-present.

Macroscopic charcoal (Figs 4-5, S1.1) was less abundant but more variable: we observed higher influx (MAC) and high background charcoal (BCHAR) values between ca. 1350-1720 CE, low values between ca. 1720-2003 CE, and a rise from ca. 2003 CE-present. Highest MAC occurred at ca. 1650-1720 CE, with a distinct charcoal layer at ca. 1650 CE). Only in the three highest charcoal peaks recorded in this layer we found charcoal pieces larger than 500 µm. In this period, three peaks were identified as statistically significant by CharAnalysis in the conservative reconstruction. The local reconstruction registered five more peaks in other phases. Inferred fire frequency (IFF, peaks/1000 years) was low, varying between 0-2, with highest values recorded at ca. 1450-1490 CE and ca. 1610-1720 CE.

Wood charcoal was dominant among the three morphological types and its amount was higher than 50% in almost all samples (Fig. 5). Up to ca. 1900 CE leaf charcoal was also numerous (10-35%). Since ca. 1900 CE the amount of leaf charcoal dropped, whereas wood charcoal was highly dominant. Grass charcoal was not numerous but in stable values (10-20%). High MAC values (statistically significant charcoal peaks representing local fire episodes) are connected with a higher abundance of vascular plants and an increased amount of wood charcoal. Wood charcoal may be an evidence of burning of trees located around the mire. We did not find charcoal pieces larger than 1 mm in the peat, which would be a more definite prove of local burning of trees, e.g. on the peatland surface (Adolf et al., 2018b). However, the amount of charcoal found during the three fire episodes is considerable, including few charcoal pieces larger than 500 µm, and suggests fires in close proximity.

Quantitative reconstructions of fire number (FN), burned area (BA) and total fire radiative power (tFRP) at ca.1450-1600 CE follow similar trends to MIC and resulted in mean annual values per 1000km^2 of 118 fires, 69 km^2 and 17559 MW, respectively. Extraordinarily high fire activity is reconstructed between ca. 1630-1730 CE (mean per 1000 km^2: FN=10’365, BA=23’962 km^2, tFRP=34’371’477 MW, Fig. 3, S1.1), which is also when MAC particles >500 µm were found, possibly indicating local fire occurrence. Since ca. 2003-present reconstructions resulted in mean values per 1000 km^2 of FN=79, BA=46.6 km^2 and tFRP=12’322 MW. Transfer functions should be applied carefully to influx values that are clearly out of the range of the calibration-dataset values (Adolf et al., 2018a).

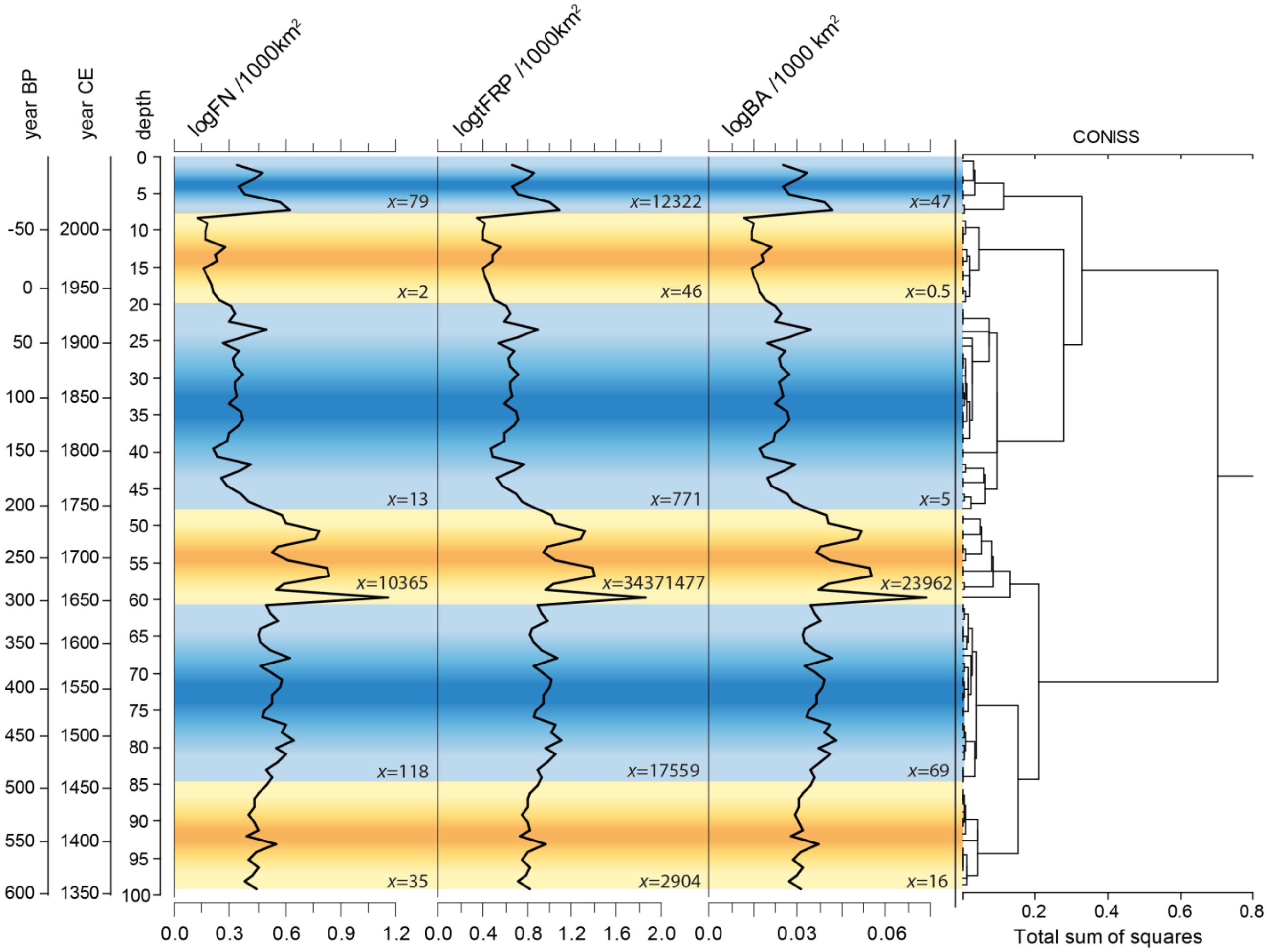

Figure 3. Output of the fire transfer function by Adolf et al. (2018b), including the reconstruction of fire number (FN), total fire radiative power (tFRP; MW) and burned area (BA; km^2) per 1000km^2. Due to large

differences in the calibrated values we used CONISS to infer the zonation and plotted the diagram on a base-10 logarithmic scale. The mean untransformed values (*x*) for each of the zones are indicated on the diagram.

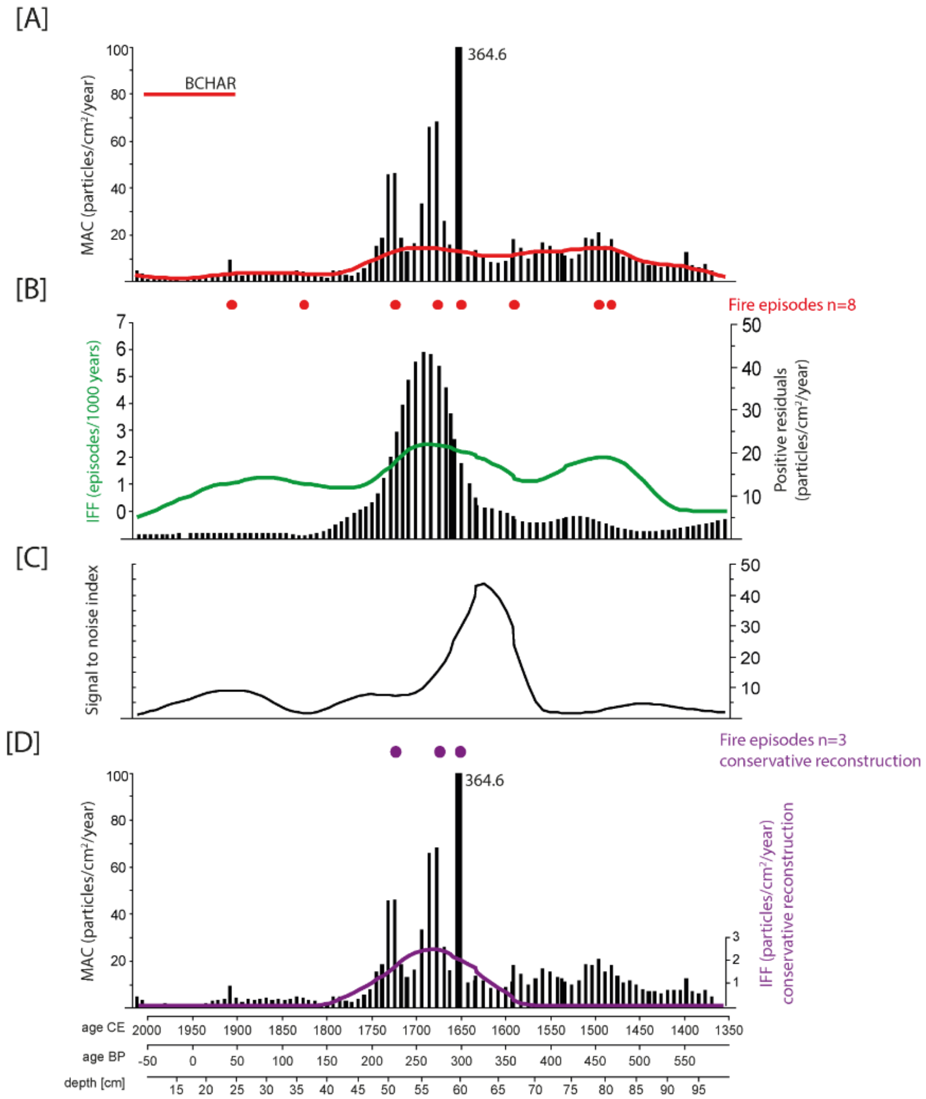

Figure 4. Summary of the fire reconstructions using CharAnalysis. [A] Macroscopic charcoal influx (MAC) and background component of the MAC series (BCHAR). [B] Positive residuals of the Bagno Kusowo MAC after subtracting the BCHAR from the MAC series. Fire episodes identified using a local threshold are show, together with the inferred fire frequency (IFF) per millennium. [C] Signal to noise index. [D] Results of the conservative reconstruction (fire episodes and IFF).

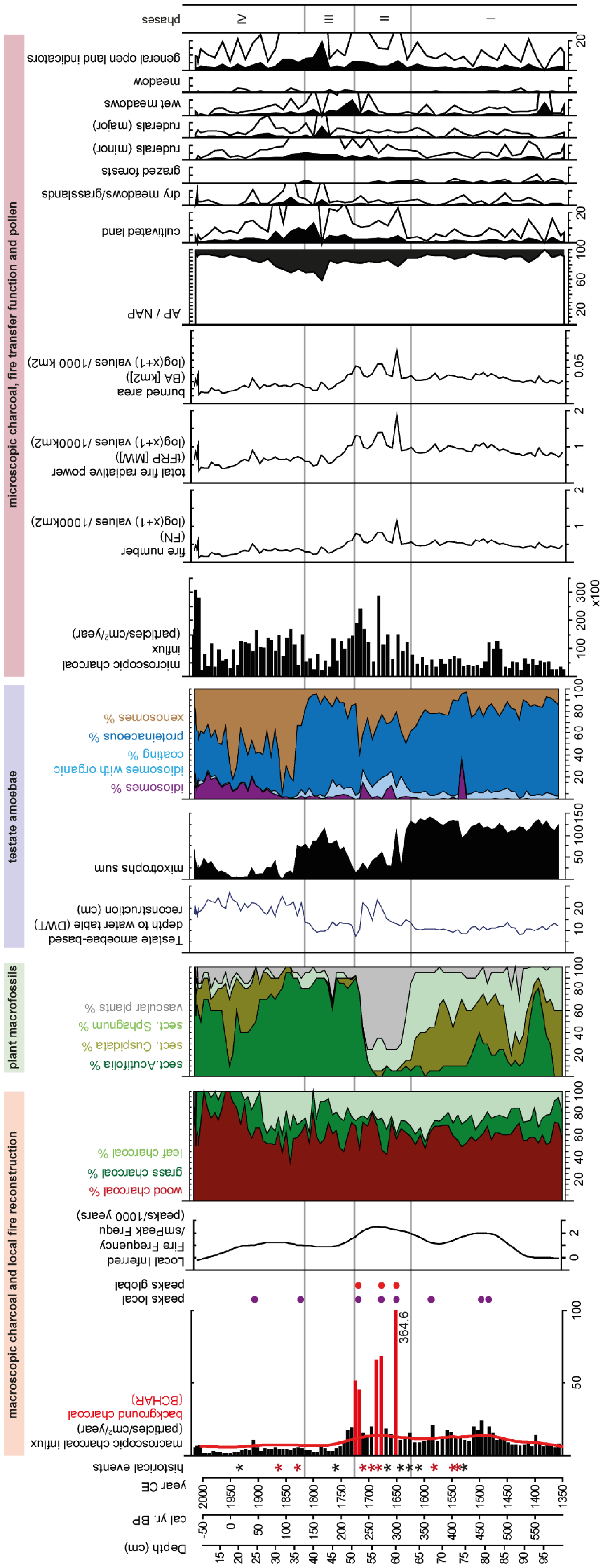
phases
I
II
III
IV
general open land indicators
meadow
wet meadows
ruderals (major)
ruderals (minor)
grazed forests
dry meadows/grasslands
cultivated land
AP / NAP
burned area (BA [km2]) (log(x+1) values /1000 km2)
total fire radiative power (tFRP [MW]) (log(x+1) values /1000km2)
fire number (FN) (log(x+1) values /1000km2)
microscopic charcoal influx (particles/cm²/year)
microscopic charcoal, fire transfer function and pollen
xenosomes %
proteinaceous %
idiosomes with organic coating %
idiosomes %
mixotrophs sum
Testate amoebae-based depth to water table (DWT) reconstruction (cm)
testate amoebae
vascular plants %
sect. Sphagnum %
sect. Cuspidata %
sect.Acutifolia %
plant macrofossils
leaf charcoal %
grass charcoal %
wood charcoal %
Local Inferred Fire Frequency /smPeak Frequ (peaks/1000 years)
peaks global
peaks local
macroscopic charcoal influx (particles/cm²/year)
background charcoal (BCHAR)
364.6
macroscopic charcoal and local fire reconstruction
historical events
year CE
cal yr. BP
Depth (cm)

Figure 5. Palaeoecological summary diagram, including historical events and local and extra-local proxies. Local proxies include macroscopic charcoal influx and output of fire reconstruction (background charcoal, significant charcoal peaks, and inferred fire frequency) based on CharAnalysis (Higuera et al., 2010) plant macrofossils, depth to water table reconstruction and testate amoebae traits. The red bars of macroscopic charcoal indicate samples where large charcoal particles >500 µm were found. Extra-local proxies include microscopic charcoal influx, fire transfer function based on Adolf et al. (2018b) (base-10 logarithmic axes, values per 1000 km^2) and pollen. Historical events include wars in the region (black stars) and fires in Szczecinek city (red stars), based on Szczecinek Historical Portal (2019).

3.2. Relationship between proxies

3.2.1. Phase I: High background charcoal and stable hydrological conditions (ca. 1350-1620 CE)

From ca. 1350 CE until the beginning of 17th century pollen data show forested landscape around Bagno Kusowo (Fig. 5). Forests were dominated by *Pinus* and *Betula* species, with some amount of *Fagus, Quercus, Alnus* and *Corylus*. Human impact, as indicated by pollen, was low with the sum of human indicators reaching a maximum of 4%. *Fagopyrum* or *Triticum*-type pollen was recorded but in low amounts and not in every analysed sample (see Fig. 3 in Gałka et al. (2014). Historical sources confirm that the area was not densely populated until the 16th century (Baziński, 2010). Local vegetation on the peatland was highly dominated by *Sphagnum* species from *sect*. Acutifolia, *sect*. Cuspidata and *sect*. Sphagnum (Fig. 5). The reconstructed depth-to-water table (DWT) oscillating between 8 and 13 cm suggests relatively wet conditions. Mixotrophic species and those possessing proteinaceous shells were dominant in testate amoeba (TA) communities (Fig. 5).

After ca. 1560 CE the pollen record suggests substantial vegetation changes. *Betula* became dominant in the forest composition for a short time and *Pinus* abundance decreased. Afterwards, pollen indicative of open land and human activities increased (e.g. *Secale*). Three local fires occurred and from the beginning of the phase wood charcoal was dominant, but later leaf charcoal got more abundant. The amount of grass charcoal decreased by the end of the phase and the local fires were associated with the dominance (peaks) of wood charcoal, suggesting burning of tree wood in the local forests.

3.2.2. Phase II: Vascular plants expansion, fires and dry shift (ca. 1620-1720 CE)

In Phase II, arboreal pollen (AP) decreases slightly and *Betula* declines, while *Pinus* becomes dominant, suggesting that forests became more open and heliophilous (Fig. 5, see details in Fig. 3 in Gałka et al. (2014). Other tree species declined, while the amount of cultivated land and open land indicators slightly increased. NMDS (S1.3) and Pearson correlations (S1.4) confirm that pollen was not correlated to MIC, but MIC was connected with low water tables. Local proxies suggest significant changes (Fig. 5), such as a sudden decrease of *Sphagnum* species and the spread of vascular plants on the surface of the peatland. Subsequently, TA possessing idiosomic shells with organic coating increased. This group was composed of the dry indicator *Assulina* species (see Fig. 5 in Gałka et al. (2014), that seem to be fast pioneers migrating quickly to dry habitats (Lamentowicz and Mitchell, 2005).

In this phase three significant fire events occurred (ca. 1650 CE, 1680 CE and 1720 CE, conservative and local reconstructions). Those peaks were the most distinct in the sequence and the first of them was the highest of the entire record (364.6 particles/cm^2/year). Moreover, wood charcoal was the most abundant charcoal morphotype, suggesting burning of the forest in the mire area. Fire events (lag0 in cross-correlations, Fig. 6, S1.2) were significantly positively correlated with vascular plants, testate amoebae possessing proteinaceous shells and mixotrophs, whereas *S. sect*. Acutifolia, xenosomes and idiosomes were significantly negatively correlated. Positive relations between MAC and vascular plants are also visible in the NMDS (S1.3). This first fire event led to a decrease in abundance of mixotrophs, species that have been shown to be very responsive to shading by vegetation, e.g. vascular plants (Marcisz et al., 2014; Payne et al., 2016; Creevy et al., 2018) or dust deposition (Fiałkiewicz-Kozieł et al., 2015) as those disturbances may have a negative influence on their endosymbionts. A drop of the water table (from 15 cm to 24 cm) was simultaneous with another charcoal peak. We assume that due to drought and runoff changes in the area, peatland was more susceptible to fires, which could spread into the nearby forests, promoting further fires.

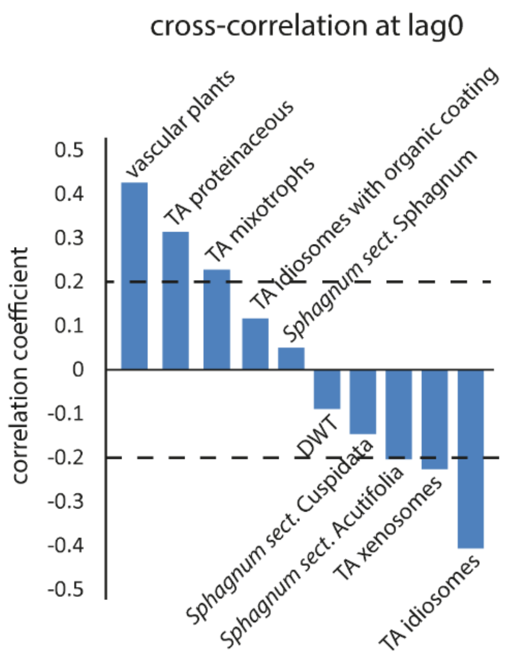

Figure 6. Correlograms showing correlation coefficients between macroscopic charcoal influx and local proxies – plant macrofossils, depth to water table reconstruction (DWT), and testate amoebae (TA) traits at lag0. Correlation coefficients outside the dashed lines are significant at $P = 0.05$. Complete cross-correlation analysis results for each of the groups are available in the Fig. S1.2.

3.2.3. Phase III: Low background charcoal and wet conditions (ca. 1720-1820 CE)

At the beginning of phase III high AP (83%) suggests rather closed forests, while in the middle of the phase (ca. 1780 CE) forests contracted (AP 69%, Fig. 5). *Pinus* and *Betula* declined and herbs such as Poaceae and *Artemisia* expanded together with crops (e.g. *Secale* or *Fagopyrum*), suggesting increasing arable and pastoral farming activities, that reached their apex during this phase at around 1750-1800 CE (see Fig. 3 in Gałka et al. (2014). From ca. 1720 CE, fire activity declined and MIC, MAC and BCHAR values decreased. *Sphagnum* was again dominant on the peatland surface, with *S. sect.* Acutifolia as the main component. Reconstructed water table rose (values between 7 and 13 cm) and TA communities changed back to the composition from before the disturbances – mixotrophs and TA possessing proteinaceous shells strongly dominated.

3.2.4. Phase IV: Low background charcoal and dry conditions (ca. 1820-2010 CE)

In this phase fire activity in the region was high as MIC values increased. In the last 200 years BCHAR is lowest (Fig. 5), suggesting less fires in the proximity of the bog. Up to 1900 CE water tables were low (<20 cm). A local fire ca. 200 years ago was again related to a decrease of mixotrophs and TA with proteinaceous shells. Moreover, *Sphagnum* abundance was at its maximum in this period (95-100%). Afterwards, the abundance of *S. sect.* Acutifolia dropped and *S. sect.* Cuspidata spread on the peatland surface. Among TA, idiosomes and xenosomes dominated. Forests recovered, open land and pastoral and arable farming declined during this phase (Fig. 5). The last fire (local reconstruction) occurred at ca. 1900 CE. Mostly wood charcoal was found in the peat, pointing to fires in the remaining forests and/or burning trees on the peatland. Higher abundance of vascular plants may be related to drainage and peat extraction, but those practices were not long-lasting. Human pressure was weaker than before and no marked changes occurred in and around the mire. For instance, oligotrophic *Sphagnum* species cover maintained on the peatland, mixotrophs got more abundant and water table started rising in the last 40 years, suggesting recovery of the bog, most likely in response to decreasing land use activities.

4. DISCUSSION

4.1. Regional fire history and vegetation patterns

Bagno Kusowo bog development may be linked with the history of the Szczecinek city (founded in 1310 CE, located 15 km from the bog) and the region that both witnessed many cataclysms in the last millennium: wars, invasions, plagues and frequent fires (Fig. 5; Gaziński (2010). Fire activity was rather low until the 16th century, and human pressure was not intensive. However, fire activity slightly increased at ca. 1450-1500 CE, around 1550 CE and at ca. 1580-1600 CE. Dramatic fires (1537, 1540, 1547 and 1583 CE) and burning of 27 witches (1581-1592 CE) in Szczecinek are reported in historical sources (Szczecinek Historical Portal, 2019). Moreover, a 150-year-long military conflict at the border with Poland that started in 1536 CE and influenced the economy of the city. Increased fire activity in the 16th century was also recorded in other peatlands in northern Poland, where increased burning was associated with permanent human occupation (Marcisz et al., 2015; Marcisz et al., 2017). Our transfer function reconstructions support this increase in fire occurrence, where mean fire number per year rise from 35 to 118 fires/1000km^2 during ca. 1450-1650 CE. In adjacent regions, human-induced fires connected with forest clearings were reported in Germany and around the Baltic (Barber et al., 2004; Sillasoo et al., 2011; Brown and Giesecke, 2014). The subsequent period 1600-1720 CE was politically very unstable and during the Thirty Years' War (1618-1648 CE; Wilson (2011) regional fire activity increased, forests declined and cultivated and open land indicators expanded. It may be that increased fire activity was at least partly connected to battles and military activities in the region and the city. Because of further dramatic fires recorded in Szczecinek in 1682, 1696 and 1710 CE, a ban on the construction of wooden houses in the city was issued in 1711 CE (Szczecinek Historical Portal, 2019). Stable conditions in the second part of 18th century are reflected in the Bagno Kusowo vegetation record and reconstructed mean fire numbers per year are below 100. The 19th century began with forest declines and expansions of open land vegetation such as Poaceae, *Artemisia* and crops (*Secale, Triticum*-type and *Hordeum*, Gałka et al. (2014). Politically stable times and good hydrological conditions enabled more intensive agriculture. Soon after, regional fires increased and historical sources mention two fires in the city: in 1835 CE and 1861 CE (Szczecinek Historical Portal, 2019) which might have been connected with droughts in the region. However, fires in the region did not influence the forest composition around the mire, when forests recovered. The comparison of reconstructed fire number (FN) for the topmost peat section (Fig. 3) with fires registered in the European Forest Fire Information System (EFFIS, 2019) revealed that charcoal-inferred FN values from Bagno

Kusowo are within the range of observed fire occurrences for the study region (the area of Szczecinek Country; 139.2 fires per 1765.39 km^2) during the past 15 years, validating the transfer functions of Adolf et al. (2018b) for our study site.

4.2. Influence of fires on local vegetation, hydrology, and testate amoebae morphological traits

Fire reconstruction at Bagno Kusowo suggests that local fires (MAC) occurred regularly during the past 650 years (Figs. 3-5) and were most probably limited to the nearby forests and/or to the bog margin (wood charcoal reaching >60%, leaf charcoal perhaps reflecting crown fires). No trace of burning peat as described in other studies (Kuhry, 1994; Sillasoo et al., 2011; Magnan et al., 2012) was found at our site. Major changes in the local vegetation composition – expansion of vascular vegetation, mainly *Eriophorum vaginatum* and *Baeothryon cespitosum*, on the surface of the mire – occurred ca. 1620 CE, and were followed by a change in testate amoeba (TA) community composition and increasing local fires. *Sphagnum sect.* Sphagnum (mostly *S. magellanicum*) dominated over the *S. sect.* Cuspidata (e.g. *S. cuspidatum*) and this change can be assigned to cooling and water table lowering to which *S. magellanicum* is better adapted, due to wider ecological amplitude (Hölzer, 2010). Similar changes have been observed in other peatlands in the Pomerania region: Stążki (Lamentowicz et al., 2011) and Słowińskie Błoto (Lamentowicz et al., 2009), where cooling was associated with a reduction in precipitation which together favoured *E. vaginatum* expansion. The following hydrological instability in Bagno Kusowo led to the establishment of *E. vaginatum* which is mostly forming tussocks and, therefore, may be regarded as an indicator of water-level instability (Tobolski, 2000; Silvan et al., 2004). We hypothesized, that fires were the factor triggering change in local vegetation composition, favouring vascular vegetation. Our results show that the change in peatland vegetation have been possibly initiated by cooling climate and water table lowering. However, subsequent fires exacerbated further spread of vascular vegetation (mainly *E. vaginatum*) on the surface of the peatland.

A rapid, although transient, increase in abundance of idiosomes with organic coating occurred after the expansion of vascular plants ca. 300 years ago (Fig. 5). This group was composed of TA species belonging to genus *Assulina* (Tab. 1), mainly *A. muscorum* (see Fig. 5 in Gałka et al. (2014)), recognized as dry indicators found in dry hummocks in different geographical locations (Mazei and Tsyganov, 2006; Amesbury et al., 2016). Next to hydrological preferences, small size of *A. muscorum* (28-60 µm) may also be of high importance for the fast spread of this species as small TA are able to migrate quickly to suitable micro-habitats (Fournier et al., 2015; Marcisz et al., 2016). *Assulina* sp. are one of only few TA possessing tests that can survive acetolysis and are commonly observed in pollen slides (Payne et al., 2012). Hence, in the natural environment their resistant tests may allow them to survive during unfavourable conditions. Moreover, they tolerate well low pH (Swindles and Roe, 2007) and it has been underlined that drought-induced acidification of peatlands can progress quickly after water table lowering (van Haesebroeck et al., 1997). A peak of abundance of idiosomes with organic coating has been registered soon after the first local fire in ca. 1650 CE. Burning was most probably connected with forest clearing (dominance of wood charcoal) and the establishment of fields and meadows by humans as reflected in pollen data (increase in cultural indicators; Fig. 5). Land opening may have resulted from battles and accompanying fires in the vicinity of the bog or, more likely, field establishment as a consequence of increased nutrition needs due to population growth.

Qin et al. (2017) studied short-term responses of TA to wildfire and showed that xenosomes were more abundant after fire, whereas the amount of idiosomes dropped. The reason for this response might be that xenosomic shells are hard and more resistant to disturbances than other shell types (Qin et al., 2017). In Bagno Kusowo, xenosomes peaked just before the fire, while during and after the fire their abundance decreased. From the four groups of TA shell types, only those possessing proteinaceous shells were significantly positively correlated with fire incidence (Fig. 6). In contrast to the results of Qin et al. (2017) and our hypotheses, NMDS and cross-correlations show that the presence of xenosomes and idiosomes was connected with low water tables throughout the study period; moreover, these species were negatively correlated to fire (Fig. 6, S1.3). However, Qin et al. (2017) did not analyse TA assemblages before the fire event, therefore it is unknown if the shell composition recorded by the authors was an actual response to fire or to some other factors like changes in local hydrology or trophy connected to fire incidence. Similarly to xenosomic shells, tests made of biosilica with organic coating are resistant (Payne et al., 2012), therefore, it is possible that disturbances can trigger higher abundances of species possessing this type of shells. Idiosomes with organic coating were more abundant during the fire period, but their positive relation to fire events was not statistically significant (Fig. 6).

Long-term studies on the response of TA to fires in N Poland underlined that fire events, initiated by peatland droughts, triggered a change in TA communities by promoting small species over big ones and eliminating mixotrophs (Marcisz et al., 2016). Similarly to previous observations we recorded a drop of mixotrophs after the first big fire event (Fig. 5) which is in agreement with our hypotheses; however, their abundance was still quite high during the fire and, consequently, they were significantly correlated with fire disturbance (Fig. 6, S1.2). Mixotrophs are lately in the focus of short- and long-term studies as they are promising bioindicators in paleoecological and ecological studies of peatlands. Because of their sensitivity to light intensity, they may be used as disturbance (Marcisz et al., 2016) or landscape openness indicators (Payne et al., 2016; Creevy et al., 2018). Mixotrophs are especially important for peatland functioning because, as phototrophs, they contribute to photosynthetic carbon (C) fixation, and therefore it has been suggested that reduced abundance of mixotrophs with climate warming may lead to reduced C fixation in peatlands (Jassey et al., 2015). As predators of decomposers, they influence organic matter decomposition in peatlands (Jassey et al., 2015). High abundance of mixotrophs is often linked with good hydrological conditions, hence, it is not surprising that this group of species declined together with the expansion of *E. vaginatum* and water table lowering. High amount and density of vascular plants and extended hummocks formation causes increased shading of the wetter hollows. As mixotrophs' endosymbionts use light during the photosynthesis process (Jassey et al., 2015), shading is disadvantageous for their survival. Fires nearby the site and wind erosion from open areas may cause deposition of dust and mineral particles on the surface of the peatland, but it has been shown that dust or tephra deposition does not disturb some of the TA, because those possessing agglutinated tests may incorporate such small particles when building their shells (Fiałkiewicz-Kozieł et al., 2015). Mixotrophs, however, possess proteinaceous shells and do not use such particles in the process of shell formation. Because they depend on light availability, dust deposition and shading may have detrimental or even disastrous consequences for mixotrophs. Additionally, droughts connected with fire occurrence may cause declines of mixotrophs as observed in response to anthropogenic peatlands drainages in the past 200 years (Fournier et al., 2015; Lamentowicz et al., 2015; Marcisz et al., 2016).

The effect of fire and water table lowering on Bagno Kusowo was short-lasting, and soon after the three largest fire events at ca. 1730 CE, *Sphagnum* population recovered and the water table rose. This change triggered an immediate appearance of TA possessing proteinaceous shells and mixotrophs that reacted to better hydrological conditions and higher light availability, the latter in response to deforestation (decrease in AP, Fig. 5). A decline of those TA types occurred after ca. 1820 CE, together with water table lowering, and they were exchanged by xenosomes. Even though water table fluctuated, *Sphagnum* still dominated over vascular plants. In the top peat section, the composition of *Sphagnum* communities changed compared to before the fires – *S. sect.* Acutifolia dominated as opposed to previously abundant *sect*. Cuspidata and *sect*. Sphagnum.

Similar shifts have been observed in other Polish peatlands where, as an effect of human impact, *S. fallax* replaced pristine populations with *S. magellanicum* (Linje mire, Marcisz et al. (2015) and with *S. fuscum* and *S. rubellum* (Gązwa mire, Gałka et al. (2015). The reason for this difference may be that disturbances in Bagno Kusowo (318 ha) were short-lasting and the bog managed to recover and maintain (at least partly) the initial *Sphagnum* composition (Gałka et al., 2017a), whereas long-lasting disturbances in Linje (6 ha) and Gązwa (204 ha) mires were so pronounced that a return to pre-disturbance vegetation composition was impossible (Gałka et al., 2015; Marcisz et al., 2015). It has been underlined that the size of the peatland is important for recovering from disturbances: large peatlands are in general more resistant to disturbances than small ones (Strack, 2008).

5. CONCLUSIONS

We show that peatlands' vegetation can recover from low-intensity and short-lasting disturbances and, to some extent, advantage "pristine" vegetation cover with *Sphagnum* communities over the vascular vegetation. Our data suggest that microbial communities in peatlands are highly responsive to disturbances. Testate amoeba trait composition changed substantially, as traits common before disturbance (mixotrophy and proteinaceous shells) recovered only for a short time to greatly decrease subsequently. This implies that testate amoebae are good bio-indicators of past and present disturbances, specifically because they appear less resilient than plant communities. In general, the knowledge about specific traits of testate amoebae and their relationships with environmental conditions is still scarce and hence more studies are needed to disentangle the linkage between trait responses and variability in forcing factors, such as vegetation changes, fires, droughts and other disturbances. Human activity changes under global warming conditions may significantly increase fire risks in Central Europe, a region that currently does not suffer from severe and frequent fires. Improved knowledge about the influence of fire on vegetation composition and microbial communities in *Sphagnum*-dominated peatlands is, therefore, crucial for sustainable conservation and management plans and policies.

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Author contributions

ML and MG conducted field work, provided peat core and palaeoecological data sets (plant macrofossils, testate amoebae and pollen), and dated the samples. KM and WT applied for the FIRECO project to perform additional charcoal analyses. KM performed charcoal analyses, age-depth modelling, statistical analyses and prepared figures. DC and CA helped with statistical analyses and interpretation of charcoal data. KM wrote the manuscript to which all authors contributed with discussions, critical comments and writing.

Data accessibility

Charcoal data produced for this paper will be stored in the Global Charcoal Database (www.paleofire.org).

References

Adámek, M., Bobek, P., Hadincová, V., Wild, J., Kopecký, M., 2015. Forest fires within a temperate landscape: A decadal and millennial perspective from a sandstone region in Central Europe. Forest Ecology and Management 336, 81-90.

Adolf, C., Doyon, F., Klimmek, F., Tinner, W., 2018a. Validating a continental European charcoal calibration dataset. The Holocene 28, 1642-1652.

Adolf, C., Wunderle, S., Colombaroli, D., Weber, H., Gobet, E., Heiri, O., van Leeuwen, J.F.N., Bigler, C., Connor, S.E., Gałka, M., La Mantia, T., Makhortykh, S., Svitavská-Svobodová, H., Vannière, B., Tinner, W., 2018b. The sedimentary and remote-sensing reflection of biomass burning in Europe. Global Ecology and Biogeography 27, 199-212.

Amesbury, M.J., Swindles, G.T., Bobrov, A., Charman, D.J., Lamentowicz, M., Mallon, G., Mazei, Y., Mitchell, E.A.D., Payne, R.J., Roland, T.P., Turner, E.T., Warner, B.G., 2016. Development of a new pan-European testate amoeba transfer function for reconstructing peatland palaeohydrology. Quaternary Science Reviews 152, 132-151.

Archibald, S., Lehmann, C.E.R., Gómez-Dans, J.L., Bradstock, R.A., 2013. Defining pyromes and global syndromes of fire regimes. Proceedings of the National Academy of Sciences 110, 6442-6447.

Barber, K.E., Chambers, F.M., Maddy, D., 2004. Late Holocene climatic history of northern Germany and Denmark: peat macrofossil investigations at Dosenmoor, Schleswig-Holstein, and Svanemose, Jutland. Boreas 33, 132-144.

Benscoter, B.W., Greenacre, D., Turetsky, M.R., 2015. Wildfire as a key determinant of peatland microtopography. Canadian Journal of Forest Research, 1133-1137.

Berglund, B.E., Ralska-Jasiewiczowa, M., 1986. Pollen analysis and pollen diagrams, In: Berglund, B.E. (Ed.), Handbook of Holocene Palaeoecology and Palaeohydrology. John Wiley & Sons, Chichester, pp. 455-484.

Bronk Ramsey, C., 2008. Deposition models for chronological records. Quaternary Science Reviews 27, 42-60.

Brown, K.J., Giesecke, T., 2014. Holocene fire disturbance in the boreal forest of central Sweden. Boreas 43, 639–651.

Clark, J.S., Lynch, J.A., Stocks, B.J., Goldammer, J.G., 1998. Relationships between charcoal particles in air and sediments in west-central Siberia. The Holocene 8, 19-29.

Clark, J.S., Merkt, J., Muller, H., 1989. Post-glacial fire, vegetation, and human history on the northern alpine forelands, south-western Germany. Journal of Ecology 77, 897-925.

Colombaroli, D., Ssemmanda, I., Gelorini, V., Verschuren, D., 2014. Contrasting long-term records of biomass burning in wet and dry savannas of equatorial East Africa. Global Change Biology 20, 2903-2914.

Conedera, M., Tinner, W., Neff, C., Meurer, M., Dickens, A.F., Krebs, P., 2009. Reconstructing past fire regimes: methods, applications, and relevance to fire management and conservation. Quaternary Science Reviews 28, 555-576.

Creevy, A.L., Andersen, R., Rowson, J.G., Payne, R.J., 2018. Testate amoebae as functionally significant bioindicators in forest-to-bog restoration. Ecological Indicators 84, 274-282.

Dise, N.B., 2009. Peatland Response to Global Change. Science 326, 810-811.

EEA Report, 2012. European Environment Agency: Climate Change, Impacts and Vulnerability in Europe, as Indicator- Based Report 12.2012.

EFFIS, 2019. European Forest Fire Information System, http://effis.jrc.ec.europa.eu/applications/fire-history/, [last visited: 12.01.2019].

Feurdean, A., Veski, S., Florescu, G., Vannière, B., Pfeiffer, M., O'Hara, R.B., Stivrins, N., Amon, L., Heinsalu, A., Vassiljev, J., Hickler, T., 2017. Broadleaf deciduous forest counterbalanced the direct effect of climate on Holocene fire regime in hemiboreal/boreal region (NE Europe). Quaternary Science Reviews 169, 378-390.

Fiałkiewicz-Kozieł, B., Śmieja-Król, B., Ostovnaya, T.M., Frontasyeva, M., Siemińska, A., Lamentowicz, M., 2015. Peatland microbial communities as indicators of the extreme atmospheric dust deposition. Water Air and Soil Pollution 226, 97.

Finsinger, W., Tinner, W., 2005. Minimum count sums for charcoal-concentration estimates in pollen slides: accuracy and potential errors. The Holocene 15, 293-297.

Fournier, B., Lara, E., Jassey, V.E.J., Mitchell, E.A.D., 2015. Functional traits as a new approach for interpreting testate amoeba palaeo-records in peatlands and assessing the causes and consequences of past changes in species composition. The Holocene 25, 1375-1383.

Gałka, M., Miotk-Szpiganowicz, G., Goslar, T., Jęśko, M., Van der Knaap, W.O., Lamentowicz, M., 2013. Palaeohydrology, fires and vegetation succession in the southern Baltic during the last 7500 years reconstructed from a raised bog based on multi-proxy data. Palaeogeography Palaeoclimatology Palaeoecology 370, 209-221.

Gałka, M., Miotk-Szpiganowicz, G., Marczewska, M., Barabach, J., van der Knaap, W.O., Lamentowicz, M., 2015. Palaeoenvironmental changes in Central Europe (NE Poland) during the last 6200 years reconstructed from a high-resolution multi-proxy peat archive. The Holocene 25, 421-434.

Gałka, M., Tobolski, K., Górska, A., Lamentowicz, M., 2017a. Resilience of plant and testate amoeba communities after climatic and anthropogenic disturbances in a Baltic bog in Northern Poland: Implications for ecological restoration. The Holocene 27, 130-141.

Gałka, M., Tobolski, K., Górska, A., Milecka, K., Fiałkiewicz-Kozieł, B., Lamentowicz, M., 2014. Disentangling the drivers for the development of a Baltic bog during the Little Ice Age in northern Poland. Quaternary International 328-329, 323-337.

Gałka, M., Tobolski, K., Lamentowicz, Ł., Ersek, V., Jassey, V.E.J., Van der Knaap, W.O., Lamentowicz, M., 2017b. Unveiling exceptional Baltic bog ecohydrology, autogenic succession and climate change during the last 2000 years in CE Europe using replicate cores, multi-proxy data and functional traits of testate amoebae. Quaternary Science Reviews 156, 90-106.

Gaziński, R., 2010. Dzieje Szczecinka. Tom I (do 1939 roku). Wydawnictwo Jasne, Pruszcz Gdański.

Higuera, P.E., Brubaker, L.B., Anderson, P.M., Hu, F.S., Brown, T.A., 2009. Vegetation mediated the impacts of postglacial climatic change on fire regimes in the south-central Brooks Range, Alaska. Ecological Monographs 79, 201-219.

Higuera, P.E., Gavin, D.G., Bartlein, P.J., Hallett, D.J., 2010. Peak detection in sediment–charcoal records: impacts of alternative data analysis methods on fire-history interpretations. Int. J. Wildl. Fire 19, 996–1014.

Hölzer, A., 2010. Die Torfmoose Südwestdeutschlands und der Nachbargebiete, Weissdorn - Verlag Jena, Jena.

Jassey, V.E.J., Chiapusio, G., Binet, P., Buttler, A., Laggoun-Defarge, F., Delarue, F., Bernard, N., Mitchell, E.A.D., Toussaint, M.-L., Francez, A.-J., Gilbert, D., 2013. Above- and belowground linkages in Sphagnum peatland: climate warming affects plant-microbial interactions. Global Change Biol 19, 811-823.

Jassey, V.E.J., Signarbieux, C., Hättenschwiler, S., Bragazza, L., Buttler, A., Delarue, F., Fournier, B., Gilbert, D., Laggoun-Defarge, F., Lara, E., Mills, R.T.E., Mitchell, E.A.D., Payne, R.J., Robroek, B.J.M., 2015. An unexpected role for mixotrophs in the response of peatland carbon cycling to climate warming. Scientific Reports 5, 16931.

Jensen, K., Lynch, E.A., Calcote, R., Hotchkiss, S.C., 2007. Interpretation of charcoal morphotypes in sediments from Ferry Lake, Wisconsin, USA: do different plant fuel sources produce distinctive charcoal morphotypes? The Holocene 17, 907-915.

Kettridge, N., Turetsky, M.R., Sherwood, J.H., Thompson, D.K., Miller, C.A., Benscoter, B.W., Flannigan, M.D., Wotton, B.M., Waddington, J.M., 2015. Moderate drop in water table increases peatland vulnerability to post-fire regime shift. Scientific Reports 5, 8063.

Kothieringer, K., Walser, C., Dietre, B., Reitmaier, T., Haas, J.N., Lambers, K., 2015. High impact: early pastoralism and environmental change during the Neolithic and Bronze Age in the Silvretta Alps (Switzerland/Austria) as evidenced by archaeological, palaeoecological and pedological proxies. Zeitschrift für Geomorphologie 59, 177 – 198.

Kuhry, P., 1994. The role of fire in the development of Sphagnum-dominated peatlands in western Boreal Canada. Journal of Ecology 82.

Kuneš, P., Pokorný, P., Šída, P., 2008. Detection of the impact of early Holocene hunter-gatherers on vegetation in the Czech Republic, using multivariate analysis of pollen data. Vegetation History and Archaeobotany 17, 269-287.

Lamentowicz, M., Gałka, M., Lamentowicz, Ł., Obremska, M., Kühl, N., Lücke, A., Jassey, V.E.J., 2015. Climate change over the last 4000 years in a Baltic bog in northern Poland revealed by a trait-based approach, biotic proxies, and stable isotopes. Palaeogeography Palaeoclimatology Palaeoecology 418, 261-277.

Lamentowicz, M., Gałka, M., Pawlyta, J., Lamentowicz, L., Goslar, T., Miotk-Szpiganowicz, G., 2011. Climate change and human impact in the southern Baltic during the last Millennium reconstructed from an ombrotrophic bog archive. Studia Quaternaria 28, 3-16.

Lamentowicz, M., Milecka, K., Gałka, M., Cedro, A., Pawlyta, J., Piotrowska, N., Lamentowicz, Ł., van der Knaap, W.O., 2009. Climate and human induced hydrological change since AD 800 in an ombrotrophic mire in Pomerania (N Poland) tracked by testate amoebae, macro-fossilis, pollen tree-rings of pine. Boreas, An international journal of Quaternary research 38, 214-229.

Lamentowicz, M., Mitchell, E.A.D., 2005. The ecology of testate amoebae (Protists) in Sphagnum in north-western Poland in relation to peatland ecology. Microbial Ecology 50, 48-63.

Magnan, G., Lavoie, M., Payette, S., 2012. Impact of fire on long-term vegetation dynamics of ombrotrophic peatlands in northwestern Quebec, Canada. Quaternary Research 77, 110-121.

Marcisz, K., Colombaroli, D., Jassey, V.E.J., Tinner, W., Kołaczek, P., Gałka, M., Karpińska-Kołaczek, M., Słowiński, M., Lamentowicz, M., 2016. A novel testate amoebae trait-based approach to infer environmental disturbance in Sphagnum peatlands. Scientific Reports 6, 33907.

Marcisz, K., Gałka, M., Pietrala, P., Miotk-Szpiganowicz, G., Obremska, M., Tobolski, K., Lamentowicz, M., 2017. Fire activity and hydrological dynamics in the past 5700 years reconstructed from Sphagnum peatlands along the oceanic–continental climatic gradient in northern Poland. Quaternary Science Reviews 177, 145-157.

Marcisz, K., Lamentowicz, Ł., Słowińska, S., Słowiński, M., Muszak, W., Lamentowicz, M., 2014. Seasonal changes in Sphagnum peatland testate amoeba communities along a hydrological gradient. European Journal of Protistology 50, 445-455.

Marcisz, K., Tinner, W., Colombaroli, D., Kołaczek, P., Słowiński, M., Fiałkiewicz-Kozieł, B., Łokas, E., Lamentowicz, M., 2015. Long-term hydrological dynamics and fire history over the last 2000 years in CE Europe reconstructed from a high-resolution peat archive. Quaternary Science Reviews 112, 138-152.
Marlon, J.R., Bartlein, P.J., Daniau, A.L., Harrison, S.P., Maezumi, S.Y., Power, M.J., Tinner, W., Vannière, B., 2013. Global biomass burning: a synthesis and review of Holocene paleofire records and their controls. Quaternary Science Reviews 65, 5-25.
Mazei, Y., Tsyganov, A.N., 2006. Freshwater testate amoebae. KMK, Moscow.
Mitchell, E.A.D., Payne, R.J., Lamentowicz, M., 2008. Potential implications of differential preservation of testate amoebae shells for paleoenvironmental reconstruction in peatlands. Journal Of Paleolimnology 40, 603-618.
Oksanen, J., Blanchet, F.G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., Minchin, P.R., O'Hara, R.B., Simpson, G.L., Solymos, P., Stevens, M.H.H., Szoecs, E., Wagner, H., 2017. vegan: Community Ecology Package. R package version 2.4-2.
Payne, R., Lamentowicz, M., Van der Knaap, W.O., Van Leeuwen, J.F.N., Mitchell, E.A.D., Mazei, Y., 2012. Testate amoebae in pollen slides. Review of Palaeobotany and Palynology 173, 68-79.
Payne, R.J., Creevy, A., Malysheva, E., Ratcliffe, J., Andersen, R., Tsyganov, A.N., Rowson, J.G., Marcisz, K., Zielińska, M., Lamentowicz, M., Lapshina, E., Mazei, Y., 2016. Tree encroachment may lead to functionally-significant changes in peatland testate amoeba communities. Soil Biology & Biochemistry 98, 18-21.
Qin, Y., Payne, R., Gu, Y., Mazei, Y., Wang, Y., 2017. Short-term response of testate amoebae to wildfire. Applied Soil Ecology 116, 64-69.
R Development Core Team, 2011. R: A Language and Environment for Statistical Computing, Vienna: R Foundation for Statistical Computing.
Reimer, P.J., Bard, E., Bayliss, A., Beck, J.W., Blackwell, P.G., Bronk Ramsey, C., Buck, C.E., Cheng, H., Edwards, R.L., Friedrich, M., Grootes, P.M., Guilderson, T.P., Haflidason, H., Hajdas, I., Hatté, C., Heaton, T.J., Hoffmann, D.L., Hogg, A.G., Hughen, K.A., Kaiser, K.F., Kromer, B., Manning, S.W., Niu, M., Reimer, R.W., Richards, D.A., Scott, E.M., Southon, J.R., Staff, R.A., Turney, C.S.M., van der Plicht, J., 2013. IntCal13 and Marine13 radiocarbon age calibration curves 0e 50,000 years cal. BP. Radiocarbon 55, 1869–1887.
Sillasoo, U., Väliranta, M., Tuittila, E.S., 2011. Fire history and vegetation recovery in two raised bogs at the Baltic Sea. Journal of Vegetation Science 22, 1084-1093.
Silvan, N., Tuittila, E.-S., Vasander, H., Laine, J., 2004. Eriophorum vaginatum plays a major role in nutrient immobilisation in boreal peatlands. Annales Botanici Fennici 41, 189–199.
Stockmarr, J., 1971. Tablets with spores used in absolute pollen analysis. Pollen et Spores 13, 615-621.
Stoffer, D., 2016. Applied Statistical Time Series Analysis R package version 1.7.
Strack, M., 2008. Peatlands and climate change. International Peat Society, University of Calgary, Canada.
Swindles, G.T., Roe, H.M., 2007. Examining the dissolution characteristics of testate amoebae (Protozoa: Rhizopoda) in low pH conditions: Implications for peatland palaeoclimate studies. Palaeogeography, Palaeoclimatology, Palaeoecology 252, 486-496.
Szczecinek Historical Portal, 2019. Szczecinek Calendar (in Polish), http://szczecinek.org/kalendarium.html [access date: 09.01.2019], In: Szczeciński Portal Historyczny im. Karla Tuempla (Ed.).
Tinner, W., Conedera, M., Ammann, B., Gaggeler, H.W., Gedye, S., Jones, R., Sagesser, B., 1998. Pollen and charcoal in lake sediments compared with historically documented forest fires in southern Switzerland since AD 1920. The Holocene 8, 31-42.
Tinner, W., Hu, F.S., 2003. Size parameters, size-class distribution and area-number relationship of microscopic charcoal: relevance for fire reconstruction. The Holocene 13, 499-505.
Tobolski, K., 2000. Przewodnik do oznaczania torfów i osadów jeziornych. PWN, Warszawa.
Tuittila, E.S., Väliranta, M., Laine, J., Korhola, A., 2007. Quantifying patterns and controls of mire vegetation succession in a southern boreal bog in Finland using partial ordinations. Journal of Vegetation Science 18, 891-902.
Turetsky, M.R., Benscoter, B., Page, S., Rein, G., van der Werf, G.R., Watts, A., 2015. Global vulnerability of peatlands to fire and carbon loss. Nature Geosci 8, 11-14.
Umbanhowar, C.E., McGrath, M.J., 1998. Experimental production and analysis of microscopic charcoal from wood, leaves and grasses. The Holocene 8, 341-346.

van Haesebroeck, V., Boeye, D., Verhagen, B., Verheyen, R.F., 1997. Experimental investigation of drought induced acidification in a rich fen soil. Biogeochemistry 37, 15-32.
Vannière, B., Blarquez, O., Rius, D., Doyen, E., Brücher, T., Colombaroli, D., Connor, S., Feurdean, A., Hickler, T., Kaltenrieder, P., Lemmen, C., Leys, B., Massa, C., Olofsson, J., 2016. 7000-year human legacy of elevation-dependent European fire regimes. Quaternary Science Reviews 132, 206-212.
Watson, E.J., Kołaczek, P., Słowiński, M., Swindles, G.T., Marcisz, K., Gałka, M., Lamentowicz, M., 2017. First discovery of Holocene Alaskan and Icelandic tephra in Polish peatlands. Journal of Quaternary Science 32, 457-462.
Whitlock, C., Larsen, C., 2001. Charcoal as a fire proxy., Tracking environmental change using lake sediments. Terrestrial, algal, and siliceous indicators. J. P. Smol, H. J. B. Birks, and W. M. Last, Eds., Dordrecht: Kluwer, pp. 75-97.
Wilson, P.H., 2011. Thirty Years' War (1618–1648), The Encyclopedia of War. Blackwell Publishing Ltd.

Appendix S1

Quaternary Science Reviews

Responses of vegetation and testate amoeba trait composition to fire disturbances in and around a bog in central European lowlands (northern Poland)

Katarzyna Marcisz*[1,2,3], Mariusz Lamentowicz[2,3], Mariusz Gałka[3,4], Daniele Colombaroli[1,5], Carole Adolf[1,6], Willy Tinner[1]

[1] Institute of Plant Sciences and Oeschger Centre for Climate Change Research, University of Bern, Altenbergrain 21, CH-3013 Bern, Switzerland

[2] Laboratory of Wetland Ecology and Monitoring, Adam Mickiewicz University in Poznań, Krygowskiego 10, 61-680 Poznań, Poland

[3] Department of Biogeography and Palaeoecology, Adam Mickiewicz University in Poznań, Krygowskiego 10, 61-680 Poznań, Poland

[4] Department of Geobotany and Plant Ecology, Faculty of Biology and Environmental Protection, University of Lodz, 12/16 Banacha Str., Lodz, Poland

[5] Department of Geography, Royal Holloway, University of London, UK

[6] Department of Zoology, Long-Term Ecology Laboratory, University of Oxford, UK

* Correspondence: Katarzyna Marcisz, Laboratory of Wetland Ecology and Monitoring, Adam Mickiewicz University in Poznań, Krygowskiego 10, 61-680 Poznań, Poland, e-mail: marcisz@amu.edu.pl

Supplementary Figures

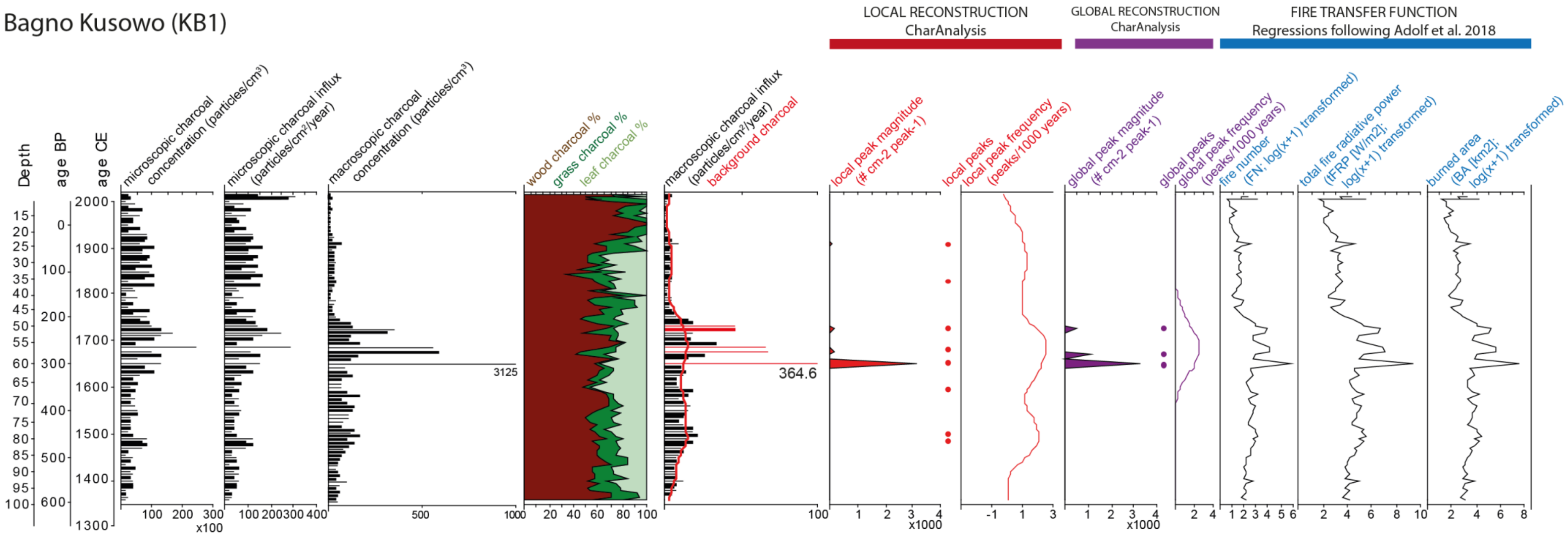


Fig. S1.1 The results of the fire reconstruction from CharAnalysis program based on macroscopic charcoal (MAC). We smoothed MAC values with a robust LOWESS (Locally Weighted Scatterplot Smoothing, 100-year smoothing window) to identify background charcoal (BCHAR). BCHAR may reflect regional fire activity or reworked charcoal (Long et al., 1998; Whitlock and Larsen, 2001). We chose robust LOWESS smoothing over LOWESS because of higher local signal-to-noise index (Higuera et al., 2009). Afterwards, we obtained residuals (charcoal peak series) by subtracting the BCHAR component from the raw CHAR record, and separated the noise component from the peaks using both locally and globally defined threshold. This enabled to identify statistically significant charcoal peaks that likely reflect local fire episodes. The locally defined threshold is based on the 90th percentile of the noise distribution using a Gaussian mixture model (Higuera et al., 2010). A local threshold was used because changes in local vegetation composition and changes in fuel availability may have influenced charcoal production (Marlon et al., 2008; Morales-Molino et al., 2015; Tinner et al., 2005). The globally defined threshold value is based on the 99th percentile of the noise distribution and is, therefore, a more conservative estimation used to separate the noise component that may be an effect of random variability, distant fires, sediment mixing or redeposition (Long et al., 1998; Whitlock and Larsen, 2001). Inferred fire frequency (IFF, fire episodes per 1000 years) was reconstructed using a global threshold to define trends in biomass burning (Colombaroli et al., 2010; Higuera et al., 2009). We used fire transfer functions following Adolf et al. (2018) in order to reconstruct annual fire number (FN), total fire radiative power (tFRP; W/m^2) and burned area (BA; km^2). The results are based on the following regression equations: $\log_{10}(FN+1)=2.1802*\log_{10}(tMACi+1)+0.207$; $\log_{10}(tFRP+1)=3.2172*\log_{10}(tMACi+1)+1.1002$; $\log_{10}(BA+1)=2.6429*\log_{10}(tMACi+1)+0.712$. According to the calibration study, the reconstructions estimate those parameters around the study site at the radius of 40 km for FN and tFRP (extra-local scale reconstruction) and 180 km for BA (regional-scale reconstruction) (Adolf et al., 2018). Here, the results are presented as log(x+1)-transformed values. The red bars of macroscopic charcoal indicate samples where large charcoal particles >500 µm were found.

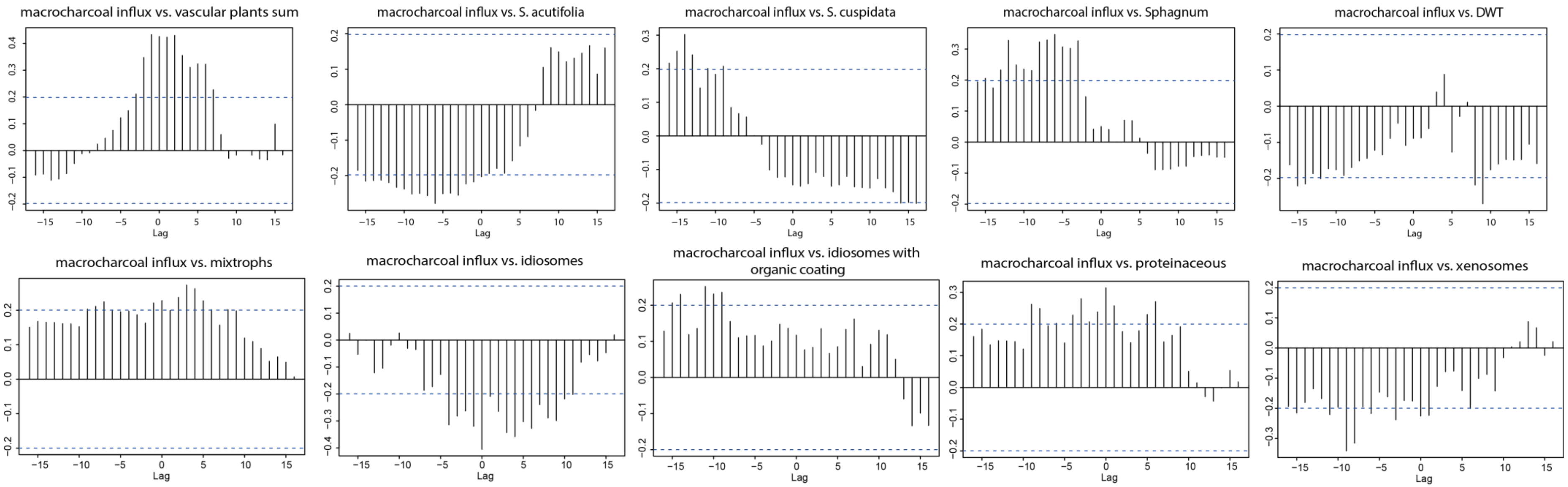
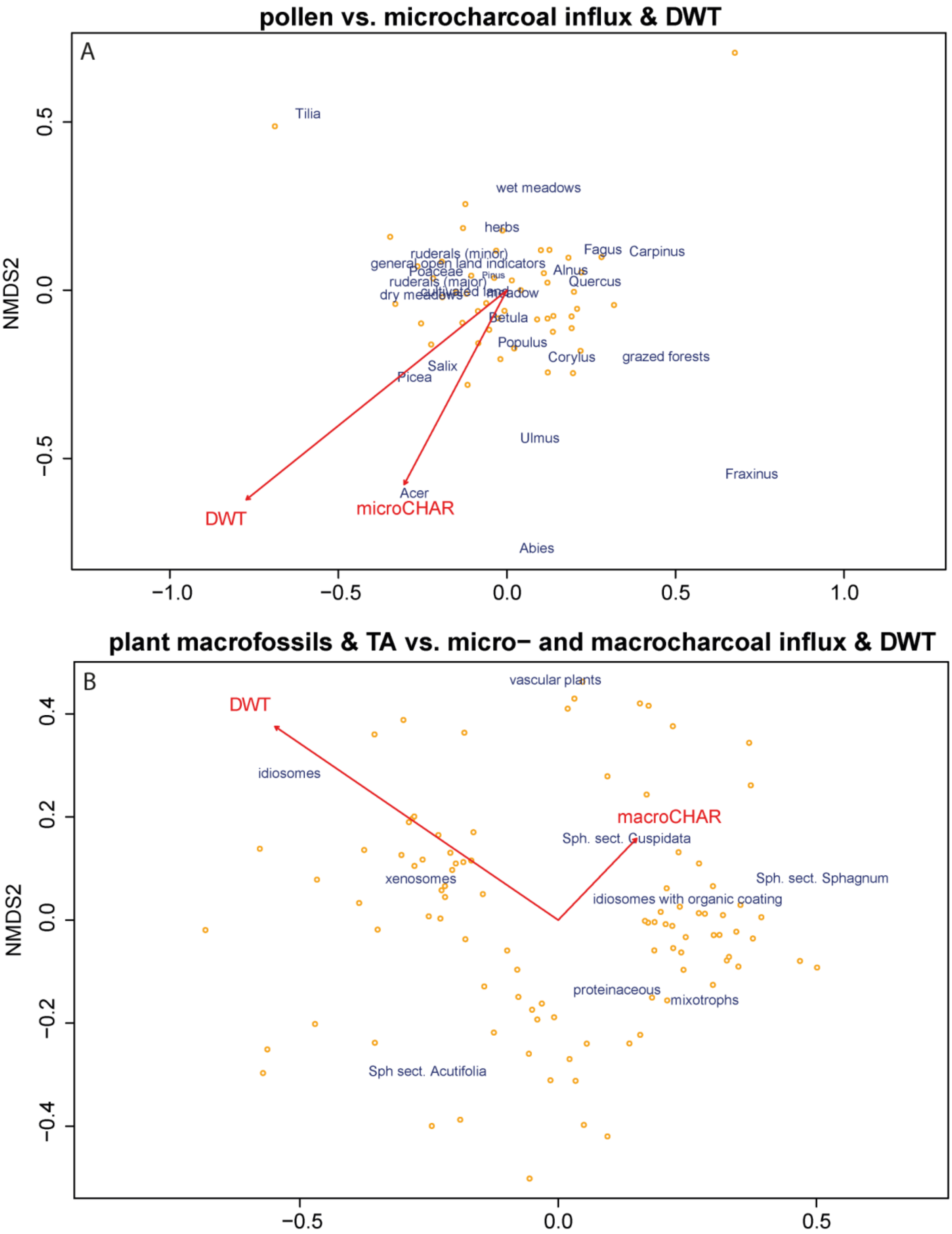


Fig. S1.2 Cross-correlation diagrams showing relationship between macroscopic charcoal influx and local proxies – plant macrofossils, depth to water table reconstruction (DWT), and testate amoebae traits (mixotrophs, idiosomes, idiosomes with organic coating, proteinaceous, xenosomes). Correlation coefficients outside the dashed lines are significant at $P = 0.05$.


pollen vs. microcharcoal influx & DWT
A
NMDS2
0.5
0.0
−0.5
−1.0
−0.5
0.0
0.5
1.0
Tilia
wet meadows
herbs
ruderals (minor)
general open land indicators
Poaceae
ruderals (major)
Pinus
cultivated land
meadow
dry meadows
Fagus
Carpinus
Alnus
Quercus
Betula
Populus
Corylus
grazed forests
Salix
Picea
Ulmus
Fraxinus
Acer
microCHAR
DWT
Abies
plant macrofossils & TA vs. micro− and macrocharcoal influx & DWT
B
NMDS2
0.4
0.2
0.0
−0.2
−0.4
−0.5
0.0
0.5
vascular plants
DWT
idiosomes
macroCHAR
Sph. sect. Cuspidata
Sph. sect. Sphagnum
xenosomes
idiosomes with organic coating
proteinaceous
mixotrophs
Sph sect. Acutifolia

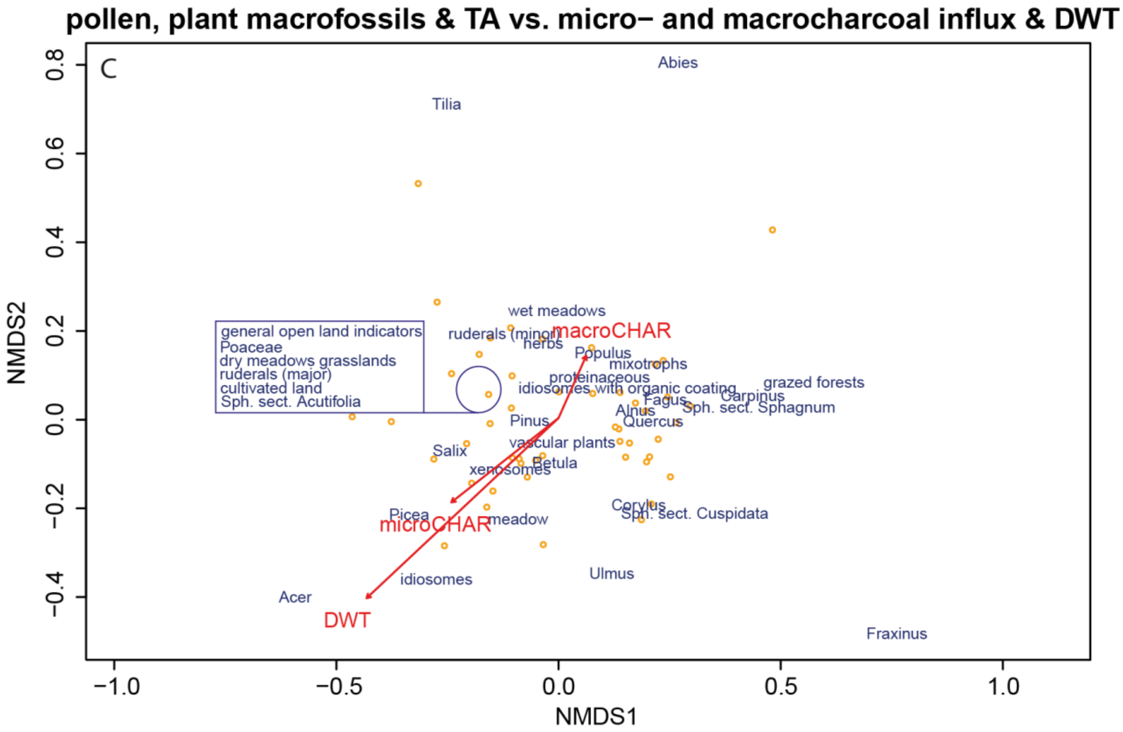


Fig. S1.3 Non-metric multidimensional scaling (NMDS) computed for regional (A), local (B) and all (C) proxies. Stress values for both diagrams were low (regional = 0.175, local = 0.169, all = 0.172, weak ties).

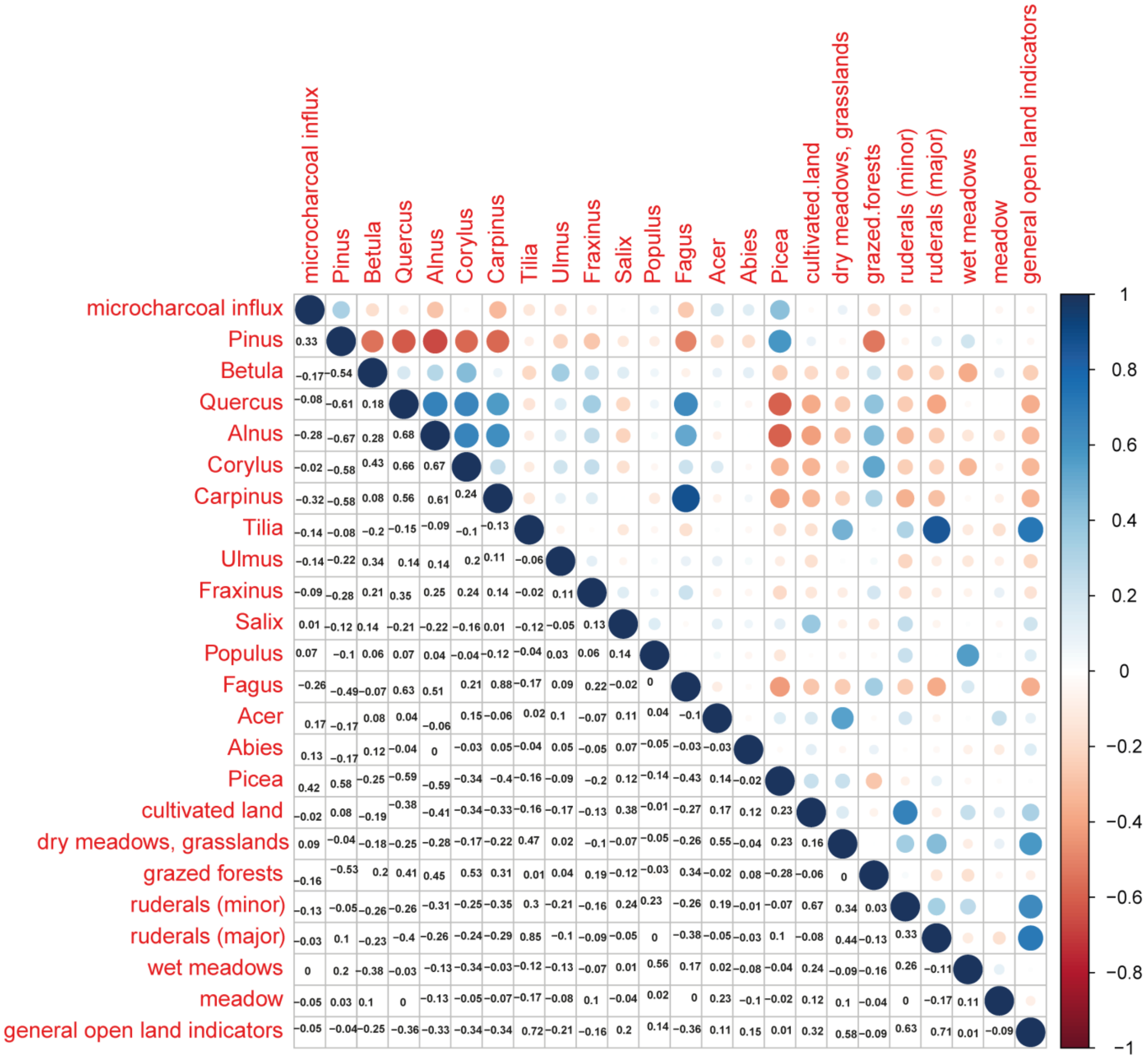


Fig. S1.4 Pearson's correlation matrix for regional proxies – microscopic charcoal influx and selected pollen types (trees and groups of pollen indicators described in S1.5).

Supplementary Tables

Tab. S1.5 List of pollen taxa included in the summary diagram of human impact. Classes of land-use category follow Poska et al. (2004).

Land-use category	Indicator taxa
Cultivated land	*Centaurea cyanus*, Cerealia type, *Hordeum* type, *Fagopyrum esculentum* type, *Juglans*, *Secale*, *Triticum* type
Dry meadows, grasslands	*Campanula* type, *Calluna vulgaris*, *Juniperus*
Grazed forests	*Pteridium aquilinum*
Ruderals (minor)	Brassicaceae, *Plantago lanceolata*, *Plantago major*, *Plantago media*, *Polygonum aviculare* type, *Rumex acetosa* type, *Rumex acetosella* type, *Urtica*
Ruderals (major)	*Artemisia*, Chenopodiaceae
Wet meadows	Cyperaceae, *Filipendula*
Meadow	*Cirsium*/*Carduus*, *Potentilla* type, Ranunculaceae undiff., *Ranunculus acris* type, *Trifolium* type
General open land indicators	Apiaceae, *Aster* type, Poaceae undiff.

References:

Adolf, C., Wunderle, S., Colombaroli, D., Weber, H., Gobet, E., Heiri, O., van Leeuwen, J.F.N., Bigler, C., Connor, S.E., Gałka, M., La Mantia, T., Makhortykh, S., Svitavská-Svobodová, H., Vannière, B., Tinner, W., 2018. The sedimentary and remote-sensing reflection of biomass burning in Europe. Global Ecology and Biogeography 27, 199-212.

Colombaroli, D., Henne, P.D., Kaltenrieder, P., Gobet, E., Tinner, W., 2010. Species responses to fire, climate and human impact at tree line in the Alps as evidenced by palaeo-environmental records and a dynamic simulation model. Journal of Ecology 98, 1346-1357.

Higuera, P.E., Brubaker, L.B., Anderson, P.M., Hu, F.S., Brown, T.A., 2009. Vegetation mediated the impacts of postglacial climatic change on fire regimes in the south-central Brooks Range, Alaska. Ecological Monographs 79, 201-219.

Higuera, P.E., Gavin, D.G., Bartlein, P.J., Hallett, D.J., 2010. Peak detection in sediment–charcoal records: impacts of alternative data analysis methods on fire-history interpretations. Int. J. Wildl. Fire 19, 996–1014.

Long, C.J., Whitlock, C., Bartlein, P.J., Millspaugh, S.H., 1998. A 9000-year fire history from the Oregon Coast Range, based on a high-resolution charcoal study. Can. J. For. Res. 28, 774-787.

Marlon, J.R., Bartlein, P.J., Carcaillet, C., Gavin, D.G., Harrison, S.P., Higuera, P.E., Joos, F., Power, M.J., Prentice, I.C., 2008. Climate and human influences on global biomass burning over the past two millennia. Nature Geosci 1, 697-702.

Morales-Molino, C., Vescovi, E., Krebs, P., Carlevaro, E., Kaltenrieder, P., Conedera, M., Tinner, W., Colombaroli, D., 2015. The role of human-induced fire and sweet chestnut (Castanea sativa Mill.) cultivation on the long-term landscape dynamics of the southern Swiss Alps. The Holocene 25, 482-494.

Poska, A., Saarse, L., Veski, S., 2004. Reflections of pre- and early-agrarian human impact in the pollen diagrams of Estonia. Palaeogeography Palaeoclimatology Palaeoecology 209, 37-50.

Tinner, W., Conedera, M., Ammann, B., Lotter, A.F., 2005. Fire ecology north and south of the Alps since the last ice age. The Holocene 15, 1214-1226.

Whitlock, C., Larsen, C., 2001. Charcoal as a fire proxy., Tracking environmental change using lake sediments. Terrestrial, algal, and siliceous indicators. J. P. Smol, H. J. B. Birks, and W. M. Last, Eds., Dordrecht: Kluwer, pp. 75-97.