



Warm Younger Dryas summers and early late glacial spread of temperate deciduous trees in the Pannonian Basin during the last glacial termination (20–9 kyr cal BP)

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ABSTRACT

This paper focuses on the last glacial termination vegetation and climate reorganization of the Eastern Pannonian Plain via the multi-proxy paleoecological analysis of Kokad mire in Eastern Hungary. Grains size, sediment chemistry and magnetic susceptibility records are compared with the pollen and plant macrofossil records on the basis of which biome and quantitative summer mean temperature reconstructions are provided and discussed with other climate records of the region. Biome assignments indicated (graminoid and forb) tundra vegetation from 19,440 cal yr BP with the local presence of *Betula pendula*, *B. pubescens*, *B. nana*, and *Pinus sylvestris*. A rapid biome shift to cool coniferous forest took place at 16,200 cal yr BP, and a second biome shift was identified at 14,740 cal yr BP when cool mixed forest developed and persisted into the Early Holocene. The most prominent feature of the record was the early post last glacial maximum (LGM) establishment (17,700 cal yr BP) and expansion (14,700 cal yr BP) of elm (*Ulmus*) and hazel (*Corylus*) supporting the phylogeographical evidence for extra-Mediterranean refugia in the Pannonian Basin. The fungal spore record indicated the presence of large grazing mammals locally after the LGM until ~16,780 cal yr BP. Their disappearance predated the biome shift to cold coniferous forest and the final increase of forest fires. Pollen based summer temperature reconstruction suggested relatively warm summers (~14.5 °C) by 19,440 cal yr BP, and buffered July mean temperature fluctuations throughout the last glacial termination in this region with < 1 °C decrease in summer mean temperatures during the Younger Dryas stadial, and ~2.2 °C warming in the Early Holocene. Our comprehensive summary of the basin's Late Pleniglacial (24,000–14,600 cal yr BP) and late glacial paleoenvironmental and paleoclimate records showed a partially wooded landscape with higher woody cover in Western Hungary. Several loess and lake archives confirmed that in this region of Europe the warming after Heinrich event 1 (around 16,200 cal yr BP) had similar amplitude to the late glacial warming.

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1. Introduction

Studying the last glacial termination history of lowland vegetation and climate change in the Pannonian Basin is a rewarding task, as sedimentary basins with well-preserved lake or peat

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deposits from this period are scarce. (Fig. 1, Buczkó et al., 2009). At the same time, this is a crucial interval in the basin's history with the spread of Epigravettian cultures with specialized hunting traditions on the still surviving megafauna elements (Dobosi, 2004; Pazonyi, 2004; Lengyel, 2014, 2016; Lengyel and Wilczyński, 2018; Böskén et al., 2018), their cultural collapse and transformation with the changing environment, diminishing food resources and rapidly changing terrestrial biomes. Human populations became more stationary, or at least their northward connections were less intense during the last glacial maximum (LGM), and a drastic drop in the amount of stone implements were noticed at archaeological sites (Lengyel, 2009; Markova et al., 2009). This is also the time, especially after 15,000 cal yr BP, when loess accumulation halted in the Pannonian Basin resulting in the loss of an important paleoclimate archive for this fast warming period (Sümegei, 2005a,b; Stevens et al., 2011; Sümegei et al., 2013, 2018, Sümegei and Náfrádi, 2015; Újvári et al., 2017; Marković et al., 2018). According to present knowledge, Epigravettian settlements were dominantly placed at the border of the lowland and hill zone, with most sites located between 150 and 300 m a.s.l., and usually at an intermediate position between the dry and more open forest steppe, steppe tundra and the denser forested foothills of the Carpathian Mountains from where a wide-ranging view over the surrounding area was possible (Lengyel, 2014; Hauck et al., 2018).

On the other hand, the Pannonian Basin was a special place during the last glacial termination as its macroclimate was warmer both in winter and summer than the surrounding hills and mountains, conditions that facilitated the early spread of the warm adapted temperate flora and fauna (Willis et al., 1995, Willis and van Andel, 2004; Jamrichová et al., 2014; Sümegei et al., 2018). Evidences for such early temperate vegetation expansions are the cave charcoal records of Rejtek (Stieber, 1967, 1969; Sümegei and Náfrádi, 2015), the lake sediment archive of Bátorliget Mire (Willis et al., 1995) and the macrocharcoal assemblages of embryonic late glacial (LG) soils in the Bodrog-Tisza Interfluve (Csongor et al., 1980; Borsy et al., 1981, 1985) that demonstrated the late glacial presence and expansion of hazel (*Corylus avellana*), elm

(*Ulmus*), lime (*Tilia* sp.), maple (*Acer* sp.), beech (*Fagus sylvatica*), hornbeam (*Carpinus betulus*) and oak (*Quercus* sp.) (Fig. 1).

Even though sand movements during the late glacial indicate that climatic fluctuations had a strong effect on total vegetation cover in the basin, and aridity was a key factor in controlling vegetation cover in the sandy areas (Borsy et al., 1981, 1982; Lóki et al., 1994; Gábris, 2003; Buró et al., 2016) especially during the Younger Dryas stadial, the few available lake sediment pollen records from the Great Hungarian Plain (GHP) do not show a distinct vegetation change during this stadial phase (Bátorliget, Kismohos, Ócsa; Fig. 1). Chironomid-inferred July mean temperature reconstructions from the surrounding Carpathian Mountains suggest that July temperatures decreased less than 1 °C in the South Carpathians (Tóth et al., 2012), with more pronounced summer cooling in the North Carpathians (Hájková et al., 2016). Diatom-inferred lake-ice extent reconstruction furthermore indicated that seasonality change with extended and colder winters was likely the driving factors in environmental change in the south Carpathian Region (Buczkó et al., 2012). The muted nature of the lowland vegetation change implies that accumulated heat during the shorter growing season was likely not prohibitive for temperate tree growth due to the remaining high summer temperatures; the major limiting factor was likely available moisture, the supply of which was however maintained in the alluvial plains of the GHP. In this respect it is important to note that seasonally inundated areas occupied more than 25% of Hungary until water regulation measures in the mid-19th century (Dunka et al., 1996).

There are thus many important questions that need better understanding in connection with the last glacial termination (Termination 1) climate, ecosystem and human interactions in the Pannonian Basin. What tree species survived the LGM locally in micro- and mesoclimatically favourable locations? When did warming lead into biome shifts in the plain? What vegetation types replaced each other? How forested was the lowland landscape during the late glacial interstadial? When did large herbivore populations decline, and how did they influence the herb biomass in the plain? These exciting questions can be studied in lake and

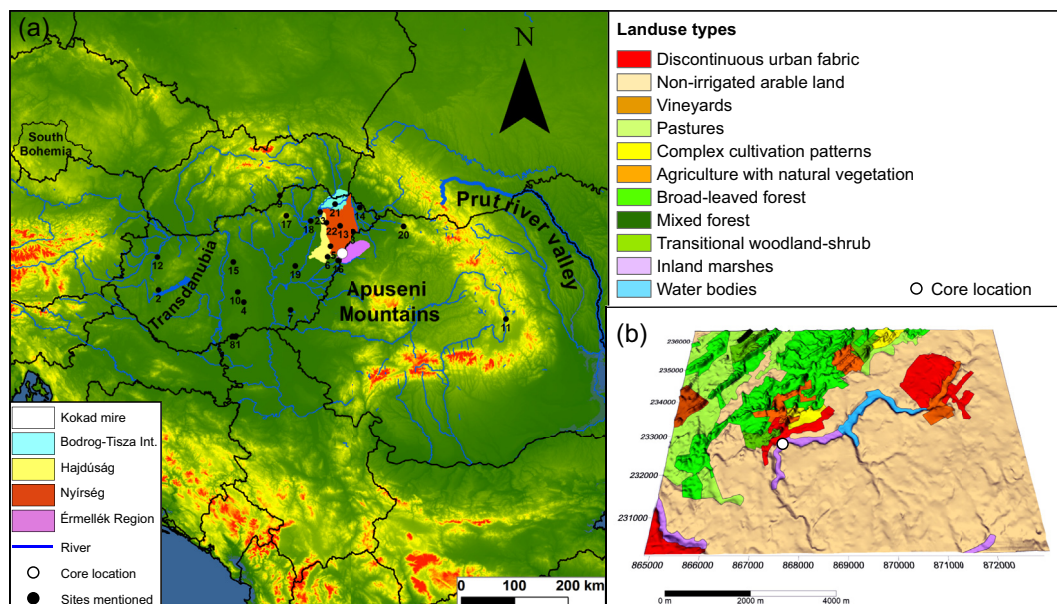


Fig. 1. Location of Kokad mire in East-Central Europe (ECE) and 3D digital elevation model of the study area; (a) location of Kokad mire in ECE and other sites mentioned in the text; (b) major land cover types on the basis of Corine Land Cover 2018 (CLC, 2018), coordinates are according to the EOVI Hungarian coordinate system; 1) Madaras; 2) Balatonederics; 3) Bátorliget; 4) Bócsa; 5) Debrecen-Brickyard; 6) Derecske Brickyard; 7) Kardoskút Fehér Lake; 8) Katymár; 9) Kismohos; 10) Kolon Lake; 11) Lake St Anne; 12) Mezőlak-Szélmező; 13) Nagymohos; 14) Nyíres-tó; 15) Ócsa; 16) Pocsaj; 17) Rejtek; 18) Sarló-hát; 19) Sárrét; 20) Steregoiu; 21) Tiszacsermely; 22) Tiszavasvár-Szorgalmatos; 23) Tokaj.

mire sediments in the Érmellék Region (Fig. 1) where deflation hollows were formed at the border of two geomorphological units: the Nyírség sand region and the Érmellék alluvial plain. Kokad mire (Fig. 1) occupies one of these valleys, and its sediment extends back to ca. 20,000 years. In this study we aim to contribute towards answering these questions using multi-proxy paleoecological methods and focusing especially on the vegetation and climate changes.

2. Regional setting

Kokad mire (47°24'10" N, 21°55'43" E; 112 m a.s.l.) is located in the Érmellék geographical region of the GHP, in the western side of the Ér river valley (Fig. 1). The mire itself developed at the boundary of three sedimentary complexes: the large sand-covered alluvial fan of the Nyírség (4500 km², Fig. 1), the loess mantled Hajdúság (1100 km²) and the alluvial silt dominated Érmellék Region (1600 km²). Rich in abandoned paleochannels, this latter region has been a mire land until the 1960's when canalisation of the area started and several formerly seasonally inundated areas were transformed into plough lands (Benedek, 1958). During the Late Quaternary Érmellék was fed by rivers that drained the Northeast Carpathians and the Apuseni Mountains. The ancient channel of the Szamos and Tisza rivers flowed along the south-eastern margin of the Nyírség (Borsy, 1990; Nádor et al., 2007) until an abrupt avulsion in the Tokaj area has changed the position of the Tisza into its current course around 16–18 kyr cal BP (Timár et al., 2005). The ancient riverbed formed a 10–15 km wide erosional plain. Kokad mire occupies a basin created by deflation within the erosional plain (Fig. 1). The mire is covered by reed-swamp today; its water is alkaline and rich in molluscs.

The natural vegetation of the study area was dominated by wetland habitats both in the Southern Nyírség and Érmellék regions until water regulation measures started (Nyírség: 1892, Érmellék: 1960). The flora of Érmellék consists of 1048 higher plant species, 47.3% of which are temperate European and Eurasian species (Karácsonyi, 1996). Before drainage, sand dune valleys were occupied by shallow eutrophic ponds, sedge and reed dominated mires, swamps and wet meadows (Benedek, 1960; Borsy, 1961). Dune tops originally supported either steppe oak forests (*Melampyro debreceniensi-Quercetum roboris* and *Festuco rupicolae-Quercetum roboris*) or sand steppes (*Festuco vaginatae-Corynephorretum*) depending on the ground water level (Borhidi et al., 2012). Secondary sand steppes were formed after forest clearance and under intensive grazing (*Thymo serpylli-Festucetum pseudovinae*, *Potentillo arenariae-Festucetum pseudovinae*). The dominant canopy component was originally pedunculate oak (*Quercus robur*), but nowadays grazed forest stands are dominated by silver lime (*Tilia tomentosa*), field elm (*Ulmus minor*), field maple (*Acer campestre*), tatar maple (*A. tataricum*), European wild pear (*Pyrus pyraster*) and poplar (*Populus* sp.). The shrub layer of these forests is species rich (*Crataegus monogyna*, *Ligustrum vulgare*, *Rhamnus cathartica*, *Cornus sanguinea*, *Pyrus pyraster*, *Prunus spinosa*). Interdune hollows were originally occupied by Willow and Birch Carr (with *Hottonia palustris*, *Carex umbrosa* and *C. hartmanii*). Nowadays these are restricted to a few localities. Tree plantations are frequent and are mostly dominated by black locust (*Robinia pseudoacacia*), the aerial extent of which has increased considerably in the last two decades (Bölöni, 2014). Steppe grasslands on sand surfaces were originally the natural components of the steppe oak forests. Today some unploughed areas preserve their natural species composition with *Festuca rupicola*, *Pulsatilla flavescens*, *Iris arenaria* and *Onosma arenaria*. Loess mantled areas of the Hajdúság region originally supported loess steppe and salt marshes in derasion valleys (Borhidi et al., 2012). According to vegetation surveys (Borhidi et al.,

2012), the Hajdúhát area was probably naturally treeless; chernozem soils dominate here. Other surveys assume the former presence of loess oak woods (*Aceri tatarici-Quercetum roboris*) that alternated with loess grasslands in an oak forest steppe landscape (Zólyomi, 1989).

The climate of the region is temperate continental. Mean annual precipitation is around 570 mm, annual mean temperature is around 9.8 °C (average values in Debrecen for 1901–2000). July mean temperatures fluctuate between 19 and 20 °C, and January mean temperatures are around –3 °C. These values exceed the average values of the GHP that are above 21 °C for July and around 11 °C annually using the data between 1981 and 2010 (Bihari et al., 2018). Mean annual precipitation is between 500 and 550 mm in the GHP (Bihari et al., 2018).

The dominant soil types are chernozem, brown earth and alluvial soils including steppe solonch (Appendix 1).

3. Material and methods

A 595-cm long undisturbed sediment core with 7-cm diameter (Kokad-2) was obtained from the south-eastern part of the mire in 2008 using a modified Livingstone piston corer (Fig. 1). The bottom 40-cm was sampled with a Russian corer. Sediment lithology was described in the laboratory using the Troels-Smith sediment description system (Troels-Smith, 1955). In this paper we present the analytical research results of the last glacial termination deposits between 190 and 635 cm.

The chronology of Kokad-2 core is based on 23 AMS ¹⁴C measurements made at the Poznań Radiocarbon Laboratory (Poland) and at the Laboratory of Climatology and Environmental Physics, ATOMKI (Hungary). ¹⁴C ages were calibrated into calendar years using the Calib Rev. v. 7.0.4. software and the Intcal13 calibration curve (Reimer et al., 2013). Age-depth modelling was done with the Bacon package in R using Bayesian probability statistics (Blaauw and Christén, 2013).

For magnetic susceptibility measurements, individual core segments were split into two halves in the laboratory. One half core was photographed, described, and used for MSCL core logger derived magnetic susceptibility at 5-mm resolution. The other half core was cut contiguously into 1-cm half cylinders. Organic content measurements were done on 1 cm³ sub-samples taken at 2-cm intervals. Samples were dried at 105 °C for 2 h, followed by ignition at 550 °C for 3 h (Heiri et al., 2001). Wet weight, dry weight and weight loss-upon-ignition (LOI) were determined and used for bulk density and organic content calculations.

Major and trace elements were analysed at 4-cm intervals. The chemical extraction technique had two-steps following Bengtsson and Enell (1986). These extraction steps are described in Vincze et al. (in press). Element concentrations were measured using inductively coupled plasma atomic emission spectrometry (ICP-AES). In this paper we present the element concentrations of the first step only that mainly represent the autigenic sediment fraction, i.e. compounds precipitating from the water column under changing pH and redox conditions in the lake (Mackereth, 1965).

Grain-size measurement methods were described in detail by Vincze et al. (in press). Samples at 4-cm interval were measured in a Horiba Partica 950 LA laser particle sizer. Grain-size classification followed Blott and Pye (2012).

Plant macrofossil analyses were done on the entire sediment core using large volume, 5 cm thick sediment samples (average volume 23 cm³) on the basis of which wetland succession has been reconstructed recently by Vincze et al. (in press). Here we focus on the time interval between 20,000 and 9000 cal yr BP and present selected macrofossil components only. For the macrofossil analysis, samples were soaked in 10% NaOH and wet-sieved using a 250 µm

mesh. Terrestrial and aquatic plant remains were hand-picked systematically from the residues under a stereomicroscope (Olympus SZ 51) and identified to the lowest possible taxonomic level.

Macrocharcoal analysis was done contiguously on 1 cm³ sub-samples taken at 1-cm intervals. Following deflocculation and bleaching with 10% (NaPO₃)₆ and 5% NaOCl, samples were sieved through a 160 μm mesh. The residue was washed into a white porcelain evaporating dish and examined under a binocular microscope (Leica M80 at X60 magnification) equipped with a video camera. Image analysis was done with the WINSEEDLE software (Regent Instruments Canada Inc. 2009) that facilitated counting the macrocharcoal particles on the screen and automatically measured their surface area. Charcoal concentrations (by number and by area) were transformed into charcoal influx (or accumulation rate, CHAR) by number. The applied charcoal peak detection and fire frequency analysis methodology is described in Vincze et al. (in press).

Samples of 2 cm³ wet sediment were prepared for pollen analysis using standard methods including treatment with HCl, NaOH, HF, acetolysis and micro-sieving at 10 μm mesh size. *Lycopodium* spore tablets of known volume were added to each sample to work out pollen concentrations (Stockmarr, 1971). Pollen and spores were identified and counted under light microscope at 400 × and 1000 × magnification. A minimum of 500 terrestrial pollen grains were counted. In several pollen slides low pollen concentration and poor pollen preservation were encountered, therefore a minimum count of 300 was used in these samples. For the identification of pollen and spores the reference database at the Department of Environmental and Landscape Geography at ELTE (Budapest) were used together with pollen atlases and keys (Moore et al., 1992; Reille, 1992, 1995; 1998; Beug, 2004). Pollen type nomenclature follows Beug (2004). Microcharcoal particles >10 μm were counted and expressed as particle accumulation rates. Statistical analysis and plotting of the pollen data was done using Psimpoll 4.27 (Bennett, 2007). Pollen assemblage zones were determined using optimal splitting by information content, while principal component analysis used square root transformed pollen data and covariance matrix. The rate of vegetation change was calculated on interpolated pollen spectra, the recalculation interval was 100 year. The distance measure was chord distance (Bennett and Humphry, 1995).

For the pollen assemblage based biome reconstructions we used the technique of Prentice et al. (1996) improved further by Tarasov et al. (1998). This latter study describes the technique how to distinguish between cool and warm steppe biomes and forest steppe. The first step is the assignment of the pollen taxa to plant functional types (PFT). We used the biome-PFT-taxon matrix published in Allen et al. (2000). Plant functional types occupy specific bioclimatic spaces that can be assigned to one or several biomes. The biome-PFT matrix is a list of biomes, indicating which PFTs are characteristic for each biome. The next step is the calculation of biome affinity scores using the formula of Prentice et al. (1996). This equation sums up the square roots of pollen percentages within a PFT, and sums up the affinity scores within a biome characterised by a set of PFTs. Eventually, the pollen sample is assigned to the biome with which it has the maximum affinity. The threshold value above which a taxon is taken into account is 0.5%. If the arboreal pollen sum is <70%, the temperate forest biome is replaced by wooded steppe (Allen et al., 2000). An alternative biome-PFT-taxon matrix was published by Binney et al. (2011) based on Bigelow et al. (2003) and Kaplan and New (2006), and was used recently in continental scale biome reconstructions (Binney et al., 2017). In this system both PFT assignments and biome names are slightly different (Appendix 2). In this paper we present the stratigraphic plot of the main biome affinity scores using both concepts, but we

do not use REVEALS-based biomization (Binney et al., 2011).

For the pollen-based July mean temperature (T_{July}) reconstruction, the European Modern Pollen Database (EMPD) was used (Davis et al., 2013). EMPD currently has information on almost 5000 surface pollen samples from throughout the Euro-Siberian and Mediterranean regions. As a first step, this dataset was harmonised taxonomically with synonym taxa merged. This resulted in 209 terrestrial pollen types for summer mean temperature reconstruction that was further reduced to the dominant 43 taxa for the modern analogue technique reconstructions (Appendix 3). Subsequently, the EMPD climate data file was used to exclude surface pollen samples where modern T_{January} is >1 °C and/or T_{July} is >25 °C. These values were very likely not exceeded during the last glacial termination and Early Holocene period in the Pannonian Basin. Surface samples with a pollen count lower than 300 for the selected 209 taxa were also excluded. In addition, a set of 40 lake surface sediment-derived modern pollen samples were added to the dataset from the South Carpathians (Appendix 3). The resultant dataset has 2687 modern pollen samples, of which 1240 are located below 600 m above sea level. We calculated percentage values for pollen taxa using the pollen counts of the 209 terrestrial pollen types. Modern T_{JJA} (mean air temperature for June, July and August) for each site was included in the EMPD climate data file. These modern values were derived from the WorldClim database with a 30-arc-second spatial resolution (Hijmans et al., 2005). The same modern climate dataset was assessed for obtaining modern T_{JJA} values for the South Carpathian lakes using the Raster package in R (Hijmans, 2016). The T_{July} range of the surface pollen dataset is 4.1–24.4 °C.

Note that the modern pollen dataset derived from EMPD is geographically uneven. Currently, Scandinavian sites are over-represented, while East European and West Siberian sites are under-represented (Appendix 3).

We developed quantitative pollen-based transfer functions for T_{JJA} using weighted averaging–partial least squares (WA-PLS) regression (ter Braak and Juggins, 1993) with five components. We used leave-one-out cross-validation (Birks et al., 1990) to evaluate the model performance and estimated performance statistics such as coefficient of determination (r²) between measured and predicted values, root mean square error of prediction (RMSEP) and maximum bias for each WA-PLS transfer function. We transformed the surface pollen data to square-roots to reduce the noise of the data (Prentice, 1980), applied randomization *t*-test (Van der Voet, 1994) for selecting the most appropriate WA-PLS component for T_{JJA} reconstructions, and calculated sample-specific standard errors for the reconstructions with a bootstrapping procedure with 1000 cycles (Birks, 2003). We performed the WA-PLS transfer functions and associated T_{JJA} reconstructions with the RIOJA package in R (Juggins, 2012). We assessed statistical significance of the WA-PLS-based T_{JJA} reconstructions with the approach involving 999 randomizations developed by Telford and Birks (2011) and conducted these significance tests with the R package PALAEOSIG (Telford and Birks, 2011). An alternative transfer function, the modern analogue technique (MAT) was also used to derive T_{JJA}. This method does not require real calibration (in contrast to the WAPLS), and is based on a comparison of past assemblages to modern pollen assemblages. The similarity between each fossil and modern pollen assemblage is evaluated by the chord distance metric (Guiot, 1990; Birks, 2012). In this study 6 modern pollen spectra that had the smallest distance were considered as the best modern analogues of the given pollen spectrum and were subsequently used for the reconstruction. If the chord distance was above a threshold defined by a Monte-Carlo method (Guiot, 1990), the modern sample was considered as bad analogue, and was not taken into account in the reconstruction. Estimates of climatic parameters were obtained by taking a

weighted average of the values for all selected best modern analogues, where the weights used were the inverse of the chord distance. MAT based T_{JJA} reconstruction and statistical tests were run in R using the RIOJA package.

In this study we focus on the reconstruction of a single climatic parameter, T_{JJA} . The aim of the reconstruction is to compare the pollen-based T_{JJA} record with the loess mollusc derived July temperature record for the LPG and LG in the Eastern GHP (Sümegei, 2005a,b; Sümegei et al., 2012, 2019). We also compare our data with a recent model-based transient climate simulation with the Community Climate System Model ver. 3 (CCSM3) coming from the TRaCE21ka experiment (Liu et al., 2009, 2014). This model has a latitude – longitude resolution of $\sim 3.75^\circ$ in the atmosphere, regridded using bilinear interpolation to a spatial resolution of $2.5 \times 2.5^\circ$. The relevant grid cell T_{JJA} data covering Kokad was obtained and plotted using the PaleoView software (Fordham et al., 2017).

4. Results and interpretation

4.1. Chronology, sediment stratigraphy and organic content

Results of the AMS ^{14}C measurements along with the dated material and calibrated age ranges (2σ) are shown in Table 1. The age-depth model is presented in Fig. 2. Dating of the biogenic carbonate section was the most problematic, as terrestrial plant macrofossils were absent in this section (c. 200–300 cm). Nine outlier dates were identified in the sequence by BACON. Most of them gave considerably younger than expected age that is likely explained by downcore penetration of monocotyledon leaves, and their unfortunate selection for dating in macrofossil poor sediment layers. Alternatively, the large surface area/sample weight ratios gave way to modern CO_2 contamination during the ^{14}C AMS dating process. Three outlier dates had critically low carbon content (<1 mg), while one charcoal sample gave unexpectedly old age at 392–394 cm and was likely reworked from the catchment. The age-depth model presented in Fig. 2 is the BACON output without any a priori classification of the dates as more reliable (e.g. charcoal or terrestrial plant macrofossil based) and less reliable (bulk sediment date prone possibly to reservoir effect). Several alternative age-

depth models could be developed using this set of AMS ^{14}C dates that show a considerable scatter. Considering the bulk radiocarbon dates in the biogenic carbonate section of the core between 213 and 300 cm (Figs. 2 and 3), an alternative model leaving out these dates would give considerably younger ages (Early Holocene) in this sediment section. However, the pollen stratigraphy (Fig. 4) indicates pine (*Pinus* Diploxylon type) and birch (*Betula*) dominance with low percentages of elm (*Ulmus*), hazel (*Corylus*) and oak (*Quercus*) pollen together with sustained high herb pollen relative frequencies (35–50%) that in comparison with other ^{14}C dated pollen records from Eastern Hungary (Fig. 1: Bátorliget, Sarló-hát, Tiszacsermely, Pocsaj P-2 & P-5, Nyíres-tó; Willis et al., 1995; Magyari et al., 2010; Borsy and Félegyházi, 1983; Félegyházi, 1998; Harrington, 1995; Sümegei, 1999) support the late glacial age of these sediment layers and the validity of the BACON derived age-depth model.

According to the age-depth model, the bottom of the sediment section is around 20,000 cal yr BP old (Fig. 2). Sediment accumulation rates were generally high during the Late Pleniglacial (LPG: 24,000–14,600 cal yr BP; Tzedakis et al., 2013) and decreased rapidly during the late glacial (LG) suggesting decreased erosional input. Average deposition time (DT) was 14 yr cm^{-1} between 20,000 and 15,000 cal yr BP (635–275 cm); followed by slower sediment accumulation and thus larger deposition times (42 yr cm^{-1}) between 15,000 and 13,530 cal yr BP (275–240 cm). Even slower sediment accumulation characterised the period between 13,530 and 9500 cal yr BP (240–201 cm; average DT: 101 yr cm^{-1}), while in the last 500 years sediment accumulation rates increased again (201–194 cm; average DT: 75 yr cm^{-1}).

The lithological column is represented in Fig. 3. The lowermost two units (635–600 cm and 600–595 cm; 20,000–19,500 cal yr BP, not shown in Fig. 3) were deposited directly after the last glacial maximum (LGM), in the Late Pleniglacial period (~GS-2.1; Rasmussen et al., 2014). The sediment is grey clayey silt with frequent black, seemingly burnt layers. This is followed by a darker, brownish coloured silty clay between 595 and 400 cm (19,500–16,500 cal yr BP) and mid-brown clayey sandy silt with occasional carbonate precipitation (400–300 cm; 16,500–15,300 cal yr BP). Organic content values are generally low in the bottom layer, between 3 and 6%, with two moderately higher

Table 1
Results of the AMS ^{14}C measurements of Kokad-2 core, Kokad mire, Hungary.

Laboratory	Dated material	Depth (cm)	^{14}C ages BP	Calibrated BP age ranges (2Φ)	Remarks
Poznań	<i>Phragmites australis</i> stems	3–4	$107,47 \pm 0,4$		modern, 0.74 mgC
Poznań	<i>Sambucus nigra</i> seed, indet. seed, macrocharcoal	58	1870 ± 30	1724–1877	
Poznań	<i>Sambucus nigra</i> seed, macrocharcoal and wood fragment	71	2250 ± 30	2156–2267	
Poznań	<i>Phragmites australis</i> stems	76–78	920 ± 40	758–924	outlier, 0.1 mgC
Poznań	Charcoal	104–107	3444 ± 33	3631–3783	
Poznań	Charcoal	115–119	3100 ± 33	3226–3383	
Poznań	<i>Phragmites australis</i> stems	121–123	915 ± 30	762–920	outlier, 0.74 mgC
Debrecen	$<180 \mu\text{m}$ fine organic matter, plant macrofossils	179	7506 ± 45	8277–8398	
Poznań	Charcoal	195–198	6699 ± 51	7481–7660	outlier
Debrecen	Biogenic carbonate	239	11412 ± 46	13133–13361	
Debrecen	Biogenic carbonate	239	11823 ± 46	13547–13762	
Poznań	Cyperaceae leaf fragments	242–244	1530 ± 50	1326–1532	outlier, 0.1 mgC
Debrecen	<i>Schoenoplectus</i> and <i>Carex</i> leaves	279	1357 ± 37	1236–1337	outlier
Debrecen	Biogenic carbonate	279	12825 ± 50	15117–15525	
Debrecen	Biogenic carbonate	279	12920 ± 49	15233–15661	
Debrecen	$<180 \mu\text{m}$ fine organic matter, plant macrofossils	326	14715 ± 59	17704–18084	outlier
Poznań	sedge leaf fragments and charcoal	392–394	25330 ± 140	28983–29780	outlier
Debrecen	moss leaves, <i>Carex</i> leaves	422	13582 ± 62	16154–16619	
Debrecen	charcoal	465	14419 ± 56	17370–17805	
Poznań	<i>Carex</i> and moss leaves, <i>Betula nana</i> fruit plus indet. plant macrofossils	498–500	10930 ± 50	12703–12929	outlier
Debrecen	moss leaves, <i>Carex</i> leaves, indet seeds	553	14326 ± 63	17212–17655	
Debrecen	moss leaves, <i>Carex</i> leaves, indet seeds	598–600	14635 ± 63	17621–18001	outlier
Poznań	wood branchlet	599–601	16280 ± 90	19416–19954	0.72 mgC

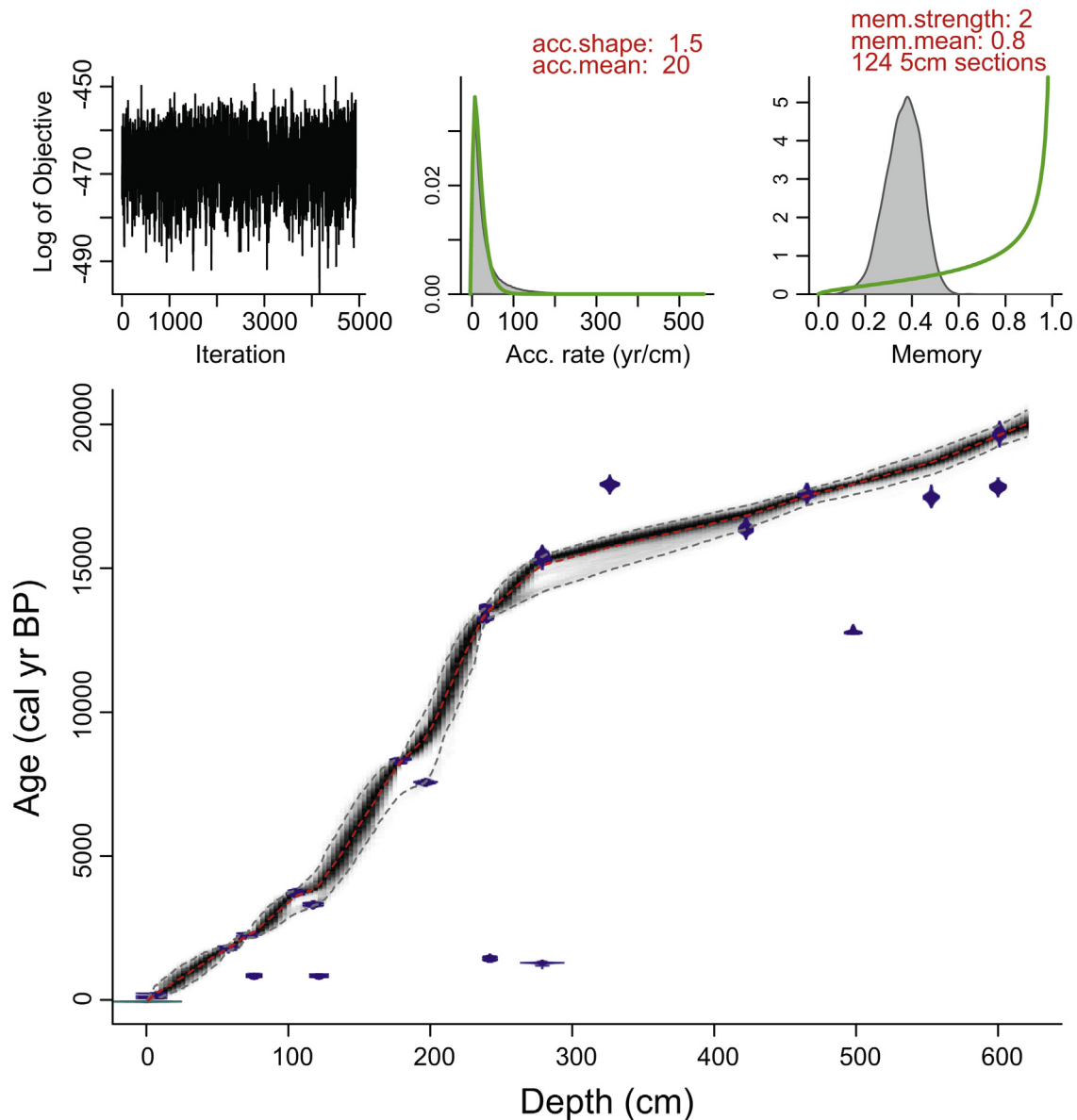


Fig. 2. Age-depth model of Kokad mire, core Kokad-2, Eastern Hungary. Bayesian age-depth modelling was performed in R using the BACON package and 23 AMS ^{14}C dates (Blaauw and Christén, 2013).

peaks (c. 11%) at 458 cm and 484 cm (17,500 cal yr BP and 17,100 cal yr BP) (Fig. 3), then decrease further above 400 cm to <5% until the Holocene. The fifth unit broadly represents the late glacial and Early Holocene (300–213 cm; 15,300–10,800 cal yr BP) where the sediment is lime rich clay with abundant ostracod and mollusc shell remains. The clayey silt unit starting above 213 cm (10,800–9000 cal yr BP) is characterised by increased organic content (5–10%) and gradually increasing silt content at the expense of clay.

4.2. Magnetic susceptibility and sediment geochemistry, inferred changes in soil, pH and oxygen availability

The magnetic susceptibility (MS) record is characterised by low values between 19,500 and 18,000 cal yr BP (595–504 cm; Fig. 3). Strongly fluctuating and high values appear between 18,000 and 16,500 cal yr BP (504–394 cm) parallel with an increase in the sulphur content of the sediment suggesting the presence of

diamagnetic pyrite and other ferrimagnetic iron sulphide minerals, e.g. greigite. This is followed by a short-term decrease in MS between 16,500 and 16,140 cal yr BP (504–362 cm). Note that a major decrease in sediment fine sand content takes place within this period, at ~16,200 cal yr BP (Fig. 3). Subsequently, a second period of increased MS values appear between 16,140–15,760 cal yr BP within a fine silt and clay dominated sediment unit, in which occasional medium sand peaks appear (Fig. 3). Between 15,760 and 14,650 cal yr BP MS values decrease, with distinctly lower values from 15,200 cal yr BP, when the Mn, Ca and S concentrations increase in the sediment (Fig. 3). From 14,650 cal yr BP MS values are generally low suggesting the cessation of magnetic mineral input or the precipitation of Fe-rich magnetic compounds.

Fe and Mn concentrations are relatively high and fluctuate from the bottom of the core to 15,700 cal yr BP (320 cm). At 16,170 cal yr BP (365 cm) both Fe and Mn show peak concentrations, while organic matter content increases together with Ca. At the same time coarse silt and very fine sand content decrease compensated

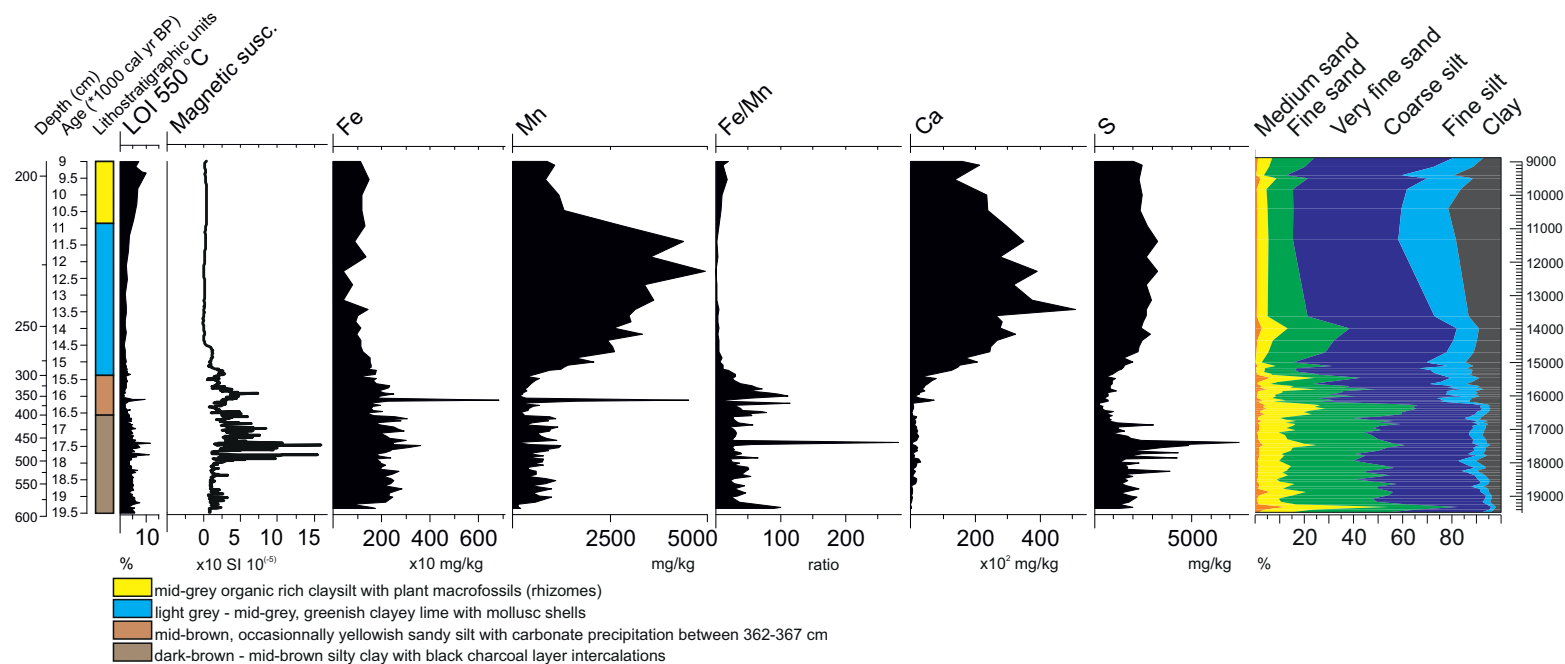


Fig. 3. Lithostratigraphic units of Kokad-2 core with the loss-on-ignition (LOI; 550 °C; %), magnetic susceptibility (MS) and selected major chemical elements (Fe, Mn, Fe/Mn, Ca, S; mg/kg). Element concentrations were measured using ICP-AES. Grain-size measurements were done using Horiba Partica 950LA particle size analyser. Grain size distribution is plotted according to the following classification: coarse sand (>0,5 mm), medium sand (0,5–0,2 mm), fine sand (0,2–0,1 mm), very fine sand (0,1–0,05 mm), coarse silt (0,05–0,01 mm), fine silt (0,01–0,005 mm), clay (<0,005 mm). MS measurement only covers the top 542 cm of the sequence.

by an increase in fine silt. Since then neither medium sand, nor MS and Ca values return to the previous level, and the sediment composition also changes from 16,500 cal yr BP (Fig. 3). These abrupt changes are indicative of a rapid environmental shift

involving accelerated input and precipitation of Ca in the lake and less intense erosion. Fe/Mn ratios show a prominent decrease from 16,200 cal yr BP (365 cm). This decrease is mainly attributable to the selective increase of Mn between 15,200 and 11,400 cal yr BP

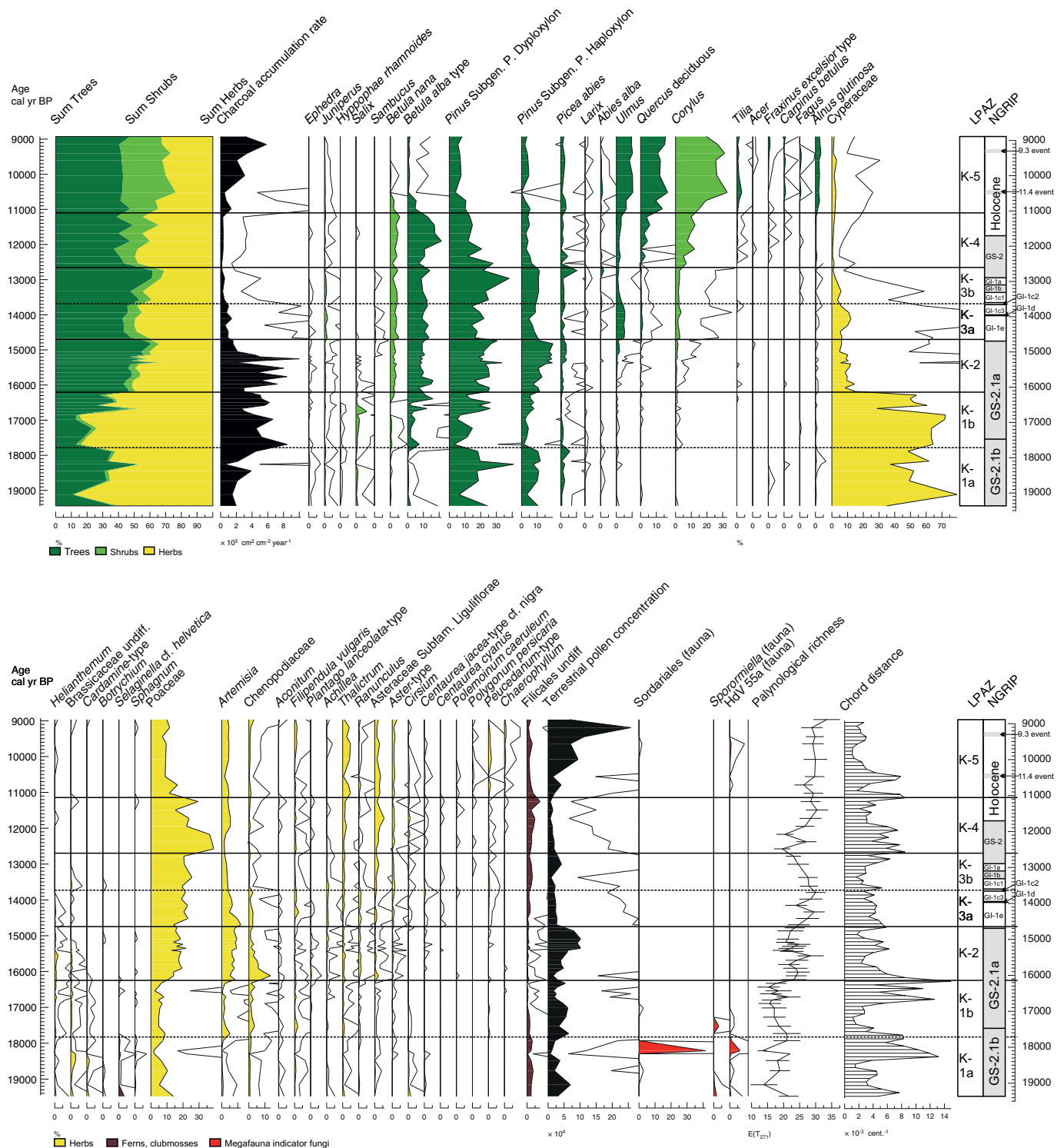


Fig. 4. Major pollen, fungal spore and green algae types from Kokad mire (core Kokad-2) plotted against calibrated BP timescale; (a) major terrestrial pollen type pollen frequencies (green and yellow) and microcharcoal accumulation rates (black); (b) major herb pollen (yellow) and pteridophyte spore (brown) frequencies, grazing indicator fungal spores (red), palynological richness and rate of change values; (c) wetland and aquatic pollen, algae and non-pollen palynomorph frequencies (blue); NGRIP: North Atlantic Greenland Ice Core Project event stratigraphy (Rasmussen et al., 2014), grey shading indicates colder climate phases; GS: Greenland stadial; GI: Greenland interstadial. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

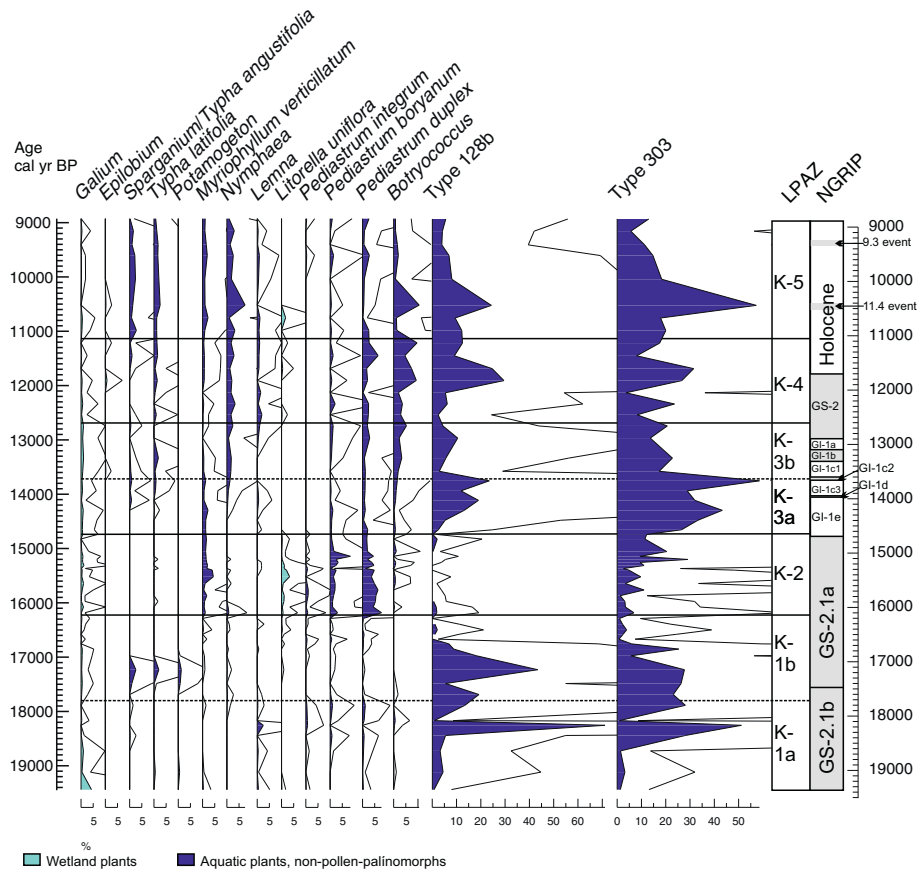


Fig. 4. (continued).

(290–220 cm) that is accompanied by massive increase in Ca and modest increase in S concentrations. High Ca values suggest strong biogenic carbonate precipitation between 15,200 and 10,000 cal yr BP (292–206 cm).

Oxygen availability at the sediment–water interface is inferred from the concentration changes of Fe and Mn, as their redox cycling depends on oxygen availability and pH at the sediment–water interface in lake and mire ecosystems (Mackereth, 1965). Fe and Mn are reduced and released into the water under anoxic conditions, while Fe and Mn oxides precipitate under oxic conditions, usually in shallow, oxygen–rich lakes during spring and autumn (Mackereth, 1965; Davison, 1993). If oxygen or other oxidizers are available, iron precipitates first due to oxidation of the ferrous to ferric iron (Bendell-Young and Harvey, 1992). Manganese precipitates by the oxidation of Mn(II) to Mn(IV), but this process requires higher redox potential. Lake water acidity has also an influence on solubility. The oxidized iron is soluble under strongly acidic (<pH3.5) environment (McBride, 1989), while Mn(IV) is soluble under pH5 (Godo and Reisenauer, 1980). Even though Fe(III) and Mn(IV) are also soluble under acidic environment, iron and manganese complexation with humic substances can strongly facilitate their precipitation (Patrick and Jugsujinda, 1992). On the basis of these considerations, the element concentration record of Kokad suggests enhanced Fe input to the lake from acidic soils (likely podzol) and enhanced precipitation of Fe compounds in the lake between 20,000 and 15,700 cal yr BP likely in line with lower pH of the water column. The increased precipitation of Mn between 15,700 and 10,500 cal yr BP points to higher oxidizer (oxygen and/or nitrate) availability at the sediment/water interface, which was mainly consumed by manganese to form Mn-oxides in a more

alkaline, carbonate rich lake period. The precipitation of Fe was less intense in this period due to lower iron input from the less acidic surrounding soils.

4.3. Pollen and plant macrofossil inferred local and regional vegetation dynamics

The **first local pollen assemblage zone** (Fig. 4) represents the time period directly after the LGM. The first analysed pollen sample is at 592 cm (19,440 cal yr BP); below this depth samples were studied for other proxies down to 635 cm, but pollen analysis was not performed on them. The first local pollen assemblage zone thus spans 19,440–16,200 cal yr BP (592–367 cm). Subzone K-1a between 19,440–17,780 cal yr BP was characterised by low terrestrial pollen accumulation rates (average AR: 712 grains cm⁻²yr⁻¹). In the pollen percentage diagram pines are the most abundant (10–48%) including Swiss stone pine (*Pinus* subgenus *P. Haploxyton*), Scots pine and/or dwarf pine (*Pinus* subgenus *P. Diploxyton*). Norway spruce (*Picea abies*) is the second most abundant followed by willows (*Salix* sp.), European alder (*Alnus glutinosa*), birches (*Betula alba* type) and green alder (*A. viridis*). In addition, *Ephedra* and common sea buckthorn (*Hippophae rhamnoides*) were typically present in this pollen zone. The woody components of the pollen assemblages in association with the low terrestrial pollen concentrations suggest generally low vegetation cover with pine and spruce trees and bare sand surfaces in the vicinity of the sedimentary basin on which both *Ephedra* and buckthorn shrubs colonized. Several cold temperate tree taxa were present in this period likely growing locally on the well-drained surfaces near the mire (*Alnus*, *Salix*, *Betula*). The sporadic presence of several

abundance of grasses (Poaceae), wormwoods (*Artemisia*) and chenopods (Chenopodiaceae). From 16,200 cal yr BP *Achillea*-type pollen and *Ranunculus* increased considerably likely suggesting a shift in the lakeshore meadow vegetation. The same time horizon marked also the disappearance of common sea buckthorn (*Hippophae rhamnoides*) and the massive decrease in sedge (Cyperaceae) pollen percentages. At the same time, crucifers (Brassicaceae undifferentiated) and bitter-cress (*Cardamine*-type) pollen also decreased pointing to a radical hydrological change. The simultaneous increase in green algae (*Pediastrum duplex* and *P. boryanum*) suggests a step-wise increase in planktonic habitats and thus likely a further water-depth increase or increasing nutrient availability in the lake water that coincided with the retreat of willows (Fig. 4b). These lakeshore trees were partially replaced by elders (*Sambucus*) from 16,200 cal yr BP. The lake was rich in submerged aquatics (*Myriophyllum verticillatum* and *M. spicatum*) in this period, and the pollen record also suggests the development of boreal shore weed (*Litorea uniflora*) dominated wet-meadows from 16,200 cal yr BP. In the plant macrofossil record, similar changes were observable (Fig. 5). The local retreat of sedges is well-reflected by the massive concentration drop of Monocotyledon undifferentiated macrofossil remains at ~16,500 cal yr BP (Fig. 5). At the same time, the organic content of the sediment decreased and Fe, Mn, Ca concentrations increased suggesting increasing nutrient in wash from the lakeshore (Fig. 3).

The **third pollen assemblage zone** (K-3) starts at 14,700 cal yr BP showing good agreement with the onset of the LG warming in Greenland (Rasmussen et al., 2014). Although this PAZ was statistically coherent, there are some characteristic pollen compositional changes that justify its subdivision into 2 subzones. In the first subzone (K-3a: 14,700–13,630 cal yr BP, 268–243 cm) the terrestrial pollen flora was characterised by the increase in temperate broadleaved pollen percentages, particularly elm (*Ulmus*) and hazel (*Corylus*), and to a smaller extent oak (*Quercus*). These woody taxa attained the highest percentages between 14,700 and 13,630 cal yr BP (av. 8.6%), when pine (*Pinus* subgenera *P. Diploxylon* and *P. Haploxylon*) pollen percentages decreased (av. 31%). Tree birches were still abundant (av. 12.6%), and elder (*Sambucus*) shrubs were likely present on the lakeshore. This pollen composition suggests the development of boreo-nemoral (mixed leaved) wooded steppes in the region. Forest patches were likely mixed pine-birch-elm (*Pinus-Betula-Ulmus*) dominated stands with the admixture of several temperate broadleaved tree and shrub taxa (e.g. *Corylus*, *Quercus*, *Tilia*, *Fagus*) and other boreal conifers (*Abies alba*, *Picea abies*). The areal extent of steppes likely did not decrease between 14,700 and 13,630 cal yr BP as suggested by the relatively high herb pollen frequencies (40–45%), but we clearly see a shift towards increasing grass (Poaceae) dominance against woodworms (*Artemisia*) suggesting a change in the steppe-tundra vegetation towards continental-type steppes. This time period broadly coincides with the GI-1edc³ sub-phases of the LG interstadial in the NGRIP ice core record (Rasmussen et al., 2014) that was dominated by warming with only one short cold episode between 14,075–13,954 b2k years (GI-1d). Non-pollen palynomorphs (NPPs) and wetland pollen types show the rapid increase of HdV-303 and HdV-128 spores in this phase suggesting a shift to a more mesotrophic environment (Fig. 4c). Furthermore, the decrease in *Pediastrum* and re-increase in sedge (Cyperaceae) pollen from 15,200 cal yr BP suggest a shift in the wetland vegetation (Fig. 4). Ostracod shell concentration increased in the deposit at the same time (Fig. 5), and the appearance of *Chara vulgaris* oogonia from 15,200 cal yr BP together with the scarcity of plant macrofossils and high Ca content (Fig. 3) suggest the development of a calcium-rich, but nutrient-poor open lake with biogenic carbonate precipitation. The only identifiable plant macrofossil in this period was common reed (*Phragmites*

australis). This also supports shallow lake conditions with high Ca input and oxidative lake bottom (see Fe/Mn ratios on Fig. 3). The onset of biogenic carbonate accumulation in the lake coincided with the micro- and macrocharcoal accumulation rate decrease from ~15,200 cal yr BP that suggests a substantial decrease in biomass burning during the early late glacial even though local woody biomass increased (Figs. 4 and 5). These changes overall suggest relatively humid conditions and less auto ignition/less flammable local biomass.

In subzone K-3b (13,630–12,710 cal yr BP, 243–231 cm) elm (*Ulmus*) and oak (*Quercus*) pollen percentages declined, while pines (*Pinus* subgenera *P. Diploxylon* and *P. Haploxylon*) increased, overall resulting in an increase in total tree and shrub pollen frequencies (Fig. 4a). At the same time terrestrial pollen concentrations increased (from 21,875 to 25,970 grains cm⁻³), while pollen accumulation rates (PAR) slightly decreased (from 516 to 328 grains cm⁻²yr⁻¹), overall suggesting that the total terrestrial vegetation cover likely did not change considerably relative to K-3a. Wormwood (*Artemisia*) and chenopod (Chenopodiaceae) pollen percentages also decreased in this period overall suggesting that the regional vegetation cover shifted towards pine-birch dominated forest steppe. Grass dominated continental steppes were likely maintained in this period that coincides with the GI-1c²¹ba phases of the late glacial interstadial in the Greenland ice core chronostratigraphy (Fig. 4). These involve 2 colder and 2 warmer episodes with slightly longer time span for the cold phases than in the previous subzone (Fig. 4). The small-scale decrease of NPPs HdV-303 and HdV-128 and gradually increasing *Pediastrum* and *Botryococcus* relative frequencies (Fig. 4c) suggest less nutrients in the aquatic environment likely with slightly increasing planktonic habitats and hence increasing water-depth in this pollen zone.

The **fourth pollen assemblage zone** K-4 (12,710–11,100 cal yr BP, 231–215 cm) is characterised by the spread of hazel (*Corylus*), grasses (Poaceae) and birches (*Betula alba* type and *B. nana*). Due to the massive increase in grass pollen, total herb pollen percentages increased; however, terrestrial PARs and pollen concentrations both decreased (av. PAR: 132 grains cm⁻²yr⁻¹, av. pollen conc.: 51028 grains cm⁻³) suggesting an overall decrease in terrestrial vegetation cover or pollen productivity. Notable is that the pollen of other temperate deciduous trees (e.g. *Tilia*, *Fraxinus excelsior*-type, *Carpinus betulus*) also increased gradually in this period. Some typical cold and warm continental steppe elements, such as wormwood (*Artemisia*) and chenopods (Chenopodiaceae) increased moderately. These pollen compositional changes suggest the spread of grass steppes together with a pine (*Pinus* *Diploxylon* type), birch (*Betula*), hazel (*Corylus*), oak (*Quercus*) and elm (*Ulmus*) dominated boreo-nemoral forests in this period that broadly covers the GS-1 stadial phase of the late glacial, but also extends into the Holocene warming. If our absolute chronology is correct, then the vegetation composition suggests that GS-1 (~Younger Dryas) growing seasons were relatively warm in this region allowing the expansion of temperate trees, but also dry, leading to the increase in steppe cover and decrease in overall vegetation cover. Micro- and macrocharcoal accumulation rates were low (Figs. 4a and 5) suggesting that fires probably did not play an important role in the pine decline at the beginning of this subzone. In the wetland environment, sedges (Cyperaceae) disappeared nearly totally from the lakeshore, while the submerged and floating aquatic vegetation was similar to the previous subzone with European white water lily (*Nymphaea alba*), whorl-leaf watermilfoil (*Myriophyllum verticillatum*), spiked watermilfoil (*M. spicatum*), duckweed (*Lemna* sp.) dominance, and with the continued presence of bulrush (*Typha latifolia*) and increased abundance of green algae (*Pediastrum duplex*, *P. boryanum*, *Botryococcus braunii*), HdV-128 and 303 fungal spores. This picture suggests a shallow mesotrophic lake with

increased trophic level from 12,200 cal yr BP.

The transition to deciduous forest dominance took place in the **fifth pollen assemblage zone** (K-5), which starts at 11,100 cal yr BP (215–194 cm). At this time a rapid increase in hazel (*Corylus*), oak (*Quercus*) and elm (*Ulmus*) took place accompanied by the rapid decrease of birches (*Betula alba* type, *B. nana*), pines (*Pinus* subgenera *P. Diploxylon* and *P. Haploxylon*) and grasses (Poaceae). This suggests the replacement of pine-birch-hazel dominated forest stands by oak, elm and hazel dominated deciduous forest stands. Notable is however that the pollen frequencies of some characteristic meadow-steppe herbs increased (e.g. *Thalictrum*, Compositae Subfam. Liguliflorae, *Achillea*, *Peucedanum*-type, *Ranunculus*, *Potentilla*) pointing to the continued presence of steppe habitats. The total tree and shrub pollen percentages did not increase over 75–80% in this Early Holocene period, also supporting the semi-open forest steppe character of the landscape in which coniferous trees likely survived into the Early Holocene as suggested by the presence of Norway spruce (*Picea abies*), fir (*Abies alba*) and larch (*Larix decidua*) pollen in addition to pines (Fig. 4a). Increased abundance of chervil (*Chaerophyllum* sp.), a typical deciduous forest understorey herb genus (e.g. *C. temulum*) also supports the local spread of oak forests. Charcoal accumulation rates were high in this period suggesting the frequent occurrence of forest fires. These fires likely played an important role in keeping the forests open. In this period, the plant macrofossil record was characterised by the increasing concentration of common reed (*Phragmites australis*) rhizomes and common stonewort (*Chara vulgaris*) and great tassel stonewort (*Tolypella prolifera*) oogonia (Fig. 5) that is in line with the gradually increasing sediment organic content, and altogether point to the presence of a shallow, lime rich mesotrophic lake at the site.

4.4. Herbivore indicator non-pollen palynomorphs

In this study we paid special attention to the recording of non-pollen palynomorphs (NPP) that involve fungal spores and mainly green algae remains. Of the rich fungal spore assemblages, Fig. 4b displays in red the grazing indicator fungal spore types Sordariales, *Sporomiella* and HdV-55a (*Sordaria* ascospore; van Geel et al., 2003). They are present only in the bottom part of the sediment, between 19,440 and 17,000 cal yr BP suggesting the local presence of large herbivores at that time.

4.5. Biome reconstruction

As described in the methods, biome scores were calculated using two slightly different biomization schemes, the results of which are presented in Fig. 6. Using the plant functional and biome assignment scheme of Prentice et al. (1992, 1996), the main biome is tundra between 19,450 and 16,200 cal yr BP that corresponds to the high abundance of sedges (Cyperaceae), grasses and arctic dwarf shrubs (*Betula nana*, *Salix*). Cool coniferous and cool mixed forest biome scores were also high, and occasionally taiga and cool mixed forest biomes keyed out, when Cyperaceae percentages were lower. A rapid biome shift appears at 16,200 cal yr BP, when Cyperaceae pollen percentages decrease, grasses (Poaceae) increase together with steppe herbs, pines, birches and deciduous trees. The tundra biome is replaced at this point by cool coniferous forest pointing to afforestation and rapid climatic improvement. Only in a few samples did taiga, cool mixed forest and cool steppe biome key out. From 14,740 cal yr BP cool mixed forest was identified predominantly throughout the sequence up to 9000 cal yr BP, with increasing cool mixed forest biome scores after 12,330 cal yr BP. Notable is that the shift to the Holocene temperate deciduous tree dominated pollen assemblages at 11,200 cal yr BP did not entail

a change in the biome assignment, only a further increase in the cool mixed forest and temperate deciduous biome scores (Fig. 6, the latter is not shown); the pollen assemblages were still grouped into the cool mixed forest biome. Since it differs from the temperate deciduous forest biome in that the latter does not contain boreal evergreen conifer trees (*Picea*, *Abies*; Prentice et al., 1992), the Early Holocene biome assignment of the Kokad pollen record reflects the survival of these boreal evergreen conifer tree taxa into the Early Holocene.

Using the more recently published alternative biome-PFT-taxon matrix (Binney et al., 2011), graminoid and forb tundra (DRYT) biome dominated between 19,450 and 17,400 cal yr BP followed by alternation between graminoid and forb tundra and cold evergreen needle leaved forest (TAIG) between 17,400 and 14,700 cal yr BP. The scores of these two biomes were the highest with occasional jumps (Fig. 6). From 14,700 cal yr BP the biome assignment is graminoid and forb tundra (DRYT) again even though the scores of cold evergreen needle-leaved forest (boreal forest) are also very high. The final biome assignment is attributable to a small increase in grasses and other herbs in this period, and it is more likely interpretable as a spread in steppe vegetation at the onset of the late glacial warming. Between 13,100 and 11,200 cal yr BP the cold evergreen needle-leaved forest biome was ubiquitous, and from 11,200 cal yr BP to 9000 cal yr BP temperate deciduous forest was reconstructed in all samples.

Comparing the results of the two methods, both point out the presence of tundra (graminoid and forb tundra) directly after the LGM until 16,200 and 17,400 cal yr BP, when a shift to cool coniferous forest or its counterpart, cold evergreen needle leaved forest was reconstructed. The main difference in the two methods is in the biome assignment during the early late glacial when cool mixed forest is reconstructed by the Prentice et al. (1996) scheme and graminoid forb tundra by the Binney et al. (2011) scheme. Given the increasing presence of temperate deciduous trees in this period, the Prentice et al. (1996) scheme seems more realistic, and not only in this period, but also throughout the entire sequence.

The pollen based biome assignment scheme of Prentice et al. (1996) and Tarasov et al. (1998) counts with the total arboreal pollen sum only in the temperate deciduous forest biome. Forest is replaced with forest steppe in case of <70% arboreal pollen frequencies. In the Kokad pollen sequence these values were constantly below this limit before 10,500 cal yr BP and only occasionally increased above 70% between 10,500 and 9000 cal yr BP, suggesting that the landscape was not covered by closed forest. Cool mixed wooded steppe and cool conifer wooded steppe biomes would therefore be more appropriate terms to express the semi-open character of the landscape during the last glacial termination. On the other hand, the presence of boreal evergreen conifers (if not far distance transported) suggest enough precipitation (α ~75%, Prentice et al., 1992) that contradicts with the wooded steppe vegetation. To resolve this contradiction, we have to reckon with the complex hydrology of the Érmellék geographical region (Fig. 1), where Kokad mire is situated. High groundwater table in the former river valleys likely created locally humid environments suitable for boreal evergreen trees.

According to Prentice et al. (1992, 1996), the tundra biome between 19,450–16,200 cal yr BP suggests a climatic limit of GDD5 (growing degree day sum above 5 °C) < 350–500 and precipitation demand between 28 and 65% (α : ratio of actual evapotranspiration to equilibrium evapotranspiration). From 16,200 cal yr BP a shift to cool conifer forest suggests an increase in GDD5 to 900 and coldest month mean temperatures between –15 and –19 °C, while from 14,740 cal yr BP the reconstructed cool mixed forest biome suggests a further increase in GDD5 (>1200), increasing coldest month mean temperatures (–2 to –15 °C) and increasing moisture availability at

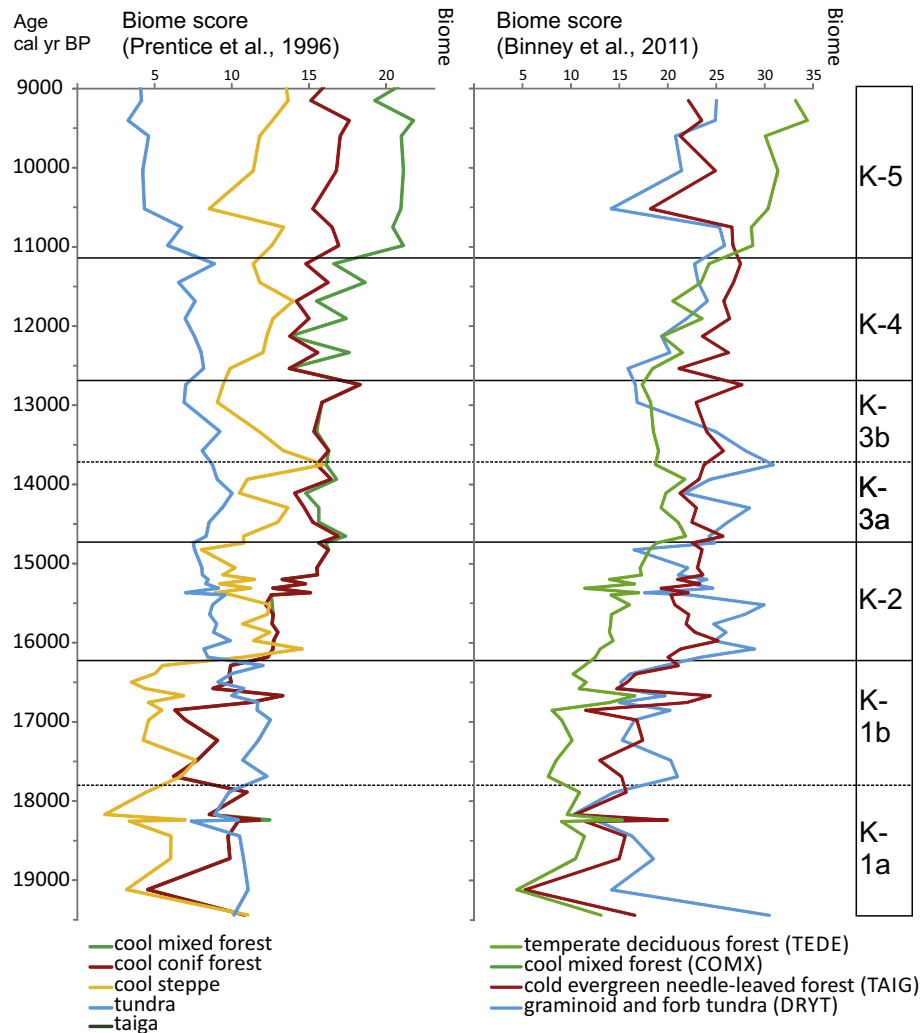


Fig. 6. Biome scores for Kokad mire (core Kokad-2) calculated using two slightly different biomization schemes; (a) biome scores and final affiliated biome based on the method of Prentice et al. (1996); (b) biome scores and final affiliated biome based on the method of Binney et al. (2011).

least locally ($\alpha > 75\%$).

4.6. Rate of vegetation change, palynological diversity and multivariate data analyses

Fig. 4b displays the chord distances of the 50-yr recalculated pollen assemblages, which measures the tempo of vegetation change through time. The values suggest that the composition of the terrestrial vegetation showed rapid changes between 18,000–18,300, 16,800–16,200, 12,650–12,050, 11,200–11,000 and 10,550–10,450 cal yr BP. These intervals coincide well with the pollen assemblage zone boundaries, but in particular highlight rapid vegetation reorganization directly after the LGM, and not during the late glacial warming. The pollen inferred vegetation diversity showed the most prominent increase at 16,200 cal yr BP from less than 20 pollen types per sample to above 25 pollen types per sample afterwards. The timing of this increase coincides with the biome shift from tundra (steppe-tundra) to cool coniferous forest. Palynological diversity decreased again in the second part of the lateglacial interstadial (GI-1) and between 13,600 and 12,100 cal yr BP (late GI-1 and GS-2), which was followed by an increase to > 28 terrestrial pollen types per sample afterwards.

4.7. Pollen-based paleoclimate reconstruction

The results of cross-validation test for the transfer function shows that the WA-PLS model ($r^2 = 0.741$, root mean square error of prediction (RMSEP) = 1.454 °C) exhibit good predictive performance and restricting the modern samples by altitude (<600 m) influences the reconstructed absolute values, and also increase model performance (Appendix 3). The MAT model has slightly better predictive performance ($r^2 = 0.825$, root mean square error of prediction (RMSEP) = 1.246 °C). The significance tests showed that both the WA-PLS and MAT T_{JJA} models are statistically significant ($p < 0.005$) as they explained more of the variance in the fossil data than most reconstructions derived from transfer functions trained on random environmental data (Telford and Birks, 2011, Appendix 3). Fig. 7 shows pollen inferred July mean temperatures at Kokad using both the WA-PLS (209 taxa) and MAT (43 taxa) based reconstructions.

The WA-PLS reconstruction shows that between 19,440 and 16,700 cal yr BP pollen-inferred summer mean temperatures were stable and fluctuated between 14.5 and 15.7 °C, while the MAT based reconstruction shows lower values and high amplitude fluctuation (Fig. 7).

The two reconstructions differ considerably in the LPG section,

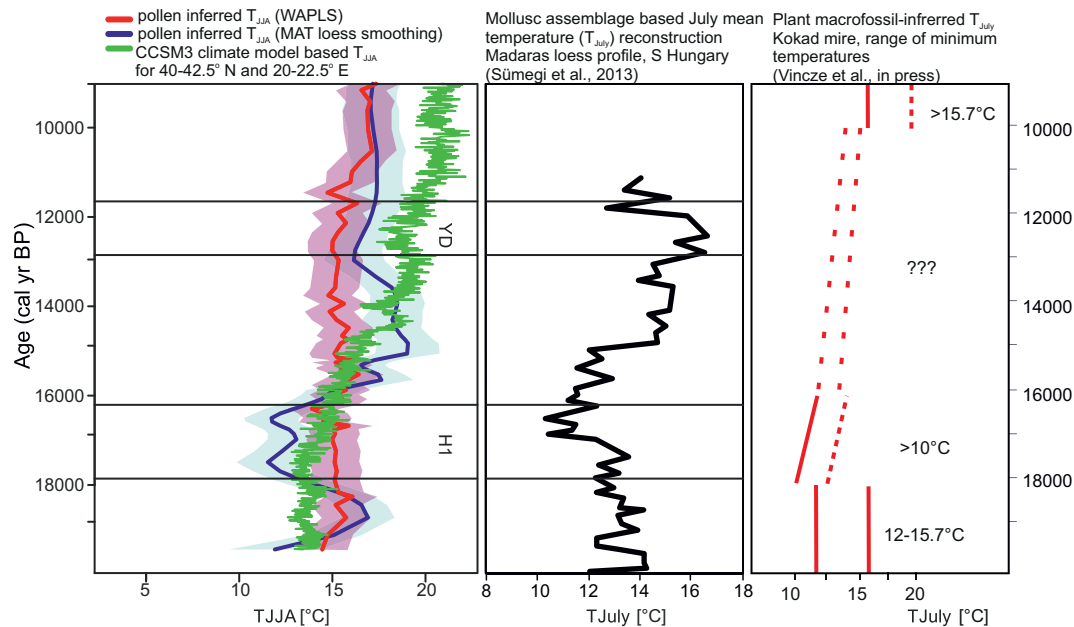


Fig. 7. Pollen-based summer mean temperature (T_{JJA}) reconstruction between 20,000 and 9000 cal yr BP at Kokad mire with climate model inferred summer mean temperatures for 40–42.5°N and 20–22.5°E using the CCSM3 climate model and the PaleoView software (Liu et al., 2009; Fordham et al., 2017). For comparison the central column shows mollusc assemblage inferred July mean temperatures (T_{July}) at the Madaras loess profile, South Hungary (Sümegei et al., 2013), while the right column displays plant macrofossil inferred minimum range of July mean temperatures from Kokad mire on the basis of Vincze et al. (in press). H1: Heinrich-1 event; YD: Younger Dryas.

with the MAT reconstruction showing a distinct cooling between 17,900–16,280 cal BP with inferred summer mean temperatures between 7.5 and 12.7 °C, while the same cold period is missing in the WA-PLS reconstruction, only minor cooling is present between 16,700 and 16,280 cal yr BP from 15 to 13.6 °C, which amplitude seems more realistic. As is shown on Fig. 7, this period coincides with Heinrich-event 1 (H1: 17,850–16,200 cal yr BP).

Following this event, July mean temperatures increased rapidly in the MAT based T_{JJA} record to 16–18 °C, while the WA-PLS method fails to display this relatively high amplitude warming, summer mean temperatures reached maximum 15.6 °C until 11,450 cal yr BP. The largest amplitude increase in the WA-PLS based summer temperature reconstruction took place between 11,450 and 10,500 cal yr BP, when T_{July} increased from 15 to 17.2 °C and stayed around this value until 9000 cal yr BP. The MAT based reconstruction, on the other hand, shows a second colder period between 13,570 and 12,330 cal yr BP and a gradual warming afterwards, but the maximum Early Holocene T_{JJA} was only 17.4 °C, which is lower than maximum reconstructed summer mean temperature during the LG (18 °C). Given the pollen compositional changes (increase in temperate deciduous taxa), this reconstruction seems less realistic.

Overall, the MAT based reconstruction shows unrealistically large amplitude fluctuation in T_{JJA} , and despite its better statistical performance, which likely derives from over-fitting (Telford and Birks, 2011), the geographical position of the selected best analogues makes extreme jumps in space (Appendix 3). The WA-PLS based reconstruction, on the other hand, does not display significant warming during the LG interstadial despite the clear vegetation change. Therefore, we may conclude that the pollen based summer temperature reconstructions can be used as a coarse approximation of the LPG and LG summer temperatures only, and their changes in case of Kokad. What is striking is the relatively warm summers by 19,440 cal yr BP (~14.53 °C) on the basis of the more realistic WA-PLS technique, and buffered July mean temperature fluctuation throughout the last glacial termination period in this region with < 1 °C decrease in July means during the GS-1

stadial, and ~2.2 °C warming in the Early Holocene.

5. Discussion

5.1. Ecosystem changes during the last glacial termination in the eastern and western Pannonian Basin, what the Kokad multi-proxy record adds to our knowledge?

Archives of the LGM and last glacial termination climate, flora and fauna of the Pannonian Basin are particularly rich, and the number of paleo-proxy records has increased considerably during the last three decades thanks to the intense loess mollusc, loess charcoal, grain size and susceptibility studies both in Eastern and Western Hungary (Bradák et al., 2011; Buró et al., 2016; Feurdean et al., 2007a,b, 2008, 2011, 2012; Jakab et al., 2005, 2009; Jankovská and Pokorný, 2008; Járjai-Komlódi, 2003; Magyari et al., 1999, 2012, 2014a,b; Medzihradský and Bajzáth, 1998; Obrecht et al., 2017; Rudner and Sümegei, 2001; Rudner et al., 2004; Sümegei, 2005a,b; Sümegei and Krolopp, 2002; Sümegei et al., 2011, 2013, 2018; Újvári et al., 2017; Willis and van Andel, 2004; Willis et al., 1995, 1997, 2000). Particularly the Madaras and Katymár loess sequences provided high time-resolution and well dated climate and biogeographical records from SE Hungary (Fig. 1), and these demonstrate that despite the clear cooling trend during the LGM, humidity increased in the southeast GHP that favoured the increase of total vegetation cover. Moreover, the survival of forest dwelling molluscs together with loess-charcoal records suggested the persistence of trees in the Pannonian Basin (Willis et al., 2000; Willis and van Andel, 2004; Rudner and Sümegei, 2001; Sümegei et al., 2012, 2018). This was accompanied by the expansion of Holarctic steppe, North-Asian xeromontane and boreo-alpine elements in the Mollusc fauna pointing to significant cooling (Sümegei, 2005b). The most peculiar feature of the southern lowland ecosystems was their aridity-driven change during the Late Pleniglacial climatic fluctuations. While the Hungarian sites show an alteration in climate, vegetation and fauna well in agreement with

stadial-interstadial fluctuations in Greenland data (Sümegei et al., 2012), the Serbian loess sequences further south lack such correlation, explained by the aridity of the climate coupled with relatively warm summers that resulted in the stable dominance of grasslands with slightly higher n-alkane inferred woody cover during GS-2, but no real forest advances at the Vojvodina sites (Marković et al., 2008, 2018; Zech et al., 2013; Sümegei et al., 2016). These conditions were explained by a southward shift in the westerlies during late MIS 3 and MIS 2 that induced wetter and warmer air masses from the Mediterranean and the Balkans (Tzedakis et al., 2006; Obrecht et al., 2017, 2019) penetrating into the basin's southern parts. This likely explains the relatively mild conditions in this region.

For the LGM, the mollusc-inferred vegetation cover was mosaic tundra and mesophilous steppe, forest-steppe vegetation in Eastern Hungary, similarly to Katymár and Madaras (Fig. 1). Ecosystem productivity was higher during the interstadial periods, despite the open character of the landscape. Notable is that none of these Serbian loess records contained wood charcoal during the LGM and deglaciation period and loess accumulation halted only at the beginning of the Holocene, around 11,000 cal b2K at Madaras (Fig. 7, Hupuczsi and Sümegei, 2010; Sümegei et al., 2012). The mollusc-inferred July mean temperatures showed gradually decreasing values after 24,000 cal b2k from 18 °C to 10–11 °C by 17,000 (~Heinrich-1 stadial), followed by an increase after 16,500 cal b2k gradually up to 15–16 °C by the late glacial interstadial (Fig. 7). The Kokad paleo-record completes this picture for the eastern GHP by indicating the local presence of birch (*Betula pubescens*, *B. nana*) and pine (*Pinus sylvestris*) trees and shrubs in the steppe tundra dominated landscape during the early post-LGM period, between 19,440–18,700 cal yr BP, and proves also the local persistence of several boreal mosses (*Pseudocalliergon trifarium*, *Drepanocladus aduncus*) and cold temperate trees (*Salix*, *Alnus*) and very early colonization of hazel (*Corylus*) in this period. Fig. 7 displays together the pollen inferred summer mean temperatures, the climate model derived data for the same period (Fordham et al., 2017; Liu et al., 2009, 2014), the mollusc inferred July mean temperatures from the Madaras loess sequence (Fig. 1; Sümegei et al., 2012) and the plant macrofossil-based July temperatures of Kokad (range of minimum temperatures) (Vincze et al., in press). According to the mollusc-inferred temperature record, average temperatures were around 12.5 °C after the LGM, between ca. 20,000 and 17,500 cal yr BP, followed by an abrupt cooling to ~10.5 °C until ca. 16,100 cal yr BP. At the same time the aquatic plant macrofossil-based July mean temperature reconstruction of Kokad suggests >14–15.7 °C soon after the LGM, until c. 18,300 cal yr BP (indicated by the presence of *Typha angustifolia* and *Typha latifolia*). This was followed by a cooling until c. 16,900 cal yr BP (Vincze et al., in press, Fig. 7). This interval broadly agrees with Heinrich-event 1, and it seems that this cold event had strong effect both on the fauna and vegetation of the Pannonian Basin, as the pollen inferred summer mean temperatures also display a cold period between 17,900 (16,700) and 16,200 cal yr BP at Kokad mire, when summer mean temperatures drop to 10 °C with the modern analogue technique (MAT), while the WA-PLS method implies a shorter and weaker cooling between 16,500 and 16,200 cal yr BP down to ~13.6 °C. Unfortunately, aquatic remains did not provide information about July mean temperatures from 16,500 cal yr BP, only chemical data (Fe/Mn ratio and Ca increase) indicate significant changes around Kokad (Vincze et al., in press). It is noteworthy that not all paleo-records indicate cooling at this time in the basin. For example, neither the Madaras loess sequence, nor the Nagymohos and Fehér Lake sediment archives (Fig. 1) indicate cooling or biome reorganization in the same period (Sümegei et al., 2013, 2018; Magyari et al., 2014a). At Madaras the mollusc-inferred July mean

temperatures stayed above 14.5 °C in this period. On the other hand, some Serbian loess records and the Lake St Anne pollen record in the Eastern Carpathians indicate cooling and drying and the re-expansion of junipers (*Juniperus* sp.) in the Eastern Carpathians at this time (Marković et al., 2008; Magyari et al., 2014b). Overall, several paleo-archives show that the last cold interval prior to the late glacial warming was associated with Heinrich-event 1, and the ecosystem impacts of this cold interval likely terminated around 16,500–16,200 cal yr BP.

Our study site Kokad lies north of the aforementioned loess sequences, in a different geographical unit (Érmellék), where the nearest loess-mollusc records are in the Hajdúság (Fig. 1). The Debrecen-Brickyard sequence covers the time of the last glacial termination period (Sümegei, 2005b) and its species-poor mollusc fauna was dominated by cold-loving xero-montane and arctic-alpine species (*Columella columella*, *Vallonia tenuilabris*) indicating steppe environment with periodic cooling and warming. The inferred July mean temperatures ranged 12.9–13.2 °C between c. 19,300 and 17,000 cal yr BP (see also Fig. 7), which is in agreement with the lower estimates of the paleoclimate model data and agrees better with the MAT-derived mean summer temperatures (Fig. 7). The mollusc inferred July temperatures increased to c. 15–16 °C at 17,000 cal yr BP, and a further much more robust change in the fauna was found at 16,100 cal yr BP (13,380 ± 200 ¹⁴C years) when cryophilous elements decreased, while cold-resistant and mild climate indicators increased (e.g. *Vallonia costata*) pointing to milder conditions with >16 °C July mean temperatures. At the same time, the carbonate content of the loess increased (Sümegei, 2005b). These changes are highly similar to the observed climate changes at Kokad, however the Hajdúság loess region at Debrecen likely remained treeless or only sparsely wooded during the late glacial unlike the more humid Érmellék region. The mollusc-inferred July mean temperatures agree with the modelled values and also with the pollen based MAT reconstruction (Fig. 7). Noteworthy is that the loess sequence corroborate a major environmental shift at ~16,100–16,200 cal yr BP, i.e. prior the late glacial interstadial warming. Several loess profiles from the Hajdúság region were studied by Sümegei (2005b) and their most important finding for the LG/Holocene boundary was the turnover of the vegetation from cold to warm steppe and forest steppe. He also pointed out that the southern part of the Hajdúság (e.g. Derecske, Fig. 1) accumulated floodplain loess with higher proportion of forest-dweller species during the LGM suggesting increased woody cover, similarly to the lower-lying northern Hajdúság (Tiszavasvár-Szorgalmatos, Fig. 1).

Further west, in the Danube-Tisza Interfluvium the deposits of inter-dune hollow lakes (Bócsa and Kolon lakes) cover the LGM and the early part of the last glacial termination period (Fig. 1; Járαι-Komlódi, 1985; Borsy et al., 1991; Lóki et al., 1995; Sümegei et al., 2011). These pollen records indicate pine-birch forest steppe vegetation during the last glacial termination. The local presence of tree birch (*Betula* sp.) was confirmed in Lake Kolon by the recovery of epidermis fragments at 18–19 and 13–14 kyr cal BP (Sümegei et al., 2011). This vegetation picture is quite similar to Kokad between 20 and 14.7 kyr cal BP, but the resolution of these pollen records is generally low, and their dating control is weak (except Lake Kolon, Sümegei et al., 2011). The 16.2 kyr cal BP shift from tall forb steppe-tundra and cold conifer forest steppe to cold conifer forest steppe and continental grassland mosaic (with deciduous tree admixture) at Kokad (Fig. 6) is for example not well-expressed in these records, and a notable difference appears during the late glacial interstadial, when temperate deciduous taxa show a much more pronounced increase at Kokad (Fig. 4a). The most prominent feature of the Kokad paleobotanical record is without any doubt the early expansion of elm (*Ulmus* sp.) and hazel (*Corylus*) during the late glacial and the relatively vague expression of the short and

longer term cooling events of the late glacial. Moving further west to the Balaton region, the paleo-archives suggest that shrub birch (*Betula humilis*) and pine tree (*Pinus* sp.) remains were abundant in the terminal part of the Late Pleniglacial, between 16 and 17 kyr cal BP and both common reed (*Phragmites australis*) and bulrush (*Typha latifolia*) were present suggesting that July mean temperatures exceeded 13 °C, similarly to Kokad (Kolstrup, 1980; Jakab et al., 2005, Jakab and Sümegei, 2011; Sümegei et al., 2011). During the late glacial boreal and arctic brown moss dominated rich fen vegetation developed in association with pine (*Pinus* sp.) and shrub birches (*Betula nana* and *B. humilis*), on the basis of which the terrestrial vegetation was inferred to be similar to the modern boreal forest/tundra ecotone region (Sümegei et al., 2008a). The pollen record overall suggested larger pine forest cover in Transdanubia than in the Eastern GHP, but mesophilous deciduous trees did not expand, apart from a small increase in hazel (*Corylus*) during the late glacial (Juhász, 2007). Another extensive wetland area that hosts late glacial sediments is Sárrét in Transdanubia (Fig. 1; Willis, 1997; Sümegei et al., 2008b; Molnár et al., 2013). Similarly to Lake Balaton, pines (*Pinus* sp.), birches (*Betula* sp.), silver fir (*Abies alba*) and Norway spruce (*Picea abies*) must have been the dominant tree species in this region, which was forested during the late glacial according to the pollen record. None of the so far studied sequences have good enough chronology to pinpoint the Younger Dryas, but it is likely that a short-term increase in birches (*Betula* sp.) and grasses (Poaceae) mark this time interval suggesting that pine forests were either burnt down or killed by winter cooling and birch spread in this period together with the steppe-tundra vegetation. Compared to Kokad, this site shows stronger vegetation fluctuation during the late glacial (Molnár et al., 2013), but mesophilous deciduous trees do not expand, suggesting colder summers and lower vegetation season temperatures in this region. The Transdanubian part of the Pannonian Basin has also some alluvial landscapes, to some extent similar to Érmellék. An infilled meander at Mezőlak-Szélmező was studied for both pollen and plant macrofossils in this region (Fig. 1, Ilon et al., 2006; Juhász and Szegvári, 2007). The pollen record of this relatively well-dated sediment sequence extends back to ca. 16,000 cal yr BP, and similarly to other Transdanubian sites shows the dominance of pine and birch during the late glacial, with an initial juniper (*Juniperus* sp.) and willow (*Salix* sp.) dominated phase. This is the only pollen sequence in Transdanubia that shows the early expansion of hazel (*Corylus*), from ca. 13,000 cal yr BP, similarly to Kokad. Overall, it seems that small sites with similar geomorphological setting show similar late glacial vegetation change in the lowlands of the Pannonian Basin, so the early expansion of hazel at both localities supports its early late glacial spread in the mixed leaved boreal forests of Hungary. Another similarity is the absence or weak expression of pollen compositional change during the Younger Dryas. The pollen inferred forest cover was higher in this region (AP~80%), similarly to other Transdanubian sites.

This comprehensive summary of the basin's Late Pleniglacial and late glacial paleobotanical and biotic proxy based paleoclimate records shows a wooded landscape to different extent: a much more forested landscape in Transdanubia, with ubiquitous pine, birch, spruce and larch dominance, but with significant contribution also of the cool temperate trees, such as willow, alder and poplar. Several loess and lake archives confirm that in this region of Europe the warming after Heinrich event-1 (around 16,200 cal yr BP) had similar amplitude to the late glacial warming and this warming had a strong summer warming component. Biome shift from steppe-tundra to cool coniferous forest took place at several sites at this time, suggesting that forest expansion started earlier in this region than the late glacial warming (Magyari et al., 2014a, b, Sümegei et al., 2013, 2018), and this expansion also favoured the

spread of temperate trees as we will show in the next section.

5.2. The question of temperate tree refugia in the Pannonian Basin and dispersal in light of the pollen, plant macrofossil and population genetic records

Even though direct, plant macrofossil or wood-charcoal evidence for temperate tree refugia in the Pannonian Basin during the LGM (including the Carpathian Mountains) is still missing, and the question of temperate tree survival beyond the 45°N latitude is debated (Tzedakis et al., 2013), species distribution modelling and phylogeographic data both indicate the potential presence of some temperate tree species with continental character in the Pannonian Basin (*Ulmus laevis*, *U. glabra*, *Tilia cordata*, *Quercus robur*; Svenning et al., 2008), and these species are often called cryptic northern survivors (Varga, 2010; Schmitt and Varga, 2012). As demonstrated by Sümegei et al. (2013), Magyari et al. (2014a,b), Feurdean et al. (2007a, 2011, 2014) and others, several LGM pollen profiles show the re-occurrence of temperate trees in the pollen records during milder interstadial periods between 26 and 17 kyr cal BP, suggesting that refugial habitats of these species were likely located in relatively small distance to these sites from where migration during the relatively short warm interstadials was feasible. An increasing number of temperate and boreal mammal, butterfly, amphibian and reptile population genetic studies argued in support of northern refugia for the continental temperate fauna (summarized in Schmitt and Varga, 2012; Vörös et al., 2017), while the LGM fossil faunas also supported this inference by pointing out the combination of typical cold-adapted species with temperate faunal elements in the Pannonian Basin (Pazonyi, 2004; Sommer and Nadachowski, 2006). In light of these studies the early establishment of hazel (*Corylus*) in Eastern Hungary at ~17,700 cal yr BP and its early expansion from 14,700 cal yr BP can be considered as another supporting evidence for extra-Mediterranean refugia for this species. In this context, it is important to mention that hazel macrocharcoal has been found and dated to 12,900 ± 360 ¹⁴C years (14,780–15,990 cal BP years) in fossil soils of the Nyírség blown sand area directly north of Kokad (Borsy et al., 1982). This finding proves its local presence during the very early phase of the late glacial interstadial and supports the pollen based evidence for its early late glacial expansion in the Eastern GHP. The European-scale phylogeographical study of hazel (*Corylus avellana*) also supports possible refugial populations in the Northern Balkan, although Hungarian populations were not studied (Palmé and Vendramin, 2002). The SE European haplotypes in hazel were not restricted to the very southernmost Balkans, but went as far north as Romania and Croatia suggesting survival in the northern part of this region. Continental-scale mapping of pollen records also support its presence in East-Central Europe by 15,000 cal yr BP and even earlier, and expansion of local Balkan populations (Brewer et al., 2017). It is also notable that hazel was one of the exceptions in the study of Bhagwat and Willis (2008) whose biogeographical trait did not fit with the typical northerly survivors. Its ability to spread fast was explained by bird mediated seed dispersal. Another continental temperate tree taxon for which early post LGM expansion was demonstrated by the Kokad pollen record is elm (*Ulmus*) (Fig. 4a). Species distribution modelling suggested LGM refugial populations in the Southern Pannonian Basin for Wych elm (*U. glabra*) and European white elm (*U. laevis*), but phylogeographical studies in these two species are rare due to a considerable drawback of its populations in the 20th century due to a pathogen fungus causing the Dutch Elm Disease (Collin et al., 2000). Nonetheless, the Pannonian Basin provide evidence for its glacial survival in MIS-3 (ca. 60-30 kyr cal BP) pollen records (Nádor et al., 2011), while several MIS 3 paleolithic sites revealed its charcoal and pollen remains in

the Romanian Carpathians and Trans-Carpathians Region, mainly in the Prut Valley (Cărciumaru, 1989).

The important refugial role of the Pannonian Basin and within it the Eastern GHP with its sand dune region in the Nyírség has been noted also at a famous protected mire called Bátorliget. It is located just 55 km to north-east of Kokad (Fig. 1) and detailed pollen study of this locality suggested the late glacial regional presence of hornbeam (*Carpinus betulus*), hazel (*Corylus*), elm (*Ulmus*) and oak (*Quercus*), while the first charcoal pieces of the same taxa were recovered as early as ~9450 cal yr BP here (Willis et al., 1995; Rudner et al., 2004). Although this site does not extend back to the LGM, its diverse geomorphology and the refugial character of its modern fauna and flora with several cold adapted glacial relict boreo-alpine species (e.g. *Ligularia sibirica*) surviving in the mire, while warm-adapted Sub-Mediterranean species prevailing on the southern sand dune slopes (e.g. *Tilia tomentosa*), render this area ideal for long-term maintenance of both temperate and boreal species.

5.3. LGM and late glacial biomes in the eastern GHP

In case of Kokad, biome assignments using both biome-PFT-taxon matrices suggested (graminoid and forb) tundra vegetation until 16,200 cal yr BP with the demonstrated presence of *Betula pendula*, *B. pubescens*, *B. nana*, and *Pinus* sp. in the vicinity of the mire. Overall, the biome assignment does not overestimate the abundance of trees in this early post LGM period, and given the presence of trees and shrubs, it is likely that forest-tundra or forest-tundra ecotone would be more appropriate biome assignment.

Compared to the general Eurasian pattern (Binney et al., 2017), where the expansion of forest biomes and woody plant cover in general was underway by 15 kyr cal BP, the Kokad site shows an earlier afforestation, from ~16,200 cal yr BP relative to the sites near to us. A moderate drop in woody PFTs occurs in Europe (west of 40°E) during the 12.5 kyr cal BP time slice that represents the Younger Dryas cooling (Binney et al., 2017). This decrease is not apparent in Kokad, as discussed above. The Younger Dryas cooling is obscured in the record, even if we take into account the dating uncertainties.

5.4. Implications for the late Pleistocene herbivore populations

Our fungal spore records (Fig. 4b) showed the presence of large grazing mammals locally, around Kokad mire, directly after the LGM, but only in the first phases of the last glacial termination, until 16,780 cal yr BP. Their disappearance slightly predated the biome shift from graminoid and forb tundra to cold coniferous forest, and also predated the final increase of forest fires. This picture is very similar to the findings of studies focusing on mega-fauna–vegetation–fire relationships in Australia and North America (Gill et al., 2009; Rule et al., 2012), and support the inferred order of changes in these studies. The data suggest that at first a decrease in the population size of grazing mammals takes place, this is followed by the accumulation of herb biomass, which then initiates fires. This ecosystem disturbance assists a biome shift; in our case the expansion of cool temperate and boreal evergreen and summer green conifer dominated woodlands with some temperate deciduous trees. Furthermore, these data support the paleo-vegetation modelling results of Allen et al. (2010) in that these herbivores grazed in an environment with high annual net primary productivity (aNPP). These simulations predict relatively high productivity of boreal and summer green trees in the GHP as well, and our pollen and plant macrofossil based vegetation reconstruction also suggests that these trees (*Betula pendula*, *B. pubescens*, *Pinus sylvestris*, *Picea abies*, *Abies alba*) were indeed

present, while the highest primary producers were sedges, graminoids and forbs.

5.5. Heinrich event 1, warming at 16.2 kyr cal BP and Younger Dryas summer climate

With its position inland, but also north of the classical Mediterranean areas of Europe, the Pannonian Basin is influenced by Atlantic, Mediterranean, and continental air masses. Its present-day precipitation is dominated by Mediterranean moisture source in the GHP (57%, Bottyán et al., 2017) reaching the country mainly in late autumn and spring from the Gulf of Genoa, while the North European (7.4%) and Atlantic (14.2%) rain sources dominate in winter. After the post-LGM warming, between ca. 18–16.2 kyr cal BP, the pollen-based summer temperature reconstruction indicated ~1–2 °C cooling in summer mean temperatures ($T_{JJ\text{A}}$). Its duration and amplitude largely varied depending on the transfer function applied (Fig. 7). This cooling was however much weaker in the model hindcast (Fig. 7; Fordham et al., 2017; Liu et al., 2014) for summer, even though modelled annual rainfall and winter mean temperatures (T_{DJF}) both decreased considerably between 17,300 and 16,800 cal yr BP (see Appendix 3). No matter which transfer function is used, the pollen-based summer mean temperature showed abrupt increase with biome shift at ~16,200 cal yr BP, and a similar increase was also present in the modelled climate (Fig. 7, Appendix 3). First of all, looking at the ocean circulation patterns both in the North Atlantic (Stanford et al., 2011) and Mediterranean Seas (Martinez-Ruiz et al., 2015) at the time of Heinrich event 1, these two regions show contrasting timings for the duration of this event (North-Atlantic: 17.5–16.0 kyr cal BP; Mediterranean Sea: 16.2–15.7 kyr cal BP), with virtually complete Atlantic Meridional Overturning Circulation (AMOC) shutdown between 17.5 and 14.7 kyr cal BP (McManus et al., 2004; Stanford et al., 2006), and rapid intensification of the polar atmospheric circulation along with minor cooling in Greenland at 17.5 kyr cal BP (Rasmussen and Thomsen, 2008). According to the Greenland ice cores, polar circulation intensity ended at 16,200 cal yr BP, which timing agrees well with the observed warming and biome shift at Kokad, and also at Lake St Anne (Magyari et al., 2014b). Ca^{2+} accumulation decreased considerably at this time in the Greenland ice cores suggesting humidity increase and arctic circulation change (Rasmussen et al., 2014). About two hundred years earlier (~16,400 cal yr BP), the Black Sea sediments showed increased drainage of glacial meltwater and permafrost and higher input of terrestrial organic matter via the Volga and Dniester rivers leading to the accumulation of illite and kaolinite rich red clay (Major et al., 2006; Bahr et al., 2008; Kwiecien et al., 2009; Sanchi et al., 2014). At the same time, aeolian input increased considerably in the Western Mediterranean Sea suggesting arid conditions in the Mediterranean and North Africa and the northward migration of the ITCZ at 16,200 cal yr BP (Martinez-Ruiz et al., 2015). Despite the expected importance of the Mediterranean Sea in delivering moisture into the Pannonian Basin, it seems that warming at 16,200 cal yr BP was driven by the decrease in polar circulation and the coincident increase in accumulated heat during the growing season. As we discussed above, other paleo-proxy archives from the region also demonstrates that East-Central Europe (ECE) experienced rapid warming after Heinrich event 1 (Magyari et al., 2014b; Sümegi et al., 2013, 2018; Constantin et al., 2019). Furthermore, pollen records from lake sediments in the Southern Alps also showed rapid afforestation and treeline ascend by Scots pine, Swiss Stone pine and European larch (*Pinus sylvestris*, *P. cembra*, *Larix decidua*) and cold temperate deciduous trees, mainly birch (*Betula* sp.) from ~16,000 cal yr BP (Tinner et al., 1999; Wick, 1996; Vescovi et al., 2007) suggesting that vegetation change started at similar time in

this region as well.

Regarding the late glacial period, the pollen based summer mean temperature record of Kokad mire shows divergent trends in comparison with the CCSM3 climate model run for the same region (Fig. 7). According to the modelled climate, the late glacial (GI-1) warming at ~14,700 cal yr BP showed an increase from ~16 to 18.5 °C by 14,300 cal yr BP, while the pollen based WAPLS reconstruction showed stable temperatures around 15 °C until the Early Holocene, and the MAT method suggested temperatures around 17 °C at 15,150 cal yr BP. Comparing these results with similar pollen based warmest month mean temperature reconstructions for an Eastern Carpathian site, Steregoiu (Feurdean et al., 2008), the authors also find large variance in the inferred temperatures for the late glacial onset (16–19 °C) with minimal warming. Given the altitude of the site at 790 m a.s.l., these values are generally higher than at Kokad. Also notable is that the pollen based warmest month mean temperature (MTW) reconstruction showed very divergent values depending on the method applied, with significant Younger Dryas (YD) cooling in summers indicated only by the modern analogue vegetation method (MAV) that is similar to MAT. The WAPLS method however did not indicate summer cooling at Kokad, neither at Steregoiu (Feurdean et al., 2008), and the chironomid based July mean temperature reconstructions by Tóth et al. (2012) from the Southern Carpathian Mountains also support no or minimal cooling in summer during the YD. The pollen records at the GHP, similarly to Kokad, do not show strong vegetation change during the YD (Félegyházi, 2001; Willis et al., 1995, 1997; Kustár et al., 2016; Sümegei et al., 2011). In some records the increase of herb pollen (mainly *Artemisia* and *Chenopodiaceae*) is seen, but temperate tree taxa present during the late glacial interstadial survived, and in the case of Kokad we noticed the expansion of hazel (*Corylus*). As opposed, all alpine pollen records from the Carpathians show a definite steppe expansion and temperate and boreal tree retreat at this time (Fărcaş et al., 1999; Feurdean et al., 2007a; Magyari et al., 2012; Tanţău et al., 2006, 2014). The Northern Carpathian chironomid based July mean temperature reconstruction and other multi proxy sediment records from South Bohemia (Fig. 1) furthermore suggest that summer cooling was significant in that region, with a cold and humid early phase (Hošek et al., 2014; Hájková et al., 2016). Overall, this comparison of the region's YD paleoclimate and paleoenvironmental records suggests that as we move eastwards and southwards in the region the impact of the North Atlantic perturbation diminishes, particularly in the summer months, and we also see a lowland/mountain contrast with stronger ecosystem impacts observable in the mountain records, and slightly increasing aridity being the main environmental signal in the lowlands of East Hungary (Borsy et al., 1981). These circumstances were certainly favourable for the survival, and in some cases also for further expansion of temperate broadleaved trees on the well-drained soils of the Érmellék region.

6. Conclusions

This study demonstrated that lowland environments in the Carpathians Basin provided relatively warm mesoclimate habitats during the last glacial termination that fostered the early late glacial expansion of deciduous trees (*Ulmus*, *Corylus*, *Quercus*, *Fraxinus*, *Tilia*). Our comprehensive review furthermore demonstrated that the Younger Dryas cooling (~GS-1) had weak impact on the terrestrial vegetation in the basin thereby this area provided secondary refugial habitats for the already expanding temperate flora, and the attenuated cooling trend likely allowed the expansion of hazel (*Corylus*) shrubs already during the YD. The pollen based biome reconstructions verified the presence of graminoid and forb tundra vegetation with trees prior to 16,200 cal yr BP and directly

after the LGM. This suggests that the mammalian megafauna thrived in this biome and disappeared earlier than the biome shift. We also demonstrated that a major ecosystem turnover took place earlier in East-Central Europe than in NW Europe: cool coniferous and mixed forest developed already from 16,200 cal yr BP, when July mean temperatures increased by minimum 2 °C. Overall, we can conclude that the floodwater rich lowland environments of the Carpathian Basin were important refugial habitats as their milder climate with sufficient water supply aided tree survival.

Pollen-based quantitative climate reconstruction demonstrated relatively warm summers in East Hungary directly after the last glacial maximum, with 14–15 °C mean temperatures and buffered summer mean temperature fluctuation throughout the last glacial termination period in this region with < 1 °C decrease in summer mean temperatures during the Younger Dryas, and ~2.2 °C warming in the Early Holocene. We demonstrated that the Eurasian training set and the applied transfer function have great influence on the reconstructed temperatures, and at this stage pollen-based last glacial termination climate reconstructions from the continental region of Europe are suitable to infer the general trend of the climate change, while interpretation of the absolute climate values requires careful analysis of the model performance, positions of the modern analogues, or in case of WAPLS the climate response curves of the main woody and herbaceous pollen types on which these models are based on, as non-analogue climates and non-analogue vegetation composition obviously distort the reconstruction outputs.

Data availability

Datasets and appendices related to this article can be found at https://data.mendeley.com/datasets/ppn2vb7dt/draft?_a=55c296ea-1b30-4f75-8893-a111d8374965, an open-source online data repository hosted at Mendeley Data (Magyari, unpublished dataset).

Declaration of competing interest

None.

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Appendix ASupplementary data

Supplementary data related to this article can be found at <https://doi.org/10.1016/j.quascirev.2019.105980>.

Table 1 Results of the AMS ¹⁴C measurements of core Kokad-2, Kokad mire, Hungary. Note that outlier dates were selected by the BACON software.

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