



Hydrological dynamics and fire history of the last 1300 years in western Siberia reconstructed from a high-resolution, ombrotrophic peat archive



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ABSTRACT

Siberian peatlands provide records of past changes in the continental climate of Eurasia. We analyzed a core from Mukhrino mire in western Siberia to reconstruct environmental change in this region over the last 1300 years. The pollen analysis revealed little variation of local pine-birch forests. A testate amoebae transfer function was used to generate a quantitative water-table reconstruction; pollen, plant macrofossils, and charcoal were analyzed to reconstruct changes in vegetation and fire activity. The study revealed that Mukhrino mire was wet until the Little Ice Age (LIA), when drought was recorded. Dry conditions during the LIA are consistent with other studies from central and eastern Europe, and with the pattern of carbon accumulation across the Northern Hemisphere. A significant increase in fire activity between ca. AD 1975 and 1990 may be associated with the development of the nearby city of Khanty-Mansiysk, as well as with the prevailing positive Arctic Oscillation.

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Introduction

Northern hemisphere peatlands are important archives of past environmental change and sinks of carbon (Charman, 2002; Loisel et al., 2014). However, climate change and human impacts (e.g., wetland drainage and nutrient deposition) trigger increased emission of this stored carbon into the atmosphere (Payne et al., 2013; Ward et al., 2013). Given these ongoing stressors, there is an urgent need to better understand the various processes involved in peatland dynamics (Dise, 2010; Loisel and Yu, 2013). Paleoenvironmental approaches provide a useful perspective on the present state and long-term history of peatlands (Seddon et al., 2014), and the application of coupled biotic and abiotic proxies enables a detailed reconstruction of climate change, peatland ecosystem development, and changes in the surrounding landscape (Gałka et al., 2013).

The last millennium is a critical period for paleoenvironmental study, as it features both climatic variability, such as the Medieval Warm Period (MWP) and the Little Ice Age (LIA), and increasing anthropogenic impacts leading up to the dramatic increases in pollution

and global temperatures observed over the last 200 years (Jones and Mann, 2004). Peatland ecosystems experience various types of anthropogenic and natural disturbances, including wetland drainage, forest management, and fire (Dise, 2010). The response of peatlands to disturbance and climate change has been well studied in Europe (Lamentowicz et al., 2008, 2011; van der Knaap et al., 2011), but the paleoecology of Siberian bogs remains largely unexplored.

The hydrological dynamics of Siberian peatlands over the last millennium are of particular interest, and testate amoebae, protists that are abundant in peatlands and sensitive to hydrological conditions, can be used as a reliable proxy for the quantitative reconstruction of past variability in water tables (Hendon and Charman, 2004; Blundell et al., 2008; Booth et al., 2008; Turner et al., 2014). However, while some research has explored the ecology and taxonomy of testate amoebae in Siberian bogs (Muller et al., 2009; Kurina et al., 2010; Bobrov et al., 2013), modern calibration studies have not been carried out in this region. Such calibration data sets for testate amoebae are urgently needed so that this proxy can be utilized for the reconstruction of past hydrological variations in western Siberia.

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Several analyses of Siberian peatlands have focused on carbon accumulation (Lapshina et al., 2001; Turunen et al., 2001; Borren et al., 2004; Beilman et al., 2009; Lapshina and Plogova, 2011), but few peatland studies in this region have generated paleoecological inferences (Liss et al., 2001; Pitkänen et al., 2002; Kremenetski et al., 2003; Peregon et al., 2007a, 2007b; Bobrov et al., 2013). This is in contrast to work in northwest Europe and North America, where a large number of high-resolution, multi-proxy studies have been performed in peatlands (Blundell and Barber, 2005; Booth et al., 2006; Swindles et al., 2007; Kaislahti Tillman et al., 2010; Turner et al., 2014). The lack of such studies in Siberia is unfortunate, as Siberian peatlands cover much larger areas than in other parts of Eurasia. Moreover, paleoenvironmental records from Siberian peatlands have the potential to improve our understanding of past changes in both the continental climate of Eurasia and pristine vegetation that no longer exists in Europe (Solomeshch, 2005).

Charcoal records from peatlands have been used to reconstruct past fire activity in Europe (Sillasoo et al., 2011; Gałka et al., 2013) and North America (Lavoie and Pellerin, 2007), but only limited research of this type has been carried out in Siberia (Turunen et al., 2001), despite the global importance of peatland fires (Turetsky et al., 2015). It is believed that during the last decade, burning has increased in Siberia due to the prevailing positive Arctic Oscillation (Balzter et al., 2005). This relationship can only be verified with a paleoecological approach, since mapped fire data and instrumental weather data cover only short time scales. Over longer intervals, increased fire activity may be related to the prolonged drought events that are recorded by hydrological changes in peatlands. Charcoal data have not been regularly compared to quantitative paleohydrological reconstructions (Tweiten et al., 2009). Nevertheless, the study by Marcisz et al. (2015) showed that a coupled analysis of charcoal and testate amoebae could improve our understanding of past droughts and heat waves over long temporal scales.

In this study, we apply three methodological approaches that previously have not been used together in Siberia. (i) A testate amoebae transfer function was used for a quantitative water table reconstruction; (ii) pollen and plant macrofossils were used to reconstruct vegetation history; and (iii) a charcoal record was used to infer past fire activity. The integration of these proxies allows us to explore the response of boreal peatlands, forest communities, and fire activity to climate change. This research focus aligns well with the *PAGES-Asia2k* research program

(Ahmed et al., 2013). A modern calibration study also improves our understanding of testate amoebae ecology in the boreal region of Siberia.

Study site

The Mukhrino mire is located on the eastern bank of the Irtysh River, near the confluence with the Ob River in the middle taiga area of western Siberia, about 20 km from Khanty-Mansiysk (60°54' N, 68°42' E). This region is located in the Boreal climate zone, which corresponds to the Sub-Arctic climate zone of western Europe (Fig. 1). The mean annual temperature is -1.3°C , the coldest month being January with a mean temperature of -18.9°C ; the warmest month is July, with a mean temperature of 17.1°C . The mean annual precipitation is 553 mm (Kremenetski et al., 2003). In 2009, the Mukhrino Field Station was built at the margin of a giant mire complex. It is managed by the UNESCO Chair of Environmental Dynamics and Climate Change at Yugra State University, Khanty-Mansiysk, Russia (Elger et al., 2012). The Mukhrino mire complex is typical for the West Siberian middle taiga. It is a complex of oligotrophic-raised bogs (*Pinus sylvestris* and *P. sibirica*, *Eriophorum vaginatum*, *Ledum palustre*, *Chamaedaphne calyculata*, *Betula nana*, and *Sphagnum fuscum*) patterned with ridge-hollows (*Carex limosa*, *Scheuchzeria palustris*, *Sphagnum balticum*, *S. jensenii*, and *S. papillosum*) and oligo-mesotrophic fens (*Carex rostrata*, *Menyanthes trifoliata*, *E. russeolum*, *S. fallax*, *S. jensenii*, and *S. majus*) (Filippov and Lapshina, 2008). This area is characterized by the absence of permafrost (Bleuten and Filippov, 2008). The Mukhrino peatland has a peat thickness between 3 m and 4.5 m. Its hydrology is dependent on micro-topography and changes seasonally. During the summer, groundwater in poor fens and hollows is between 5 cm and 20 cm below the moss surface, while in raised bog areas with *Sphagnum* hummocks, the water table is 40–80 cm below the surface (Bleuten and Filippov, 2008).

Materials and methods

Field sampling

In summer 2012, a 1-m-long peat core was sampled with a long serrated knife and sliced in the field into 1-cm samples. Each slice was



Figure 1. Map of Eurasia showing the location of Mukhrino mire and indicating the range of boreal forests.

divided into four subsamples to be used in the four analyses. These peat samples were then packed into plastic bags and transported to the laboratory. They were kept refrigerated until processing.

In addition, 65 moss samples and 5 liverwort samples were collected in the summers of 2012 and 2013 in the mire around Mukhrino station for the construction of a calibration data set to be used in the testate amoebae transfer function. Surface samples were taken along a wet–dry gradient from pools to the tops of hummocks. Water table depth was measured once during the sampling campaign, together with pH and conductivity.

Chronology and peat accumulation rate

Eleven AMS (accelerator mass spectroscopy) ^{14}C dates were obtained in the Poznań Radiocarbon Laboratory (Poland) in 2013. The samples subjected to dating contained *Sphagnum* stems and leaves and these were carefully cleaned from rootlets to avoid contamination by younger carbon (Table 1). The basis for the chronology of the Mukhrino peat profile is a Bayesian age–depth model constructed using the OxCal v. 4.2 program (Bronk Ramsey, 2008), with the application of the IntCal13 (Reimer et al., 2013) and NH1 post-bomb (Hua et al., 2013) atmospheric curves. For the calculation of the model with a 0.5-cm resolution, the *P_Sequence* function with parameters $k_0 = 1$ and $\log_{10}(k/k_0) = 0.3$ was applied. The most distinct changes in the peat structural composition and pollen concentration of the profile were introduced using the *Boundary* command. The first boundaries were established at depths of 100 cm and 0 cm (the bottom and top of the model, respectively), followed by 86.5 cm and 50.5 cm (both reflecting rapid changes in pollen concentration and bulk density (cf. Fiałkiewicz-Kozieł et al., 2015)). The age of the top of profile (0 cm) was set as AD 2012.7 (the August 2012—the date of the core retrieval). Hereafter, ages are presented as mean (μ) values of the modeled ages, and expressed as AD years. The peat accumulation rate (P), expressed as cm/yr, was calculated according to the formula: $P_{\text{depth}} = 1 \text{ cm}/(\mu_{\text{depth} - 0.5 \text{ cm}} - \mu_{\text{depth} + 0.5 \text{ cm}})$.

Pollen and charcoal

Twenty-four samples (1 cm thick, each 2 cm³ in volume) were prepared with a standard preparation procedure with the application of

hydrofluoric acid to remove silica, followed by acetolysis (Berglund and Ralska-Jasiewiczowa, 1986). A *Lycopodium* tablet (20,848 spores, produced by the University of Lund) was added to each sample to enable the calculation of pollen concentrations (Stockmarr, 1971). Pollen slides mounted with glycerin were analyzed using a light microscope at 400× and 1000× magnification and counted to a sum of arboreal pollen (AP) >500 grains. Two samples with pollen concentrations <10,000 grains/cm³ were counted to <500 AP grains. Then, on the same slides, microscopic charcoal particles (10–100 μm in length) were counted at 200× magnification, along with *Lycopodium* spores, until a sum of 200 was reached (Tinner and Hu, 2003; Finsinger and Tinner, 2005). Pollen grains were identified with the assistance of the modern pollen slide collection of the Institute of Geoecology and Geoinformation of Adam Mickiewicz University in Poznań (Poland), as well as available keys and atlases (e.g. Moore et al., 1991; Beug, 2004). Percentages of pollen and spores were calculated relative to the sum of trees, shrubs, and herbs, excluding the pollen of wetland plants and dwarf shrubs. Charcoal accumulation rates (CHAR), expressed as charcoal particles/cm²/yr, were calculated by multiplying charcoal concentrations (CHAC, particles/cm³) by the sediment accumulation rate for each analyzed level (Davis and Deevey, 1964).

Testate amoebae

Fossil testate amoebae were analyzed in subsamples taken at 1 cm intervals, whereas modern testate amoebae assemblages used to create the new transfer function were examined from surface moss samples. All of these samples were prepared by sieving and back-sieving (Booth et al., 2010). The testate amoebae were analyzed at 200–400× magnification, and a minimum of 150 tests per sample were performed whenever possible (Payne and Mitchell, 2008). The identification was performed at the highest possible taxonomical resolution based on the available literature (e.g., Grospletsch, 1958; Ogdén and Hedley, 1980; Mazei and Tsyganov, 2006).

Macrofossils

For the analyses of plant macrofossils, contiguous samples of 3 cm³ (96 core samples) were analyzed at varying resolutions (2-cm

Table 1
Results of radiocarbon dating from the Mukhrino profile. Abbreviations: Poz—laboratory code of the Poznań Radiocarbon Laboratory (Poland).

| Depth [cm] | Laboratory code | Age [^{14}C yr BP] | Calibrated age, 2σ range [AD]; in brackets probability of the range of age | Material selected to date; remarks |
|------------|-----------------|------------------------------|--|---|
| 13–14 | Poz-57449 | 107.81 ± 0.34 | 1956–1957 (3.7%) | <i>Sphagnum</i> stems |
| | | pMC | 2001–2005 (91.7%) | |
| 20–21 | Poz-57451 | 110.13 ± 0.33 | 1957 (1.3%) | <i>Sphagnum</i> stems |
| | | pMC | 1996–2000 (94.1%) | |
| 31–32 | Poz-56374 | 130.35 ± 0.45 | 1961–1962 (4.9%) | <i>Sphagnum</i> stems |
| | | pMC | 1978–1980 (90.5%) | |
| 40–41 | Poz-56525 | 145.69 ± 0.4 | 1962–1963 (7.9%) | <i>Sphagnum</i> stems |
| | | pMC | 1972–1974 (87.5%) | |
| 51–52 | Poz-59502 | 70 ± 30 | 1691–1730 (24.3%) | <i>Sphagnum</i> stems; excluded from age–depth modeling |
| | | | 1810–1924 (71.1%) | |
| 56–57 | Poz-69551 | 145 ± 30 | 1668–1710 (16.3%) | <i>Sphagnum</i> stems |
| | | | 1717–1782 (29.2%) | |
| | | | 1797–1891 (33.5%) | |
| | | | 1909–1948 (16.4%) | |
| 60–61 | Poz-69552 | 140 ± 30 | 1669–1780 (43.1%) | <i>Sphagnum</i> stems |
| | | | 1798–1891 (36.8%) | |
| | | | 1909–1945 (15.5%) | |
| 69–70 | Poz-59503 | 495 ± 30 | 1400–1450 | <i>Sphagnum</i> stems |
| 79–80 | Poz-59385 | 995 ± 30 | 986–1052 (63.8%) | <i>Sphagnum</i> stems |
| | | | 1081–1158 (31.6%) | |
| 90–91 | Poz-59386 | 1270 ± 30 | 663–778 (92.3%) | <i>Sphagnum</i> stems |
| | | | 792–804 (1.3%) | |
| | | | 819–821 (0.2%) | |
| | | | 842–859 (1.6%) | |
| 99–100 | Poz-59387 | 1260 ± 30 | 669–779 (85.3%) | <i>Sphagnum</i> stems |
| | | | 791–829 (5.9%) | |
| | | | 838–865 (4.2%) | |

resolution between 0 cm and 10 cm depth; 1-cm resolution below 10 cm depth). Each sample was wet sieved through a 0.2-mm mesh, and macrofossils were identified under a binocular microscope using several keys (Grosse-Brauckmann, 1974, 1992; Tobolski, 2000; Birks, 2007; Laine et al., 2011) and reference specimens collected in Siberia. Additionally, macroscopic charcoal particles were counted wherever present.

Bulk density and ash content

Bulk density (BD; g cm^{-3}) and ash content (AC; %) were measured to characterize the physical properties of the peat. BD was determined on the basis of 5-cm³ subsamples, which were dried at 105°C for 24 h and then weighed. The dry weight (g) was divided by the fresh sample volume (cm³) (Chambers et al., 2011). AC for 94 duplicates was obtained by measuring the LOI₅₅₀, where LOI₅₅₀ is the loss on ignition at 550°C as defined by Heiri et al. (2001), and calculated using the equation $AC = 100\% - LOI_{550}$.

Numerical analyses

A Hellinger-transformed testate amoebae community matrix was used as a response matrix (Legendre and Gallagher, 2001). Redundancy analyses (RDA) were employed to relate abiotic variables (water table, pH, and conductivity) to biotic communities. The significance of the model, axes, and variables was tested using a Monte Carlo test with 999 permutations. Computations were performed in R 3.0.1 (Team, 2013), using the *vegan* package (Oksanen et al., 2011).

A quantitative water table reconstruction was developed using the local testate amoebae calibration data set from 68 moss samples

collected in the Mukhrino peatland in 2012 and 2013. The training set was based on the relative abundance (percentage of entire community in a sample) and tested using common models in paleoecology, such as partial least squares (PLS), weighted averaging (WA), and weighted averaging partial least squares (WA-PLS) (Juggins and Birks, 2012). Prior to analysis, species present in less than three samples were removed. The best performing model was assessed using RMSEP, R², and maximum bias criteria. Then, the model was used for the quantitative inference of the water table. Sample specific errors of the reconstruction were calculated using bootstrapping (Birks, 1995). Calculations as well as testate amoebae and plant macrofossil diagrams were done using C2 software (Juggins, 2003). The results of pollen analysis was summarized in diagram drawn in TILIAGraph program (Grimm, 1991).

Results and interpretation

Ecology of testate amoebae

A total of 64 testate amoebae taxa species and subspecies from 23 genera were identified at the Mukhrino mire. The most abundant taxa were *Archerella flavum* (20%), *Hyalosphenia papilio* (15%), *Assulina muscorum* (8%), and *Phryganella acropodia* (7%). The Shannon–Weiner diversity index ranged between 1.37 and 2.59. RDA revealed three clusters of species (Fig. 3A). Species composition shows that *Assulina muscorum*, *A. seminulum*, *Trigonopyxis arcua*, *Trinema lineare*, and *Arcella catinus* are correlated with low water table, whereas *Nebela carinata* is an indicator of wet conditions. *Hyalosphenia papilio* occurs in plots with higher pH and conductivity (EC), and a moderately wet environment. *Cyclopyxis arcelloides*, *Diffugia bacillifera*, *D. bacilliarum*,

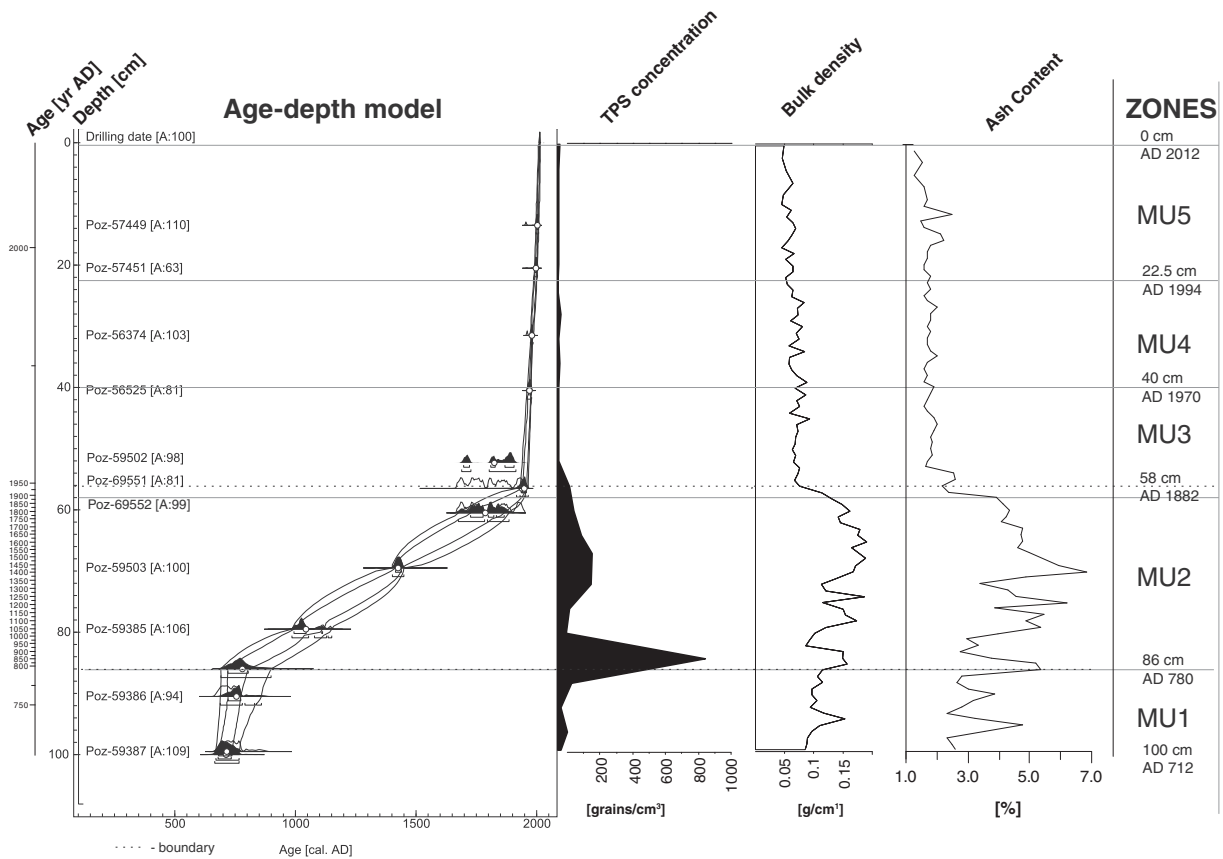


Figure 2. Age-depth model for the Mukhrino mire core with bulk density and ash content. Dates are listed on the left along the depth scale (see Table 1). Each of these is presented with individual agreement of modeled and calibrated date, which is placed in square brackets (for details, see Bronk Ramsey (2008)). Abbreviations: Poz—laboratory code of Poznań Radiocarbon Laboratory, TPS—total pollen sum.

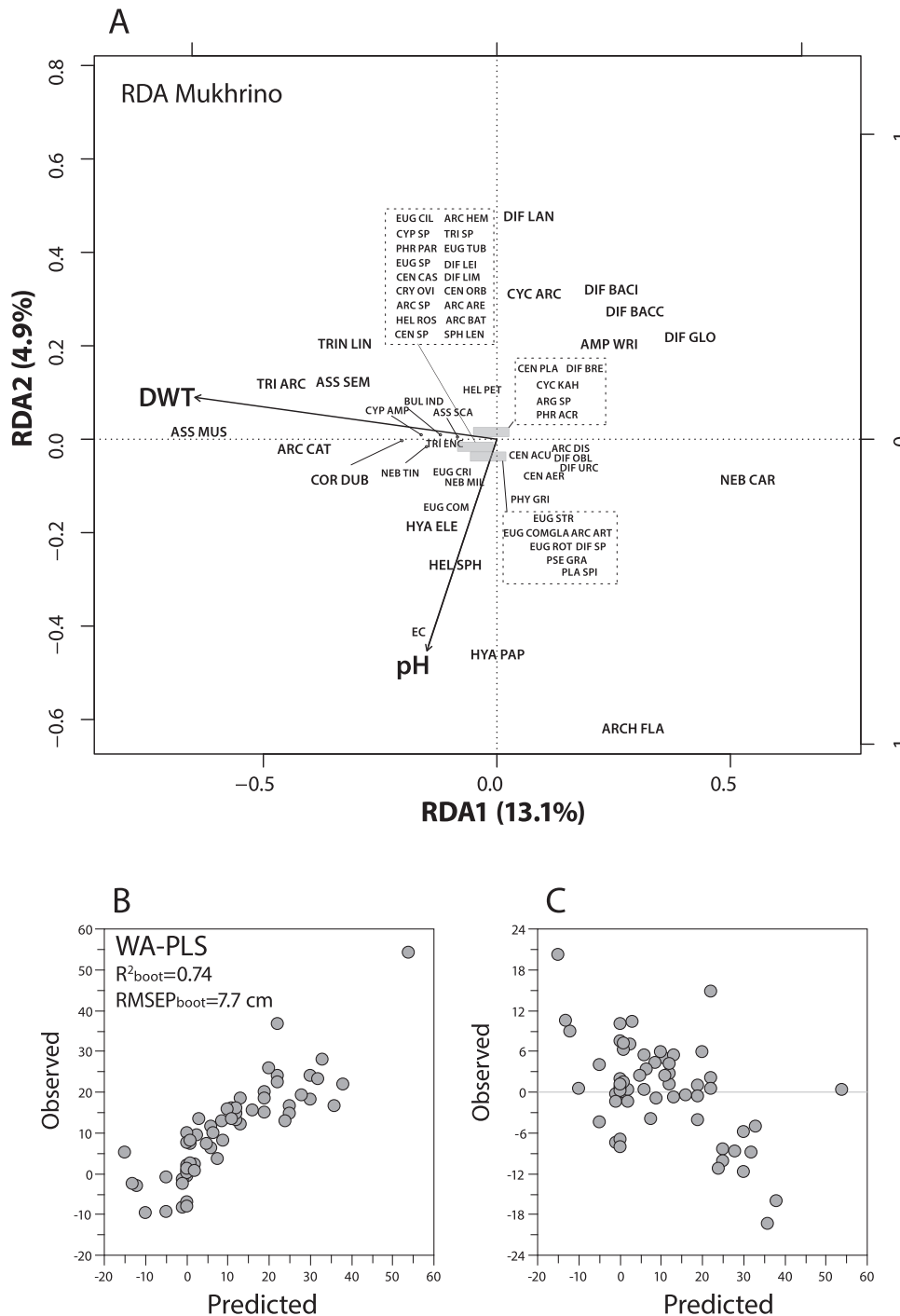


Figure 3. Result of the redundancy analysis (RDA) of testate amoeba communities (A) and measured environmental variables (pH and depth to the water table—DWT) from modern surface samples collected from Mukhrino mire. (B) observed vs. predicted model, and (C) residuals of the weighted averaging partial least squares model with bootstrap cross validation (WA-PLSboot). Species abbreviations: AMP WRI—*Amphitrema wrightianum*, ARC ARE—*Arcella arenaria*, ARC ART—*Arcella artocrea*, ARC BAT—*Arcella bathystoma*, ARC CAT—*Arcella catinus*, ARC DIS—*Arcella discoides*, ARC SP—*Arcella* sp., ARCH FLA—*Archerella flavum*, ARC HEM—*Arcella hemisphaerica*, ARGSP—*Argygnia* sp., ASS MUS—*Assulina muscorum*, ASS SCA—*Assulina scandinavica*, ASS SEM—*Assulina seminulum*, BULIND—*Bullinularia indica*, CEN AER—*Centropyxis aerophila*, CEN ACU—*Centropyxis aculeata*, CEN ORB—*Centropyxis orbicularis*, CEN CAS—*Centropyxis cassis*, CEN PLA—*Centropyxis platystoma*, CEN SP—*Centropyxis* sp., COR DUB—*Corythion dubium*, CRY OVI—*Cryptodiffugia oviformis*, CYC ARC—*Cyclopyxis arcelloides*, CYCKAH—*Cyclopyxis kahli*, CYPSP—*Cyphoderia* sp., CYP AMP—*Cyphoderia ampulla*, DIFBACC—*Diffflugia baccillarum*, DIFBACI—*Diffflugia bacilifera*, DIFBRE—*Diffflugia brevicola*, DIFGLO—*Diffflugia globulosa*, DIF LAN—*Diffflugia langeniformis*, DIF LEI—*Diffflugia leidy*, DIF LIM—*Diffflugia limetica*, DIFOBL—*Diffflugia oblonga*, DIFURC—*Diffflugia urceolata*, DIFSP—*Diffflugia* sp., EUGCIL—*Euglypha ciliata*, EUG COM—*Euglypha compressa*, EUGCOMGLA—*Euglypha compressa glabra*, EUG CRI—*Euglypha cristata*, EUG ROT—*Euglypha rotunda*, EUGSTR—*Euglypha strigosa*, EUG TUB—*Euglypha tuberculata*, EUGSP—*Euglypha* sp., HEL PET—*Heleopera petricola*, HEL SPH—*Heleopera sphagni*, HEL ROS—*Heleopera rosea*, HYAELE—*Hyalosphenia elegans*, HYA PAP—*Hyalosphenia papilio*, NEB CAR—*Nebela carinata*, NEB MIL—*Nebela militaris*, NEB TIN—*Nebela tincta*, PHRACR—*Phryganella acropodia*, PHR PAR—*Phryganella paradoxa*, PHYGRI—*Physochila griseola*, PLA SPI—*Placocista spinosa*, PSE GRA—*Pseudodiffflugia gracilis*, SPH LEN—*Sphenoderia lenta*, TRI ARC—*Trigonopyxis arcula*, TRI SP—*Trigonopyxis* sp., TRINENC—*Trinema enchelis*, TRIN LIN—*Trinema lineare*.

D. globulosa, and *Amphitrema wrightianum* are related to lower pH and conductivity. Other species are located in the middle of the hydrological gradient. The full model explains 19.2% of the variation. DWT is strongly

negatively correlated with axis 1 (13.1% variation explained), whereas pH and conductivity are negatively correlated with axis 2 (4.9% variation explained). The overall permutation test (999 random permutations)

showed that RDA was significant and axes 1 and 2 were highly significant (axis 1— $p < 0.001$, axis 2— $p < 0.002$). DWT was the most significant variable ($p < 0.001$), followed by pH ($p < 0.005$) and conductivity ($p < 0.021$).

Testate amoeba calibration data set

RDA revealed DWT as the most important variable for testate amoeba communities. Consequently, we used this variable for building the transfer function. The calibration tests show that the model performed well and generated acceptable levels of significance (Table 2). For the reconstruction, WA-PLS component 2 was selected, as it had the lowest RMSEP (7.7 cm) and highest R^2 (0.74) (Fig. 3B,C, Table 2). Subsequently, WA-PLS was applied for the quantitative estimation of the past water table dynamics.

Chronology, sediment accumulation rate, bulk density and ash content

Ten out of eleven ^{14}C dates provide a reliable age–depth model spanning the past 1300 ± 30 years, with an agreement index (A_{model}) of 82% ($A_{\text{model}} = 60\%$ is the lowest critical value; Bronk Ramsey, 2008) (Fig. 2). Date Poz-59502 was excluded; its individual agreement of 0% decreased the A_{model} below the critical value. The peat accumulation rates featured a close correspondence with peat properties. Those peat sections characterized by lower BD and AC have higher accumulation rates compared to sections with higher values for these physical parameters (Fig. 2). Significant changes in bulk density were followed by changes in plant composition, as revealed by the macrofossil analysis (Fig. 4). The highest peat accumulation rate values occurred at ca. AD 1997–2012 (1.18–1.41 cm/yr) and ca. 1970–1980 (0.89–0.9 cm/yr). Slightly lower accumulation occurred at ca. AD 1948–1970 (0.74–0.76 cm/yr) and 1980–1997 (0.64–0.65 cm/yr). The period between ca. AD 1948 and 2012 featured the lowest BD and AC (0.05–0.09 g/cm³ and 1.3–2.6%, respectively). During the oldest period (ca. AD 712–780), peat accumulated at the rate of 0.18–0.23 cm/yr. During that interval, BD was high and fluctuated between 0.09 and 0.11 g/cm³, with the exception of a distinct increase to 0.15 g/cm³. AC ranged from 2.3% to 3.9%, with one distinct peak of 4.8% at ca. AD 737. The lowest rates of peat accumulation occurred between ca. AD 780 and 1948 (0.02–0.03 cm/yr). This interval is characterized by the highest values of BD (0.09–0.19 g/cm³) and AC (2.7–6.9%, peaking at ca. AD 1425). These high BD values were strongly related to the presence of *E. vaginatum* tissues and unidentified organic matter (Figs. 2 and 4). Very low rates of peat accumulation may also suggest some discontinuities during that period, and this prompts a very careful interpretation of charcoal accumulation rates (CHAR) for this section.

Peatland and forest development

Four proxies, including plant macrofossils (Fig. 4), pollen (Fig. 5), testate amoebae (Fig. 6), and microscopic charcoal (Fig. 7), were used to reconstruct the main developmental stages of the Mukhrino bog, fire history, and changes in the composition of the surrounding vegetation. These stages were delimited visually to five zones (MU1–5).

MU1 (100–86 cm, ca. AD 712–780)

At the beginning of the record, testate amoebae indicate a high water table. *Archerella flavum* dominates, accompanied by *Hyalosphenia papilio*, *Heleopera sphagni*, and *Amphitrema wrightianum*. This assemblage suggests pool *Sphagnum* communities. DWT oscillates around 12 cm (Fig. 6).

Macrofossils indicate a relatively high groundwater table, as *Sphagnum* cf. *balticum* remains from sec. Cuspidata (Fig. 4) are typical for wet parts of the mire (e.g., carpets and lawns). *Eriophorum vaginatum* also suggests moist conditions (Hölzer, 2010).

The pollen spectra (*Pinus sylvestris* type, *Pinus sibirica* type, and *Betula*) reflect the presence of pine–birch forests, not only in this zone but in the entire profile, suggesting that vegetation composition varied little over the last 1300 years. Additional arboreal components of the forest include *Populus*, *Salix*, and *Alnus* in moist habitats, as well as “dark coniferous” forest taxa, including *Picea* sect. *Eupicea* and *Abies*. In this zone, the pollen of *Picea* sect. *Eupicea* (probably *P. abies* ssp. *obovata*) reaches its maximum values (2.5–4.5%). However, at the end of this zone (ca. AD 750), declining *Picea* percentages suggest a slight retreat of spruce.

CHAR reached 1935 particles/cm²/yr at ca. AD 730, and then decreased. CHAC oscillated between 1945 and 8690 particles/cm³.

MU2 (86–58 cm, ca. AD 780–1882)

In Zone MU2, the testate amoebae record features the disappearance of *Archerella flavum*. Concurrently, percentages of dry indicators, such as *Arcella catinus*, *Trigonopyxis arcuata*, and *Phryganella acropodia*, increase. DWT increases gradually from approximately 13 to over 40 cm.

Toward the top of this zone, *Sphagnum magellanicum* and *Eriophorum vaginatum* macrofossils indicate gradually decreasing bog surface wetness, and at the same time, *Sphagnum* cf. *balticum* disappears abruptly; *Sphagnum magellanicum* has a broad niche but generally occurs at a water table depth of ca. 24 cm (Hölzer, 2010). Wood and Ericaceae remains appear in this zone, suggesting a lower water table and the development of local shrub communities (Fig. 4).

Table 2

Transfer function performance statistics. The best model is WAPLS Component 2. Bolded values represent best performing models.

| Model | R^2 | Ave_Bias | Max_Bias | RMSEP |
|---|-------------|--------------|--------------|-------------|
| PLS | | | | |
| PLS Component 1 for WT | 0.51 | 0.33 | 40.51 | 10.34 |
| PLS Component 2 for WT | 0.64 | 0.23 | 28.31 | 8.90 |
| PLS Component 3 for WT | 0.68 | 0.07 | 23.67 | 8.49 |
| PLS Component 4 for WT | 0.67 | −0.09 | 19.52 | 8.73 |
| PLS Component 5 for WT | 0.65 | −0.26 | 16.03 | 9.47 |
| WAPLS | | | | |
| WAPLS Component 1 for WT | 0.63 | 0.34 | 23.21 | 8.60 |
| WAPLS Component 2 for WT | 0.74 | −0.28 | 17.74 | 7.70 |
| WAPLS Component 3 for WT | 0.73 | −0.91 | 15.56 | 8.43 |
| WAPLS Component 4 for WT | 0.72 | −1.08 | 17.39 | 9.06 |
| WAPLS Component 5 for WT | 0.71 | −1.15 | 16.61 | 9.59 |
| WA | | | | |
| Weighted averaging model (inverse deshrinking) for WT | 0.64 | 0.28 | 22.12 | 8.54 |
| Weighted averaging model (classical deshrinking) for WT | 0.65 | 0.36 | 16.79 | 9.18 |
| Weighted averaging model (tolerance downweighted, inverse deshrinking) for WT | 0.75 | 0.62 | 18.12 | 7.88 |
| Weighted averaging model (tolerance downweighted, classical deshrinking) for WT | 0.75 | 0.77 | 16.35 | 8.11 |

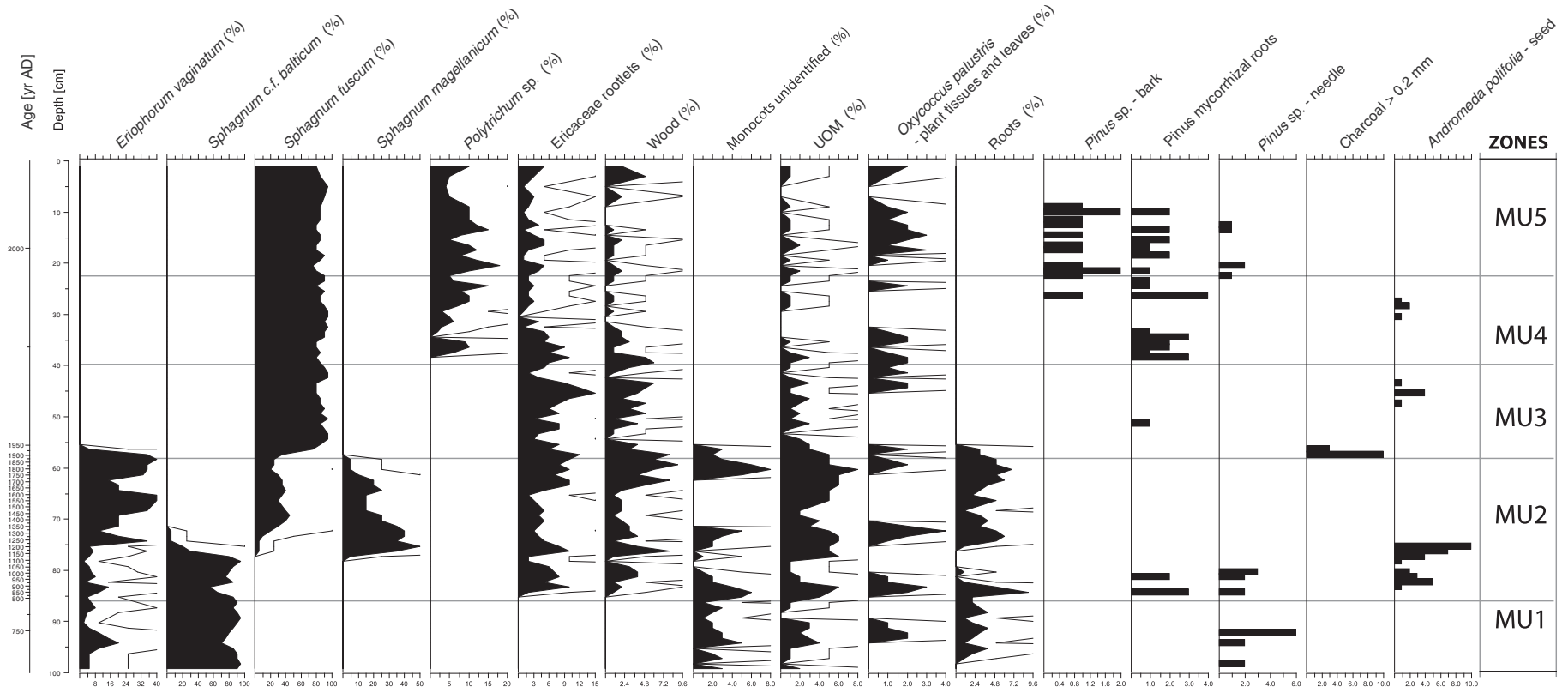


Figure 4. Plant macrofossil diagram for Mukhrino mire. Abbreviations: UOM—unidentified organic matter. Non-% variables are provided as absolute values; 5 times exaggeration is presented as white silhouette.

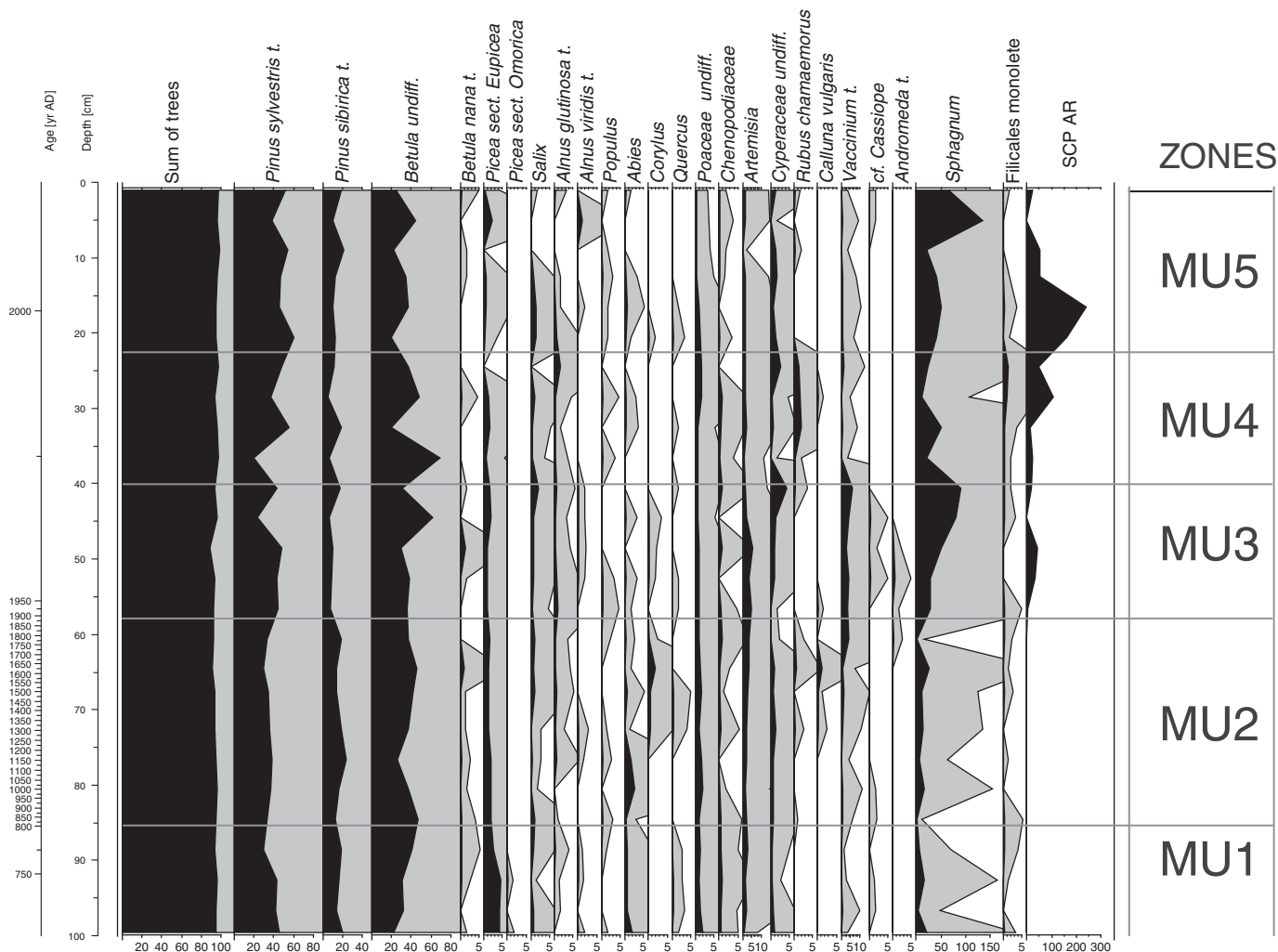


Figure 5. Pollen percentage diagram for Mukhrino mire; 5 times exaggeration is presented as white silhouette. SCP AR—spheroidal carbonaceous particles (SCPs) accumulation rate.

The pollen assemblages in Zone MU2 are similar to those of the previous zone. A minor peak in *Abies* pollen percentages (2.5%) occurs in the older part of MU2, whereas in the younger part of the zone, there is a peak in *Corylus* (1.8%; probably *C. avellana*). Such low *Corylus* pollen percentages indicate long-distance transport (cf. Tallantire, 2002).

This zone is characterized by high CHAR values (56–737 particles/cm²/yr) and a maximum of CHAC at ca. AD 1505 (29,800 particles/cm³).

MU3 (58–40 cm, ca. AD 1882–1970)

Arcella catinus percentages decline considerably in Zone MU3, whereas other dry indicators, such as *Trigonopyxis arcuata* and *Phyganella acropodia*, remain relative abundant. *Nebela militaris* first becomes abundant in this zone. This species usually indicates a higher water table than *T. arcuata* or *P. acropodia*, but the habitat was still quite dry, as indicated by the abundance of *Sphagnum fuscum*. DWT indicates a gradually increasing water table.

An abrupt transition between *Sphagnum magellanicum* and *S. fuscum* took place ca. AD 1900; this shift was accompanied by an increase in the percentages of Ericaceae, as well as higher wood remains.

In MU3, *Artemisia* reaches its highest percentages in the profile (ca. AD 1882–1966; 3.5–5.5%), possibly reflecting higher landscape openness. Spheroidal carboniferous particles (SCP) appear in this zone, suggesting coal burning in the surrounding or distant transport from industrialized areas (Swindles et al., 2015).

CHAC decreased from 7716 to 616 particles/cm³, while CHAR ranged between 264 and 637 particles/cm²/year. Macroscopic charcoal (particles >200 μm) at the depth corresponding to ca. AD 1900 indicates local fires (Fig. 4).

MU4 (40–22.5 cm, ca. AD 1970–1994)

In Zone MU4 testate amoebae assemblages, *Nebela militaris* continues to indicate a low water table, but the reconstructed water depth shows a gradual increase, reaching a value of approximately 9 cm.

At this time, the bog was dominated by *Sphagnum fuscum* (as high as 90%). *Polytrichum* first occurs in MU4, suggesting a low water table and hummock development. *Pinus* bark suggests the presence of pines in the hummocky dwarf shrub-*Sphagnum* communities. Ericaceae and wood remains decreased gradually, perhaps reflecting a higher water table.

Pollen data in MU4 feature the highest value of *Rubus chamaemorus* (max. 2%); its presence suggests the development of a hummock. SCP values increase after ca. AD 1985, likely signaling the increasing industrialization in the region (Swindles et al., 2015). CHAR increased abruptly to 6899 particles/cm²/yr in ca. AD 1975. At the same time, CHAC was 7726 particles/cm³.

MU5 (22.5–0 cm, ca. AD 1994–2012)

The macrofossil record in Zone MU5 suggests a low water table, as indicated by the stable values for *Sphagnum fuscum* and *Polytrichum*

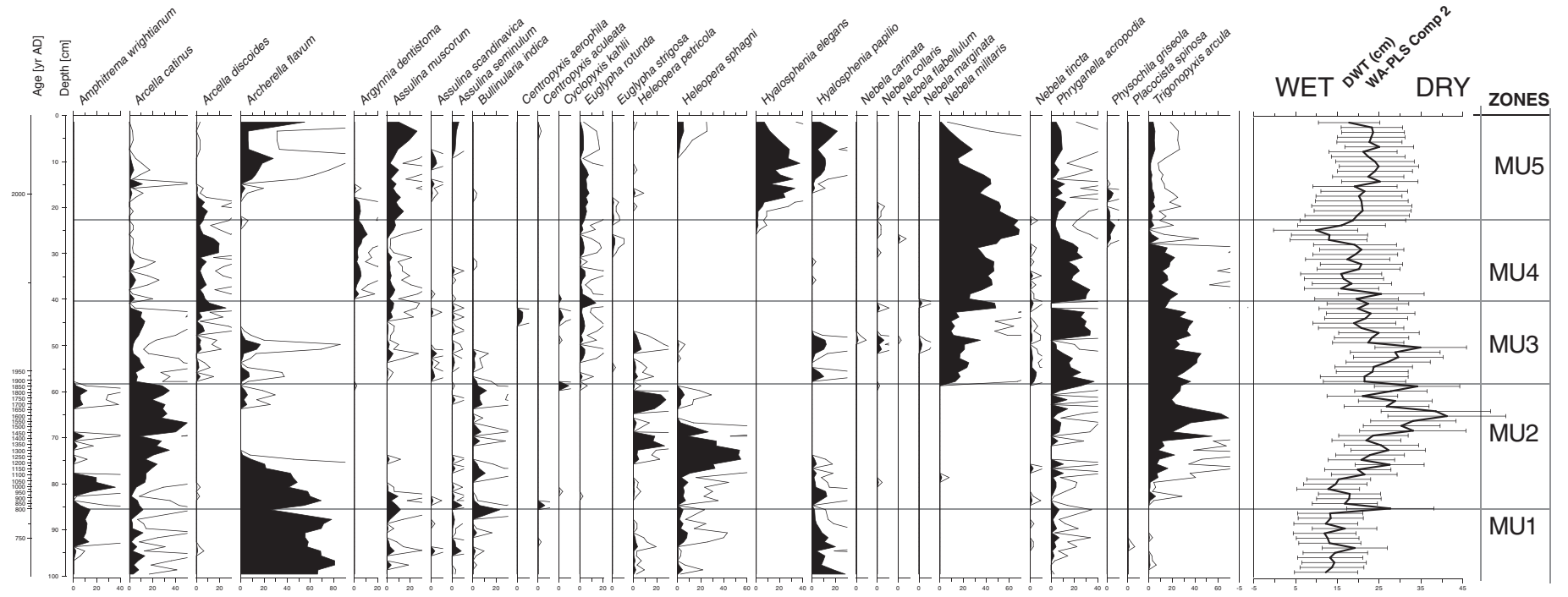


Figure 6. Testate amoebae percentage diagram for Mukhrino mire; 5 times exaggeration is presented as white silhouette. WA PLS Comp 2 (weighted averaging partial least squares component 2)—model used for the DWT (depth to the water table) quantitative reconstruction.

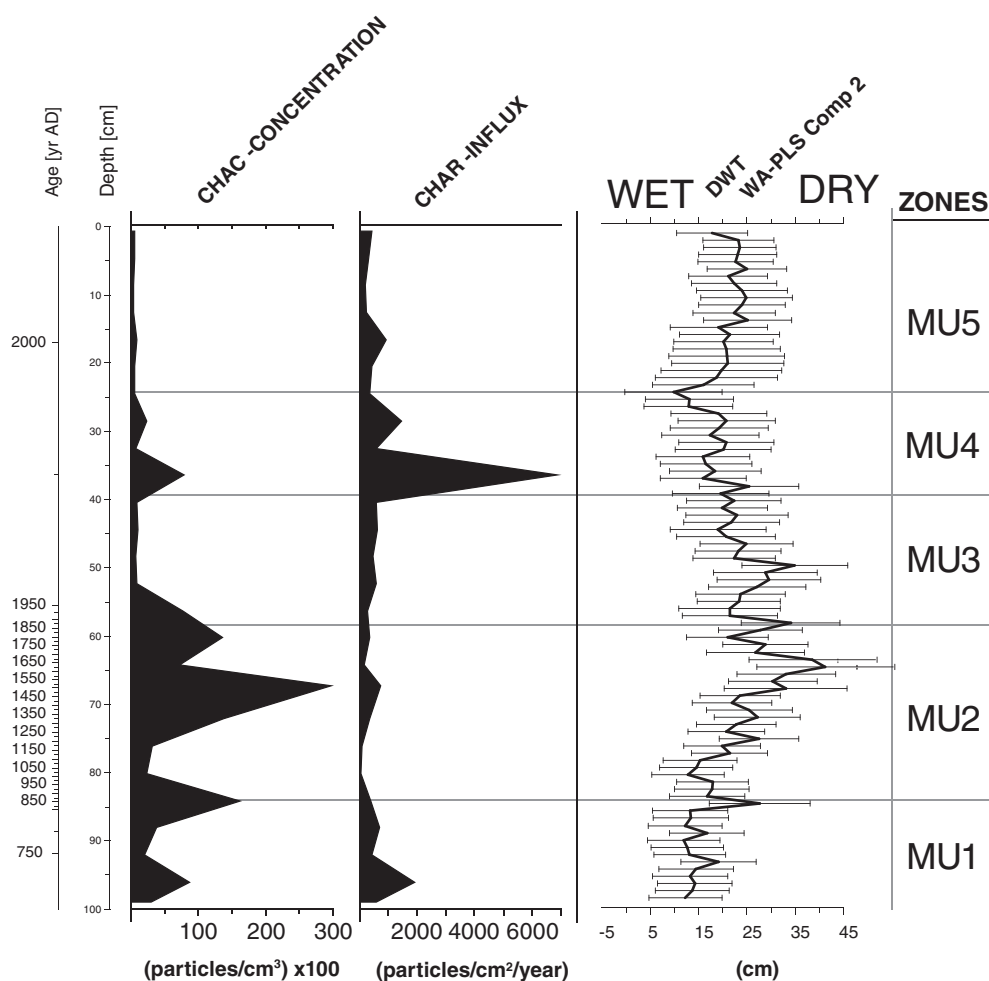


Figure 7. Summary diagram for Mukhrino mire with comparison of testate amoebae-based water table reconstruction (DWT), microscopic charcoal influx (CHAR), and microscopic charcoal concentration (CHAC). WA PLS Comp 2 (weighted averaging partial least squares component 2)—model used for the DWT (depth to the water table) quantitative reconstruction.

remains, although *Hyalosphenia elegans*, *H. papilio*, and *Archerella flavum* point to higher habitat wetness. Other species, such as *Nebela militaris*, *Phryganella acropodia*, and *Trigonopyxis arcuata*, decreased in this period.

A decrease in the *Rubus chamaemorus* pollen percentages suggests the retreat of hummock habitats from the coring location.

SCP records reveal increased coal burning between AD 1994 and AD 2000 (max. 267 particles/cm²/yr). CHAR and CHAC reached maximum values of 914 particles/cm²/yr and CHAC of 759 particles/cm³, respectively, with a decreasing trend toward the top of the zone.

Discussion

Calibration data set and ecology of testate amoebae

Numerous studies have analyzed testate amoebae ecology in various biogeographical settings in Russia (Bobrov et al., 1999; Bobrov et al., 2002; Bobrov et al., 2003; Mazei et al., 2007, 2009; Mazei and Embulaeva, 2009; Payne et al., 2012; Bobrov et al., 2013; Tsyganov et al., 2015), but there have been few such studies in Siberian peatlands (Bobrov et al., 2002; Mazei and Kabanov, 2008; Kurina et al., 2010). Our calibration study at Mukhrino mire illustrates the relationship between testate amoebae community composition and several environmental parameters. The redundancy analysis demonstrated the importance of water table depth, which is consistent with findings from other regions (Tolonen et al., 1994; Lamentowicz and Mitchell, 2005; Qin et al., 2013; Van Bellen et al., 2014). Acidity was a less important parameter, perhaps due to the limited range of the sampled habitats. The overall species

composition of testate amoebae at Mukhrino mire was not different from those described in Europe or North America (Booth, 2007; Charman et al., 2007). The most abundant species in wet parts of the gradient are the mixotrophic species *Hyalosphenia papilio* and *Archerella flavum*, as well as *Nebela carinata*. In *Sphagnum fuscum* hummocks, which were the driest part of the gradient, *Assulina muscorum*, *Trigonopyxis arcuata*, and *Arcella catinus* dominated.

A characteristic feature of this Siberian peatland is that minerotrophic species are absent, as the habitat is purely organic and very acidic. An advantage of our study is that the training set was taken from a pristine bog, large enough to exclude any bordering effect, and then applied to a core also representing pristine conditions. In Europe, in contrast, testate amoebae training sets are often collected from raised bogs that have experienced disturbance, possibly biasing reconstructions derived from them. We think that the new calibration data set from Siberia is important for its inferences concerning paleohydrological dynamics in order to better assess the processes that drive carbon accumulation. In our application of the testate amoebae transfer function to the 1300-year-long core from Mukhrino mire, the composition of the modern communities was similar to that of the fossil assemblages, and thus the transfer function could be used to reconstruct past hydrological conditions with confidence (Juggins and Birks, 2012).

Hydrology, fires, and forests in western Siberia

As the Mukhrino mire record is the first from Siberia in which the paleohydrology of the last millennium has been quantitatively

reconstructed based on a modern calibration training set, we can only relate our findings to other records from other parts of Eurasia. The dry stage at AD 780–1882 in the Mukhrino profile is similar to dry intervals described in other studies from central and eastern Europe (Lamentowicz et al., 2009; Gałka et al., 2014). In the case of Polish sites, however, unstable hydrological conditions rather than permanent drought prevailed (Marcisz et al., 2015). This may suggest that the drought increased in intensity from west to east, being most severe in continental areas like western Siberia. The recent study of Feurdean et al. (2015) provides a regional summary of paleohydrological change in bogs of central and eastern Europe and supports the interpretation of the LIA as dry in eastern sites and contrastingly wet in western sites.

Under the continental conditions of western Siberia, the influence of climate on peatlands during the LIA may have been different than was the case in oceanic western Europe. In western Europe, wet conditions may have arisen due to increased summer precipitation and a change in air circulation patterns (Magny et al., 2008, 2010). The growth of alpine glaciers during the LIA is consistent with higher moisture (Holzhauser et al., 2005), and the only existing high-resolution bog record from the eastern Swiss Alps revealed a wet trend during the LIA (van der Knaap et al., 2011). Similarly, the peatlands of the British Isles indicate moist conditions during the LIA (Charman et al., 2006). Changes in temperature may also be involved in the shifts observed in the Mukhrino mire record. Cool temperatures could have limited peat accumulation, generating changes in our proxies that are suggestive of a dry phase. The extensive carbon accumulation database from northern latitudes reveals such a trend during the LIA, with carbon sequestration rate declining during the transition from the MWP to the LIA. This was probably because the LIA featured the combination of lower temperatures and increased cloudiness, suppressing net primary productivity (Charman et al., 2013). However, given the distance between western Europe and Siberia, it may be the case that the climatic causes of dry conditions during the LIA at eastern sites were different from those operating further to the west.

Because our study is based on a single core, alternative explanations for the peatland development and peat accumulation changes should be taken into account. The patterns that we have observed could also be related to autogenic development of the peatland itself. Peat vegetation forms various distinct microhabitats in the Mukhrino mire, including very wet pools with open-water flarks overgrown by pines (so-called *ryam* forest, which is typical for raised bogs in western Siberia), and *Sphagnum* lawns. Changes in the water table may have been caused by migration (or alternative development) of those microhabitats on the peatland surface. Moreover, because the core was sampled on the margin of the flark, it is plausible that what we have interpreted as low water table conditions is instead related to the change of surface microhabitats from a pool to the flark (Zobel, 1988). It may be the case that the observed hydrological shifts are related to both internal feedbacks (Swindles et al., 2012) and allogenic forcing (Barber, 1981); additional work at Mukhrino is needed to determine the relative importance of these factors.

Fire is a key process that influences the physical and biological structure of boreal forests (Stocks et al., 2001). Wildfires affect all characteristics of the ecosystem, including species composition and diversity, biogeochemical cycles and energy flows, and carbon cycling (van Bellen et al., 2012). Wildfires in boreal ecosystems are highly dependent not only on climatic conditions (such as heat waves or hydrological stress) but also on forest management and the accumulation of woody debris (Gennaretti et al., 2013). Our study revealed a lack of dramatic shifts in vegetation in the Mukhrino area over the last 1300 years. *Pinus sylvestris*, *P. sibirica*, and *Betula* were the dominant taxa, with *Alnus*, *Picea*, *Populus*, and *Abies* as additional components (Fig. 5). However, one intriguing change is the decline of *Picea* (probably *Picea abies* ssp. *obovata*) at AD 750, a time of stable hydrological conditions and decreasing fire activity. *Picea abies* is thought to be poorly adapted to fire and drought due to its relatively thin bark and shallow root system

(Zackrisson, 1977; Niklasson et al., 2002). Thus, the parallel declines in *Picea* and CHAR in the Mukhrino record are somewhat unexpected, although paleoecological studies from Fennoscandia, where this phenomenon has been widely investigated, also feature unclear findings (Bradshaw et al., 2010). Several studies reported the expansion of *P. abies* during times of increased fire activity (Carcaillet et al., 2007; Rosén and Hammarlund, 2007; Barnekow et al., 2008; Brown and Giesecke, 2014), but others found that fire decreased prior to *P. abies* expansion (Tryterud, 2003; Ohlson et al., 2011). Additional studies spanning longer time scales are needed to better understand the relationship between *P. abies* and fire in Siberia and other boreal regions.

The charcoal record from Mukhrino mire is of particular relevance given the significant amount of carbon emitted by burning peatlands (French et al., 2004; Kasischke et al., 2005; Turetsky et al., 2015). The Mukhrino profile featured maximum CHAR values at ca. AD 1975 and two smaller peaks (at ca. AD 1984 and 2000), indicating higher fire activity during the last 60 years than at any point in the last millennium (Fig. 7). This shift may be linked with the fast development of the nearby city of Khanty-Mansiysk, which saw fast population growth starting in the 1950s. The finding of oil and gas in the region had a major impact on the development of local industry and caused a rapid influx of population from 18,000 in 1956 to 1,478,000 in 2006 (official data from the Khanty-Mansi Autonomous Okrug). This substantial increase in population not only had an impact on the development of the city itself but also contributed to the pressure on the environment in the region. Human penetration into forests increased, contributing to higher fire activity during recent decades. A key change was the completion of a bridge across the Irtysh River in around 2005, as only a few hunters visited the Mukhrino area prior to this improved access. Moreover, the nearest oil fields, located 100–200 km away, started to develop on the left bank of the Irtysh River only 5–7 years ago. Thus, it appears that fires in the Mukhrino area have experienced little human influence during most of the last 1300 years. A similar increase in fire activity over the past 60 years is noticeable in boreal forests of Canada (Stocks et al., 2002).

An alternative explanation for the observed increase in fire is that changes in climate may have caused increased burning and extended fire seasons during the last half of the twentieth century in Canada and Siberia (Wotton and Flannigan, 1993; Dale et al., 2001; Kirilenko and Sedjo, 2007). Barichivich et al. (2014) showed that rapid summer warming since the 1980s is a significant driver of increased evapotranspiration, which affects summer drought severity in the northern latitudes. In turn, drier conditions may lead to higher intensity of fires and longer growing seasons in Siberia and other boreal regions (Flannigan et al., 2013). The Arctic Oscillation (AO) also appears to influence the inter-annual variability of fire in Siberia, with higher fire activity during the positive phase of the AO (Sukhinin et al., 2004; Balzter et al., 2005, 2007). Our record provides data that can be related to AO as well as to human activity; however, we need more peat profiles from W Siberia to be sure that this is climatic forcing.

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