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Late Pleniglacial vegetation in eastern-central Europe: are there modern analogues in Siberia?

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ABSTRACT

To characterize Late Pleniglacial (LPG: 26.5–15 ka cal BP) and particularly Last Glacial Maximum (LGM: 21 ± 2 ka cal BP) vegetation and climate, fossil pollen assemblages are often compared with modern pollen assemblages. Given the non-analogue climate of the LPG, a key question is how glacial pollen assemblages and thereby vegetation compare with modern vegetation. In this paper we present three LPG pollen records from the Carpathian Basin and the adjoining Carpathian Mountains to address this question and provide a concise compositional characterization of the LPG vegetation. Fossil pollen assemblages were compared with surface pollen spectra from the Altai-Sayan Mountains in southern Siberia. This area shows many similarities with the LPG vegetation of eastern-central Europe, and has long been considered as its best modern analogue. Ordination and analogue matching were used to characterize vegetation composition and find the best analogues. Our results show that few LPG pollen assemblages have statistically significant analogues in southern Siberia. When analogue pairings occur they suggest the predominance of wet and mesic grasslands and dry steppe in the studied region. Wooded vegetation types (continental and suboceanic hemiboreal forest, continental taiga) appear as significant analogues only in a few cases during the LGM and more frequently after 16 ka cal BP. These results suggest that the LPG landscape of the Carpathian Basin was dominated by dry steppe that occurred outside the river floodplains, while wet and mesic grasslands occurred in the floodplains and on other sites influenced by ground water. Woody vegetation mainly occurred in river valleys, on wet north-facing hillsides, and scattered trees were likely also present on the loess plateaus. The dominant woody species were *Larix*, *Pinus sylvestris*, *Pinus mugo*, *Pinus cembra*, *Picea abies*, *Betula pendula/pubescens*, *Betula nana*, *Juniperus*, *Hippophaë rhamnoides*, *Populus*, *Salix* and *Alnus*. The pollen records suggest uninterrupted presence of mesophilous temperate trees (*Quercus*, *Ulmus*, *Corylus*, *Fagus* and *Fraxinus excelsior*) in the Eastern Carpathian Mountains throughout the LPG. We demonstrate that the LPG vegetation in this area was characterized by increasing grass cover and high frequency of wildfires. We conclude that pollen spectra over represent trees in the forest-steppe landscape of the LPG, furthermore pollen-based quantitative climate reconstructions for the LPG are challenging in this area due to the scarcity of modern analogues.

1. Introduction

In the last two decades several original and review papers have fuelled the debate on the nature of the Late Pleniglacial (LPG: 26.5–15 ka cal BP in this study, based on Tzedakis et al., 2013) and Last

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Glacial Maximum (LGM: 21 ± 2 ka cal BP) vegetation in the Carpathian Basin (CB) and the adjoining Carpathian Mountains (CM) (Willis et al., 2000; Rudner and Sümegi, 2001; Willis and van Andel, 2004; Jankovská and Pokorný, 2008; Zech et al., 2009, 2013; Sümegi et al., 2012a,b). Pioneering palynological and palaeozoological studies, and also some recent palaeovegetation modelling studies considered this area to be predominantly treeless: a land of continental cold steppes and tundra-steppes (Zólyomi, 1952; Járai-Komlódi, 1991; Jánossy, 1986; Harrison and Prentice, 2003). Only in the foreland zone of the Northern, Eastern and Southern Carpathians did palaeontologists/palaeoecologists infer the presence of boreal and cool-temperate trees (Stieber, 1967; Jánossy, 1986). These areas have been repeatedly recognized as important glacial refugia, from which trees started to migrate at the beginning of the Holocene (Huntley and Birks, 1983; Bennett et al., 1991; Huntley, 1993; Willis, 1994). The idea of a lowland treeless landscape was later challenged mainly by loess-charcoal, pollen, plant macrofossil and mollusc studies that provided rich evidence for the occurrence of boreal and cool-temperate trees and forest-steppe associated land snails in the CB during Marine Isotope Stages (MIS) 2 and 3, i.e. Late and Middle Weichselian including the LGM, the latter being the time of maximum glacier and ice sheet extent in the Alps and coldest loess-mollusc derived summer temperatures in the CB (Willis et al., 2000; Rudner and Sümegi, 2001; Sümegi and Krolopp, 2002; Sümegi, 2005; Peltier and Fairbanks, 2006). At the same time, an increasing number of population genetic studies provided evidence for the LGM existence of extra-Mediterranean refugia of temperate species in the Carpathians and adjoining forelands (Schmitt, 2007, 2009; Kotlík et al., 2006). Several studies argued that mesophilous temperate species likely survived in small and sporadic, meso- or microclimatically favourable azonal habitats within the extended periglacial belt, and given the restricted size and scarcity of the refugia, they have remained undetected in the reconstruction of the glacial faunas and floras based on fossil records (Birks and Willis, 2008; Schmitt and Varga, 2012).

High intraspecific genetic diversity and large genetic distances among the genotypes suggested that some plants and animals might have survived consecutive glaciations in the Carpathians, adjoining forelands and lowlands without extensive mixing among individual populations during the warm or cold periods (e.g. Palmé et al., 2003; Heuertz et al., 2004; Sommer and Nadachowski, 2006; Höhn et al., 2009; Schmitt and Varga, 2012; Temunovic et al., 2012).

Modelling of LGM tree distribution furthermore suggested that several temperate tree species potentially could have survived the LGM in the CB. Species with projected LGM distribution in the basin were *Alnus glutinosa*, *Quercus robur*, *Salix alba*, *Tilia cordata*, *Ulmus glabra* and *Ulmus laevis* (Svenning et al., 2008). Notable is that all of these species occur in alluvial forests in the Hungarian lowlands today (Borhidi et al., 2012).

Information accumulated by now suggests that during MIS 2 the CB hosted tree populations of *Pinus sylvestris*, *Pinus cembra*, *Pinus mugo*, *Picea abies*, *Larix decidua*, *Fraxinus excelsior*, *Betula pendula*, *Betula pubescens*, *Betula nana*, *Salix* sp. and *Juniperus* sp. in the river valleys and mid-mountains (Willis et al., 2000; Willis and van Andel, 2004; Bhagwat and Willis, 2008), while in the Romanian Carpathians and adjoining lowlands the LGM presence of *Pinus*, *Juniperus*, *Betula*, *Salix*, *Picea* and probably also *Larix*, *Populus tremula*, *Ulmus*, *Prunus padus*, *Quercus* and *Tilia* was inferred from early pollen increases of these trees during the Lateglacial (Feurdean et al., 2007, 2012).

What is missing, however, is a concise characterization of composition and structure of the LPG vegetation that goes beyond the reports of individual woody species and the assumption of generic steppe formations predominating in the landscape. The number of dated pollen and plant macrofossil records covering the LGM is very low in the CB and CM (Buczkó et al., 2009). Since most charcoal evidence from the CB predates or postdates the time of maximum ice-sheet extent and lowest CO_2 concentrations between ca 26.5 and 19 ka cal BP (Willis et al., 2000; Rudner and Sümegi, 2001; Clark et al., 2009; Tzedakis et al., 2013), we also need a clear demonstration of which woody species were present continuously during the coldest/driest part of the LPG.

In this paper we discuss three LPG pollen records, two from the Carpathian Basin and one from the Eastern Carpathians (Fig. 1). To obtain insights into the character of LPG plant communities and vegetation patterns in the landscape, we compare these pollen records with surface pollen assemblages recently obtained from the Altai and Sayan Mountains of southern Siberia, which are considered to be the closest modern analogues of the east-central European glacial landscapes (Chytrý et al., 2008; Jankovská and Pokorný, 2008; Kuneš et al., 2008; Pelánková and Chytrý, 2009; Schmitt and Varga, 2012). We ask whether the LPG vegetation and landscape of the CB can be considered as analogous to modern vegetation and landscape in southern Siberia and whether this comparison can improve our understanding of past ecological processes in the CB.

Finding 'good' analogues is certainly complicated by much lower CO_2 levels during the LPG (190 ppm compared to 280 ppm in the pre-industrial time; Monin et al., 2001). As it has been demonstrated by several studies, low CO_2 leads to lower photosynthetic rates and reduced water-use efficiency of plants with stronger negative effect on trees than on herbaceous plants (Harrison and Bartlein, 2012). Hence arboreal species were likely less competitive during the LPG (Harrison and Prentice, 2003), while herbaceous species may have been even more productive than at present (Allen et al., 2010). When dealing with the LPG vegetation these CO_2 generated differences in interspecific competition have to be taken into account; they certainly decrease the possibility of finding 'good' analogues.

2. Study sites

2.1. Fossil pollen sequences

2.1.1. Nagymohos peat bog, Putnok hills, NE Hungary

Nagymohos (NM, 48° 20′ 20″ N, 20° 25′ 35″ E, 297 m a.s.l.) is a 1.4 ha valley mire near the village of Kelemér in the North Hungarian Hills (Fig. 1). Two sediment cores were taken from this poor fen in 1995 and 1998 and studied by multi-proxy methods (Jakab et al., 1998; Magyari et al., 1999, 2000, 2001). The Lateglacial and LPG parts discussed in this paper comprise the 300–425 cm section of the sediment. Borehole NM-I, situated in the deepest part of the mire, was used for pollen analysis and radiocarbon dating. Borehole NM-II was situated closer to the marginal fen zone and was used for the bryophyte and anthracological analyses.

Gently rolling hills around the mire consist of sedimentary rocks, mainly Tertiary sandstone, and rarely exceed 400 m in elevation. The mire basin is underlain by Tertiary clay poor in mineral nutrients. The accumulation of groundwater in the upper horizon of the impermeable clay played an important role in the formation of the basin, which was probably caused by a landslide around 26.7 ka cal BP.

Botanical investigations revealed an impoverished flora and an underdeveloped hollow-hummock structure in Nagymohos compared to the NW European *Sphagnum*-bogs (Matus et al., 2000). The largest peat-forming association today is a birch carr (*Betulo−Sphagnetum*) that replaced the once dominant reed bed (*Calamagrostio−Phragmitetum sphagnetosum*) between 1990 and 2000 AD (Matus et al., 2000). The *Sphagnum* carpet is afloat;
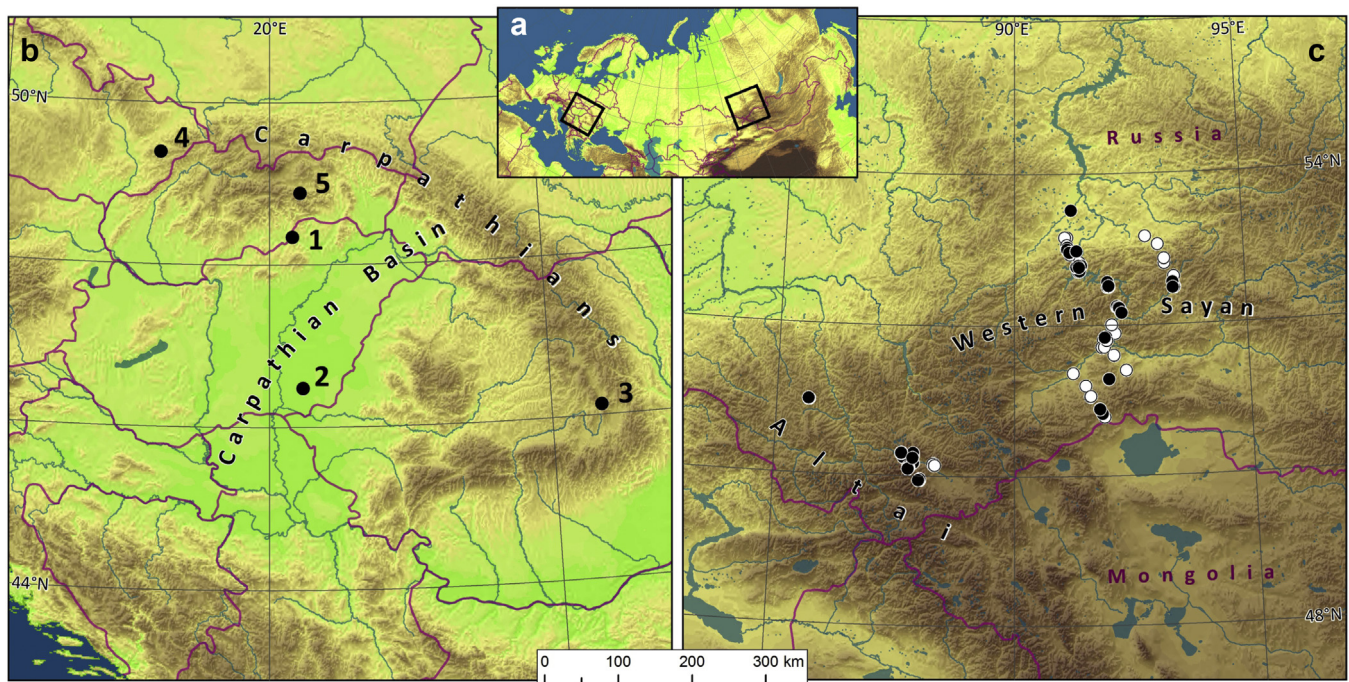
Fig. 1. Location of the studied Late Pleniglacial sequences, modern pollen samples and other sites discussed in the paper: (a) location in Eurasia; (b) Late Pleniglacial pollen sequences in eastern-central Europe − 1: Nagymohos, 2: Fehér Lake, 3: Lake St Anne (Sfânta Ana), 4: Jablůnka, 5: Šafárka; (c) surface pollen samples in the Altai and Sayan Mountains in southern Siberia − black: significant analogues, white: non-analogues.

ca 100-cm thick water column separates it from the underlying peat. The surrounding hilly country is covered by oak-hornbeam forests (*Querco petraeae−Carpinetum*) in the north-west, while the south-eastern slopes are covered with oak forests (*Quercetum petraeae−cerris*) (Hudák, 2008). The climate of the North Hungarian Hills is temperate continental. Annual precipitation (PANN) at the poor-fen site is 581 mm, mean annual temperature (MAT) 9 °C, mean temperature of the warmest month (MTWA) 19.4 °C, and mean temperature of the coldest month (MTCO) −3.5 °C (Barati et al. 1999).

2.1.2. Fehér Lake, Kardoskút, SE Hungary

Fehér Lake (FT, 46°19′35″N; 20°5′54″E, 83 m a.s.l.) is a 200 ha salt lake and inland salt marsh in the SE part of the Great Hungarian Plain (Fig. 1). Sediment cores were taken in 1995 using Russian and Livingstone piston corers. For the purpose of this study the pollen record of core FT-1 (6.3 m deep) was used. Results of the grain-size, malacological, pollen and geochemical analyses were published by Sümegi et al. (1999, 2013). According to these studies, the lake was formed ca 28 ka cal BP by channel movement of the ancient Maros river. Surface sediments around the lake consist of infusion loess to a depth of 1−2 m. This is underlain by fluvial sand. Because of its high carbonate and clay content, the surface is prone to salinization. The lake water is alkaline, and due to the strongly fluctuating water table it dries out in severely dry years.

The climate of the SE Hungarian Plain is temperate continental with Sub-Mediterranean influence (Kakas, 1960; Zólyomi et al., 1992). PANN is around 520−570 mm, MAT 10.9 °C, MTWA 22.2 °C, MTCO −1.8 °C (Szász and Tőkei, 1997). The number of sunny hours is particularly high, 2000 per year.

The natural vegetation around the lake is warm continental forest-steppe with loess steppe (2/3) and mixed oak forest of saline character (1/3) (Molnár and Bíró, 1995; Jakab, 2012).

The present vegetation of Fehér Lake consists of saline vegetation dominated by *Zannichellia palustris* subsp. *pedicellata*, *Salsola*

soda, *Suaeda pannonica*, *Bolboschoenus maritimus*s. l., *Crypsis aculeata*, *Camphorosma annua* and *Puccinellia limosa*.

2.1.3. Lake St Anne, East Carpathians, central Romania

Lake Saint Anne (SZA, Lacul Sfânta Ana, Szent-Anna tó, 46°7′35″N, 25°53′17″E, 950 m a.s.l.) is a crater lake in the Ciomatu Massif of the Harghita Mountains (Fig. 1). This study discusses the LPG and Lateglacial pollen record of an11.5-m deep core obtained in 2010 (SZA-2010), which extends back to ca 27 ka cal BP.

The lake is fed by rainwater and surface runoff from the surrounding slopes and has no outlet. Its surface area is 19.3 ha, while the watershed comprises 215 ha (Pál, 2000). The bedrock is sandstone and conglomerate that was covered by several lava domes and pyroclastic deposits of amphibole-biotite-dacite magma during the Late Quaternary (Karátson et al., 2013). The climate is temperate continental. PANN is ∼800 mm, MAT 4 °C, MTWA 15 °C and MTCO is −5 °C (Kristó, 1995). The crater is characterized by thermal inversion that results in the reverse order of the vegetation belts; deciduous forests of *Fagus sylvatica* are located above *P. abies* forests. Today the lakeshore is partly open at its NE corner and partly covered by mixed stands of *B. pendula*, *P. abies*, *Salix* sp., and *F. sylvatica*.

2.2. Training set samples

Surface pollen samples and vegetation data originate from southern Siberia, the Altai and Western Sayan Mountains (Fig. 1). A strong north−south climatic gradient runs across these mountainous areas from moderately warm and precipitation-rich areas to cold and dry areas in the intermountain basins. Along this gradient, vegetation changes from a closed taiga forest (with *Abies sibirica*, *Picea obovata*, *P. sylvestris*, *Pinus sibirica*, *P. tremula*) through forest-steppe (with woodland patches of *B. pendula*, *Larix sibirica* and *P. obovata*) to dry continental steppe at lower altitudes, or to shrubby tundra (with *Betula rotundifolia*, a species from the *B. nana*

group), herbaceous tundra or tundra-steppe at higher altitudes (Chytrý et al., 2008). Pollen samples were collected and analysed previously as part of a broader study focussing on pollen–vegetation relationships (Kuneš et al., 2008; Pelánková et al., 2008; Pelánková and Chytrý, 2009). They were taken from moss polsters, humus or topsoil in all major types of natural vegetation occurring in these areas, mainly in various types of forests, steppe and tundra. Fig. 1 shows the distribution of the surface pollen samples in southern Siberia, while Supplementary Table 1 provides brief descriptions of each vegetation type.

3. Materials and methods

3.1. Sediment coring

Overlapping core segments were obtained at each core location (Fig. 1) and stored at 4 °C until further treatment. The cores were subsampled for pollen analysis at 4–8 cm intervals.

3.2. Radiocarbon dating

Radiocarbon dating was performed on different sediment components in the LPG sections of these cores (Table 1). Where available (NM and FT), wood fragments and bryophyte leaves were preferably dated (see Magyari et al., 1999, 2001; Sümegi et al., 2013). In case of Lake St Anne (SZA) no terrestrial macroremains were found in the LPG sections of the core, therefore radiocarbon dates were derived from mixed sources: chironomid head capsules, cladocera remains and small wood charcoal particles. In the Lateglacial part of the cores terrestrial macrofossils were dated (Table 1). In addition several mollusc shells were dated from Fehér Lake (Table 1).

3.3. Laboratory preparations of fossil samples

Samples of 2 cm³ (FT, SZA) and 1 cm³ (NM) of wet sediment were prepared for pollen analysis using standard methods including treatment with HCl, NaOH, HF, acetolysis and microsieving at 10 μm mesh size (Bennett and Willis, 2001). *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 of FT and NM 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 Geography, University of Cambridge and at the Hungarian Natural History Museum were used together with pollen atlases and keys (Moore et al., 1992; Reille, 1992, 1995, 1998). The point-count method of Clark (1982) was applied to determine microcharcoal concentrations in FT and NM, while microcharcoal particles >10 μm were counted and expressed as particle accumulation rates in SZA. Statistical analysis and plotting of the pollen data was done using Psimpoll 4.27 (Bennett, 2007).

3.4. Vegetation survey and surface pollen sampling in the Altai-Sayan Mts

Collection units were 100 m² plots, in which abundances of all vascular plants were recorded; these served then for classification and description of vegetation types (Chytrý et al., 2008, 2012). Within each 100-m² plot surface pollen samples from moss polsters or litter were collected by taking five subsamples, four near corners and one in the centre, and mixed into one sample (Kuneš et al., 2008; Pelánková and Chytrý, 2009). Samples were then prepared using standard methods (Faegri and Iversen, 1989). A minimum of 500 pollen grains per sample were counted except a few poor samples. Pollen was identified with the help of a reference pollen collection and the literature (Reille, 1992, 1995, 1998; Beug, 2004). Details of the pollen analyses are described in previous papers (Kuneš et al., 2008; Pelánková et al., 2008; Pelánková and Chytrý, 2009). Data can be accessed in the European Modern Pollen Database (Davis et al., 2013).

Table 1
[14]C dates from Nagymohos and Fehér Lake, Hungary and Lake St Anne, Romania.

Depth (cm)	Material dated	[14]C BP	±	Calibrated range BP (2σ)	Median cal BP age used for modelling	±
Nagymohos (NM-I)						
315–320	Bulk peat	19,335	295	22,354–23,798	Outlier	
365–370	Bulk peat	14,246	144	16,936–17,786	17,361	425
394–399	Bulk peat	18,159	247	21,113–22,356	21,734.5	621.5
422–426	Bulk peat	21,756	267	25,161–26,862	26,011.5	850.5
Fehér Lake (FT-1)						
210–220	Biogenic carbonate (*Chara* fragments)	10,498	90	12,105–12,605	12,355	250
292–293	*Chondrula tridens* shells	13,005	49	15,139–16,305	15,722	583
400–420	*Pisidium* shells	17,715	250	20,331–21,737	21,034	703
489–490	*Chondrula tridens* shells	19,911	81	23,418–24,150	24,150	732
490–510	*Pisidium* shells	20,323	300	23,525–24,992	24,258	733
620–630	Charcoal (*Salix* sp.)	23,303	280	27,521–28,723	28,122	601
Lake St Anne (SZA-2010)						
980–982	*Sphagnum* leaves and stems, *Picea abies* needles, bract *scales*	6246	26	7155–7258	7206.5	51.5
1000–1002	Mossleaves and stems, bract scales, periderm	8216	28	9082–9286	9184	102
1036–1038	Charcoal, moss stems, periderm, bract scale	10,739	42	12,562–12,742	12,652	90
1126–1127	Cyperaceae stem/leaf fragments	14,541	67	17,371–17,976	17,673.5	302.5
1340–1342	Charcoal Cyperaceae stem fragments, chironomid head capsules, Cladocera egg	17,338	84	20,290–21,138	20,714	424
1365–1366	Cyperaceae stem fragments, chironomid head capsules, Cladocera egg	17,626	96	20,523–21,387	20,955	432
1538–1540	Moss leaves, stems, chironomid head capsules, Cladocera egg	19,717	122	23,133–23,953	23,543	410
1661–1662	Cladocera egg	21,685	163	25,400–26,713	26,056.5	656

3.5. Multivariate data analysis

Two approaches were selected to interpret fossil pollen records from the CB and CM using modern pollen assemblages from southern Siberia: principal components analysis (PCA) and analogue matching (AM). First, we harmonized the nomenclature of the pollen types in the fossil records with pollen types of the species occurring in modern vegetation in Siberia. We matched pairs of closely related taxa, which underwent vicariant speciation in Europe and Siberia, including *Abies alba–A. sibirica, Alnus viridis–A. fruticosa, B. nana–B. rotundifolia, L. decidua–L. sibirica, P. abies–P. obovata*. We also merged *P. cembra* and *P. sylvestris* types, different pollen types within families Ericaceae, Caryophyllaceae, Compositae subf. Asteroideae, Gentianaceae, Labiatae, Ranunculaceae (excl. *Ranunculus acris*-type), Rosaceae, Saxifragaceae and Umbelliferae.

Pollen counts from all fossil and modern samples were subjected to PCA ordination using the *vegan* package (Oksanen et al., 2012) of the R program (R Core Team, 2012) to compare modern and fossil pollen spectra. Square-root transformation of pollen proportions was applied prior to the analysis. Attribution of spectra to fossil or modern group was used as a covariable in the analysis to remove possible difference between these two groups caused by the taxa occurring in one area only. PCA was performed using covariance matrix.

To find the closest modern analogue to each fossil pollen sample analogue matching (AM; Simpson, 2012) was used in the *analogue* package (Simpson, 2007) in R. First, we analysed the modern training dataset for receiver operating characteristics (ROC) using defined vegetation groups for each pollen sample. This enabled us to obtain the optimal value of dissimilarity between samples, which provides the best discrimination between analogues and non-analogues (Simpson, 2012). Chord distance was used as the dissimilarity measure, resulting in 0.443 as the critical dissimilarity value (d_{crit}), above which modern-fossil sample-pairs were considered non-analogues. If there were more attributed modern vegetation analogues to a fossil sample, we took into account the first five analogues with the lowest dissimilarity values.

4. Results

4.1. Modern pollen spectra

Relative abundances of selected pollen types in the Altai-Sayan surface samples are shown in Fig. 2. Since the modern pollen assemblages have been fully described earlier (Kuneš et al., 2008; Pelánková et al., 2008; Pelánková and Chytrý, 2009), here we only mention the most important similarities and differences between the Altai-Sayan modern and the CB-CM fossil pollen assemblages.

When *P. sibirica* and *P. sylvestris* are grouped, the percentage representation of *Pinus* pollen becomes a poor indicator of modern vegetation types; it is most abundant in both taiga and hemiboreal forests, but high values are encountered also in several meadow-steppe and tundra samples, while some hemiboreal forest samples have low (<20%) values. These samples are from the areas where *Pinus* is absent and *Larix* becomes nearly universal dominant tree.

Artemisia, Chenopodiaceae and Poaceae pollen differentiate nicely the open vegetation types (especially dry steppe, steppic scrub, alpine grassland) from the woodlands. Notable is also a high proportion of *Betula* pollen types in the modern dataset (*Betula alba* and *B. nana* types); although *B. alba* type is present in most LPG pollen samples (especially NM and FT), it never attains >11%, while several taiga, hemiboreal forest, tundra, alpine grassland and

meadow steppe surface pollen samples have high relative abundances of *B. alba* and *B. nana* types (occasionally up to 50–60%).

The most conspicuous difference between the modern and fossil pollen samples is in the representation of *Juniperus*. This pollen type is infrequent in the modern samples, being no characteristic element of any vegetation type, which reflects the fact that junipers (*Juniperus sibirica* and *Juniperus pseudosabina*) are relatively rare in the Altai-Sayan region. In contrast, it is abundant in the LPG pollen assemblages of NM and SZA (values up to 20%). Finally, there are no pollen assemblages in the Altai-Sayan surface samples in which mesophilous temperate broad-leaved deciduous tree pollen types (e.g. *Quercus, Carpinus betulus, Corylus*) are present, and these species do not occur in this region, while these pollen types appear in several samples of the CB-CM Late Pleniglacial pollen assemblages (especially FT and SZA).

4.2. Late Pleniglacial pollen profiles

Detailed description of the radiocarbon dating, age–depth models, sediment and pollen stratigraphies for Nagymohos were provided by Magyari et al. (1999, 2000, 2001), the results of the Fehér Lake multi-proxy palaeoenvironmental studies were described by Sümegi et al. (1999, 2013) and those of Lake St Anne by Magyari et al. (submitted). In this paper we present a summary of the main features of all three LPG pollen records and the inferred terrestrial vegetation. In addition, we show radiocarbon dates and age–depth models in Table 1 and Supplementary Fig. 1.

4.2.1. Nagymohos

The 1.1 m long pollen sequence of Nagymohos covers a period of ca 12,250 years between 26.95 and 14.7 ka cal BP (Fig. 3, Magyari et al. 1999, 2000), suggesting very slow peat accumulation during the LPG. An additional core (NM-II) provides the plant macrofossil record between ca 26.95–18.6 ka cal BP (Fig. 4). The main feature of the pollen record is the repeated fluctuation of the arboreal pollen (AP) frequencies between local pollen assemblage zones (LPAZ), with two high AP zones (NMP-1: 26.95–24 ka cal BP and NMP-3: 21.35–18.8 ka cal BP) and two low AP zones (NMP-2: 24–21.35 ka cal BP and NMP-4: 18.8–14.7 ka cal BP). Fig. 3 demonstrates that the low AP zones match closely with the LGM and Greenland Stadial 2 (GS-2), while the others correspond with interstadials (Magyari et al., 2000). During the intervals of milder climate *Pinus* pollen frequencies often reached 70–80% and local presence of *P. cembra, P. sylvestris, P. mugo, B. nana, B. pubescens, Larix* and to a lesser extent, *P. abies* was inferred, and vegetation was found similar with the present boreal parkland forests (Magyari et al., 1999, 2000).

The macrofossil analysis demonstrated that local mire succession started with paludification; the initial stage with *P. cembra* dominating a rich fen with typical boreal brown mosses (*Calliergon richardsonii, Scorpidium scorpioides, Warnstorfia sarmentosa*) was replaced by various types of flark-fen, poor fen and tall-sedge fen vegetation during the LPG with the nearly continuous presence of *Sphagnum palustre* and *S. cuspidatum* (inferred palaeoassociations were *Carex lasiocarpa–Sphagnum* sect. *Cuspidata, Carex rostrata–Warnstorfia fluitans* and *Carex nigra–Bryum pseudotriquetrum*, see Fig. 4 and Magyari et al., 1999, 2000).

Notable is that at the end of both local pollen assemblage zones with high arboreal pollen values macrocharcoal concentrations in the sediment increased and *Pinus* pollen frequencies decreased, suggesting that the transitions to decreasing woody cover were associated with local fires likely caused by increasing drought.
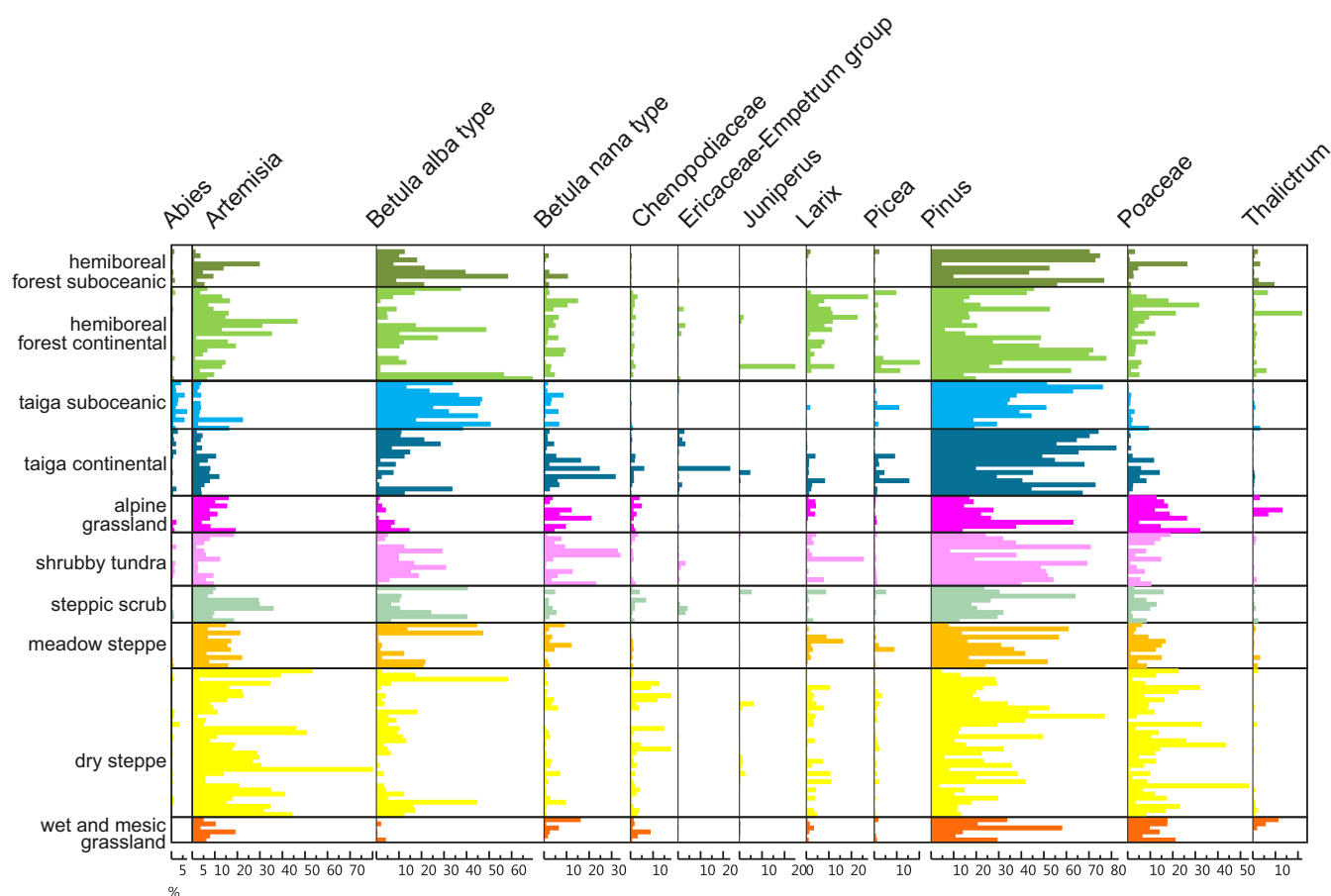
Fig. 2. Selected dominant and characteristic pollen types of the modern pollen assemblages from the main vegetation types of the Altai and Western Sayan Mountains in southern Siberia.

4.2.2. Fehér Lake

The pollen record of Fehér Lake dates back to ca 28 ka cal BP (620 cm) with pollen-bearing samples up to 13.91 ka cal BP (250 cm) and one long section of unsatisfactory pollen preservation between 263 and 323 cm (14.49—17.2 ka calBP). The pollen diagram is shown in Fig. 5. Six local pollen assemblage zones were distinguished, principally reflecting relative frequency changes in AP and the dominant terrestrial pollen taxa. Similarly to Nagymohos, the LPG pollen record is characterized by prominent fluctuation in AP, with three pollen zones characterized by high frequencies of *Pinus* subg. Diploxylon (*P. sylvestris* and *P. mugo* in our area), increased *Picea* and temperate broad-leaved tree pollen percentages (with AP values 70—80%; zones FT-1, FT-3, FT-5) and two pollen zones with decreased *Pinus* subg. Diploxylon, *Picea* and increased relative frequencies of Poaceae, *Artemisia* and *Betula* (with AP values 40—60%; FT-2, FT-4).

The oldest pollen zone was interpreted as indicative of boreal forest-steppe vegetation with *P. sylvestris* or *P. mugo*, *P. cembra* (*P.* subg. *Haploxylon* pollen) and *Larix* woods in the floodplain where water-supply was sufficient. In all pollen zones the herbaceous pollen assemblages suggested the presence of tall-herb vegetation (with *Thalictrum, Sanguisorba, Angelica, Campanula* and *Filipendula*), sand grasslands (*Armeria maritima*), boreal fens and wet meadows (*Selaginella selaginoides*) likely in the floodplain, while *Hippophaë rhamnoides* and *Ephedra* shrubs on exposed sandy surfaces in interfluvial ridges, and continental cold steppe communities (Poaceae, *Artemisia*, light-demanding Compositae) on the dry interfluvial ridges.

The pollen zone most likely correlated with the coldest/driest part of the LGM (FT-4) was characterized by Poaceae dominance

and very low *Artemisia* values compared to the earlier low AP zone of FT-2, from which the spread of grassy meadow steppes was inferred. This is an important difference between Nagymohos and Fehér Lake, as at the former site *Artemisia* maintained high relative frequencies in all LPG pollen zones.

Similarly to Nagymohos, the transitions to low AP pollen zones were characterized by microcharcoal concentration peaks suggesting that wildfires played a role in the decrease of the woody cover.

Another important feature of the Fehér Lake pollen record was the sporadic, but repeatedly increasing appearance of several mesophilous temperate tree pollen types (*Quercus, C. betulus, Acer, Fraxinus, Corylus*). These were interpreted as an indication of regional presence of these trees in micro- or meso-climatically favourable habitats in the SE Great Hungarian Plain during the milder intervals of the LPG (Sümegi et al., 2013).

4.2.3. Lake St Anne

The pollen record of Lake St Anne extends back to 25.5 ka cal BP with continuous sediment accumulation up to the present. Fig. 6 shows the LPG part (14.3—25.5ka cal BP) of the pollen record which was obtained from the core SZA-2010. In comparison with Nagymohos and Fehér Lake, AP values show less pronounced fluctuation and *Juniperus* pollen is typically present throughout the LPG and much more abundant (5—20%, often >10%). The five pollen assemblage zones covering this period mainly reflect changes in *Pinus* subg. Diploxylon (*P. mugo* and *P. sylvestris*) and Haploxylon (*P. cembra*), *Juniperus, Betula, Artemisia* and Poaceae pollen frequencies.
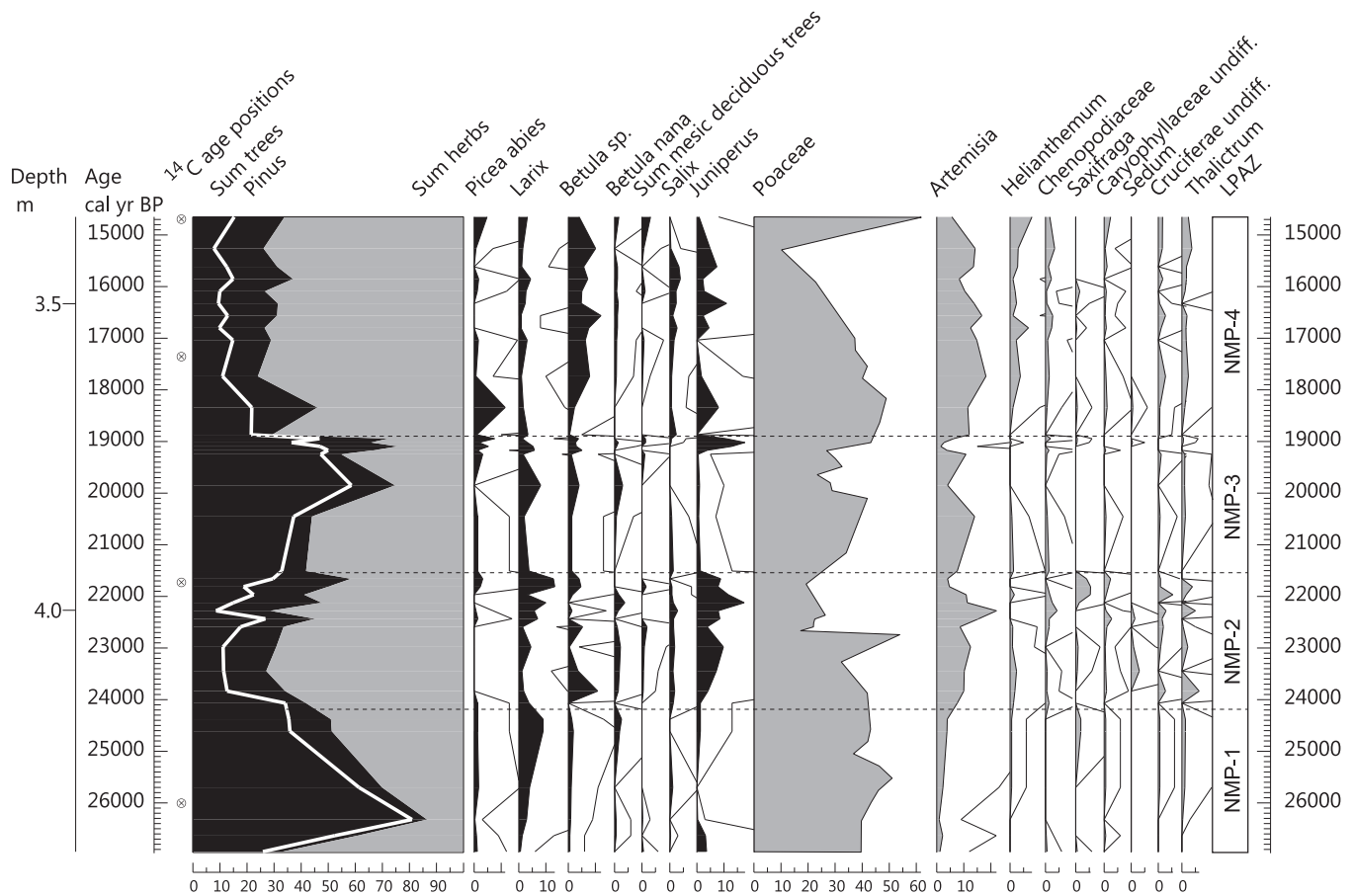
Fig. 3. Percentage pollen diagram of selected pollen taxa in the Late Pleniglacial profile of Nagymohos (394 m a.s.l., Kelemér, NE Hungary) plotted against calibrated BP age and depth. LPAZ: local pollen assemblage zones. Sum of mesophilous temperate deciduous trees includes *Quercus*, *Corylus*, *Ulmus*, *Tilia*, *Acer*, *Carpinus betulus*, *Fagus* and *Fraxinus excelsior* type.

The LPG (zones SZAP-1-4) is characterized by relatively high representation of *Pinus* subg. *Haploxylon*, *P.* subg. *Diploxylon*, *Juniperus* and Poaceae pollen and low *Artemisia* values, which in association with the herbs suggests the presence of dry and mesic hemiboreal parkland forests mainly with *P. cembra*, *P. sylvestris* and *L. decidua*, *Juniperus* shrubs, grass steppes, shrubby tundra, steppe-tundra and talus slope associations. Locally, the crater slopes likely supported shrub tundra, herbaceous alpine tundra and talus-slope vegetation with *Saxifraga*, *Soldanella*, *Ranunculus*, *Rumex*, Caryophyllaceae, *Sedum*, *Jasione* and *Thalictrum* species. Outside the cool crater mesoclimate, the presence of *Juniperus*, *P. cembra*, *L. decidua*, *P. abies*, *P. mugo*, *Betula*, *Alnus*, *Populus* and *Salix* is inferred for warmer sites from the pollen data. Notable is that during the LGM microcharcoal accumulation rates increased, suggesting the presence of woody biomass in the region even during the coldest/driest period of the last glaciation, and its more frequent burning likely in connection with enhanced drought under continental climate. *Artemisia* and Chenopodiaceae only regained abundance after 19.2 ka cal BP, which corresponds with the terminal phase of the LGM based on glacial ice-sheet extent studies (Clark et al., 2009).

4.3. Ordination of fossil and modern pollen spectra

Fig. 7 and Table 2 show the results of the principal components analysis in which the modern and fossil pollen spectra were both included. Species scores in Table 2 show that the first principal component (PC1) has high positive values for *Artemisia*, Poaceae

and *Juniperus*, while *Pinus*, *Betula* and *Picea* have large negative values suggesting that PC1 represents a steppe-coniferous forest gradient. This component thus mainly discriminates forested and treeless vegetation types, and in agreement with this division, the majority of the modern pollen samples from open vegetation types group on the right side of the ordination diagram, while those from the wooded vegetation types group on the left side (Fig. 7). There are however exceptions, e.g. several steppic scrub samples fall on the left side and several continental hemiboreal forest samples on the right, which agrees well with the partial openness of these vegetation types. PC2 has the highest positive values for *Pinus*, *Larix* and *Picea*, while *Betula* has a significant negative value. Given the merging of both *Pinus* taxa into one group, PC2 may represent a gradient in forest moisture and openness, where samples from wet and dense forest types are situated at the top, while dry and more open forest are at the bottom. As expected, relatively few of the CB Late Pleniglacial pollen samples fall on the top left part of the ordination diagram (mainly FT samples), as these assemblages are characterized by low *Betula* pollen percentages.

The proportions of variance explained by the ordination along the first two axes are 27.4 and 13.8%. These axes separate the modern samples relatively well. The position of the fossil samples on the ordination plot relative to the modern samples suggests that the LPG vegetation of Nagymohos (NM) was similar to the Siberian dry steppe and steppic scrub and occasionally to continental taiga and continental hemiboreal forest. Fehér Lake (FT) sample scores overlap mainly with wooded vegetation types: suboceanic and continental hemiboreal forest and continental taiga, but several
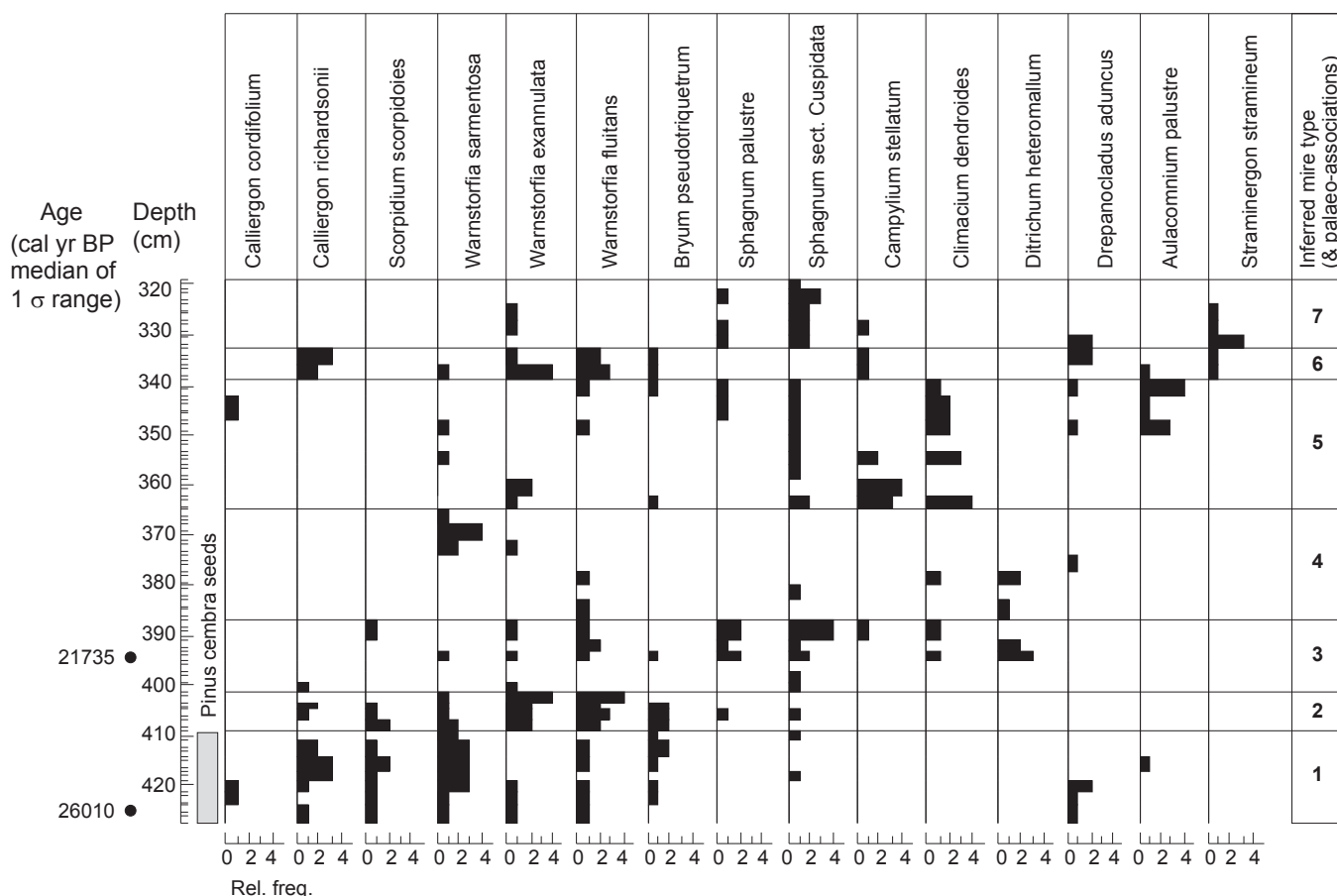
Fig. 4. Relative frequencies of the main peat forming bryophyte components in the Late Pleniglacial section of Nagymohos (NM), core NM-II (394 m a.s.l., Kelemér, NE Hungary), and presence/absence diagram of other major plant macrofossils. 1. Pine-fen, *Calliergon richardsonii* rich-fen (*Carex rostrata − Calliergon richardsonii, Carex lasiocarpa − Scorpidium scorpioides*); 2. Rich *Warnstorfia* flark-fen, flark-fen pool (*Carex lasiocarpa − Warnstorfia fluitans–Sphagnum cuspidatum, Carex nigra − Bryumpseudo triquetrum*); 3. poor-fen (*Carex lasiocarpa − Sphagnum* sect. *Cuspidata*); 4. mud-bottom, flark-fen, tall-sedge fen (*Carex echinata* (?) -*Climacium dendroides, Carex rostrata − Warnstorfia sarmentosa*); 5.rich-fen lawns & flarks, poor-fen flarks (*Carex echinata* (?) − *Climacium dendroides, Carex rostrata − Campylium stellatum, Carex lasiocarpa − Sphagnum* sect. Cuspidata); 6. *Warnstorfia* − fen, flark-fen pool (*Carex rostrata − Warnstorfia fluitans, Potametalia*); 7. poor-fen and flark-fen pool (*Carex lasiocarpa − Sphagnum* sect. *Cuspidata, Potametalia*).

fossil samples also overlap with the meadow steppe and steppic scrub samples. Clearly, the ordination plot suggests that FT was the most wooded site during the LPG. Most fossil pollen assemblages from the East Carpathian Lake St Anne (SZA) group around the zero point, show little variability and either do not overlap with modern samples or in a few cases lie near the modern samples of steppic scrub, alpine grassland, dry steppe and continental taiga, suggesting similarity with these vegetation types. Also notable is the divergence of the youngest SZA samples (younger than 17 ka cal BP). These come closer to meadow steppe and generally move towards the left side of the ordination diagram that can be explained by the increasing *Pinus* percentages in these samples suggesting increased similarity with the woody vegetation types.

Overall, PCA suggests that (1) the two mountain sites NM and SZA are similar mainly to open vegetation types and (2) they are more similar to each other than to FT; (3) FT was likely the most forested site during the LPG, at least in the surroundings of the pollen deposition site, and (4) SZA has the lowest similarity to the modern pollen samples from Siberia.

4.4. Modern analogue technique reconstruction

Receiver operating characteristics (ROC) analysis of the training dataset (Table 3) resulted in a good discrimination between vegetation groups based on pollen spectra, indicated by high area under

curve (AUC) values for all vegetation types. Application of AUC to individual vegetation types shows very good statistical performance with highly significant differences between dissimilarity values for analogues/non-analogues, except for the meadow steppe group. This may be caused by low variability within the group resulting in a low discriminant dissimilarity value (0.295).

Fig. 8 shows the results of applying the ROC methodology to the Altai-Sayan modern pollen dataset. A pair of samples was considered analogous if both were located in the same vegetation type as defined in Fig. 2, and non-analogues if each derived from different vegetation type. Kernel density estimates of the distribution of pairwise dissimilarities for the training set in Fig. 8c indicate both analogue and non-analogue pairings at relatively low dissimilarity values, but still most of the analogue pairings have very low chorddistance values (most frequent values yield 0.25). This suggests, first of all, that the modern pollen assemblages have many similarities in species composition and relative frequencies, and second, that the modern samples still discriminate the vegetation types well but at low dissimilarity values. This characteristic of the modern pollen dataset results in the determination of an optimal chord distance threshold (d_{crit}) of 0.443. Above this value modern and fossil samples are considered as non-analogues according to the ROC analysis.

The similarity of the modern pollen assemblages may be explained by two features:
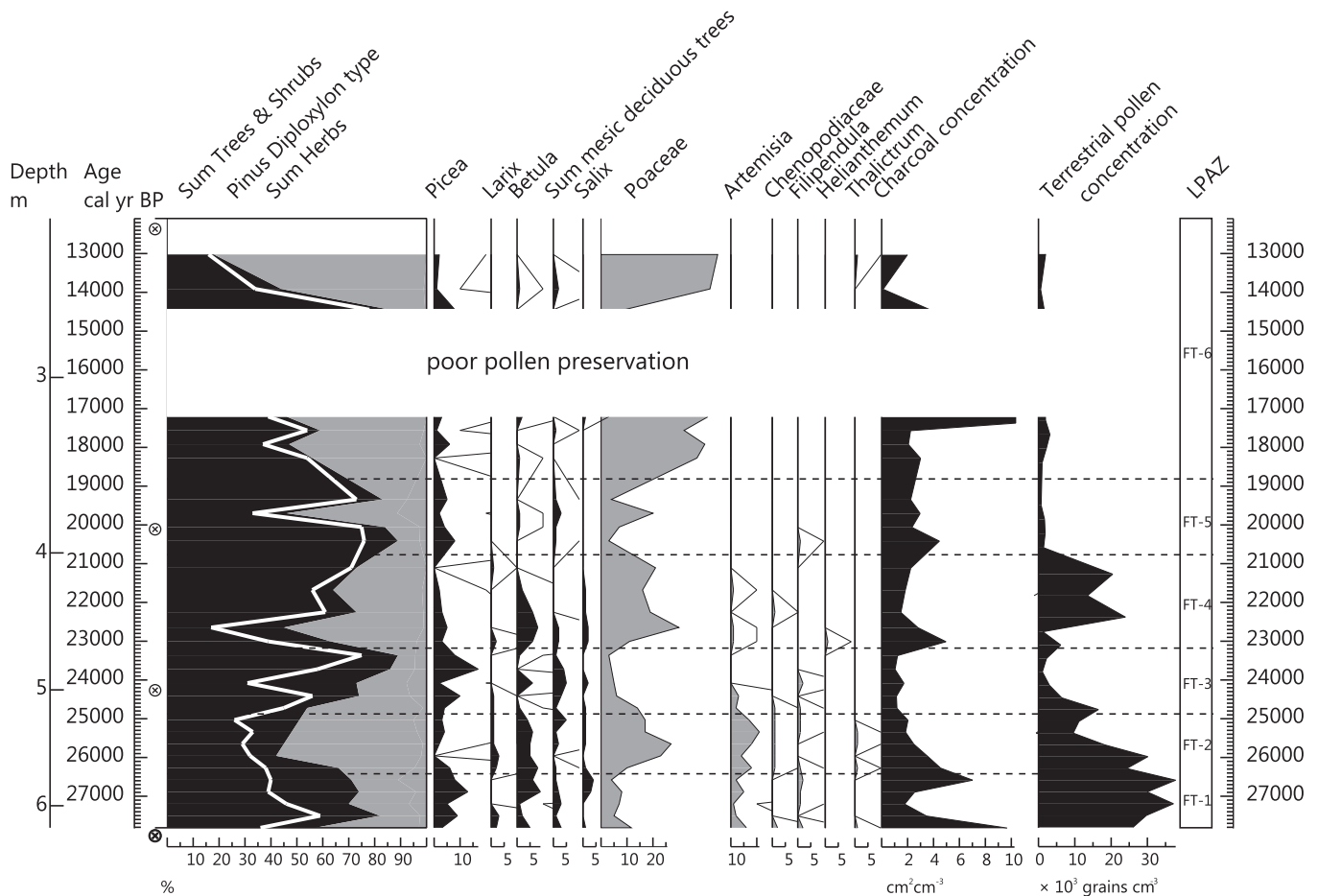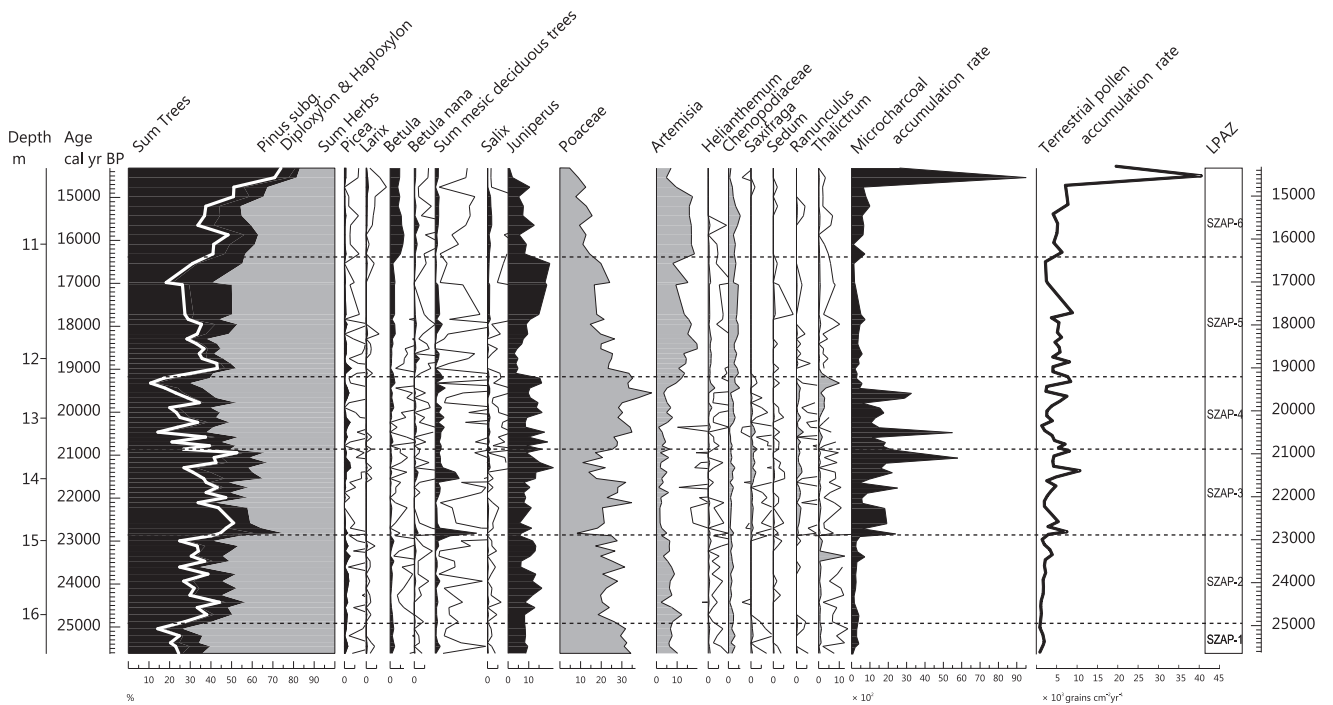
Fig. 5. Percentage pollen diagram of selected pollen taxa in the Late Pleniglacial profile of Fehér Lake (FT) (83 m a.s.l., Kardoskút, SE Hungary) plotted against calibrated BP age and depth. LPAZ: local pollen assemblage zones. Sum of mesophilous temperate deciduous trees includes *Quercus*, *Corylus*, *Ulmus*, *Tilia*, *Acer*, *Carpinus betulus*, *Fagus* and *Fraxinus excelsior* type.

1) Taxonomic harmonization of the modern and fossil pollen data resulted in the merging and occasionally removal of several pollen types from the modern pollen dataset (see Supplementary Table 2, e.g. *Pinus* subg. *Haploxylon* was merged with *Pinus* subg. *Diploxylon*), which decreased the dissimilarity of the modern spectra.
2) The modern pollen assemblages came from a relatively small geographical mountainous area (ca 400 × 400 km) where complex topography results in marked vegetation changes at small distances. These sharp vegetation changes are however partially masked by pollen transport to larger distances (uphill pollen transport, regional pollen rain).
3) Furthermore, pollen spectra are markedly biased in vegetation producing less pollen (generally treeless vegetation), where regional pollen component originating from all vegetation types in a broader area (sensu Sugita, 2007) may create substantial part of the pollen spectrum.

When applying d_{crit} 0.443 in the analysis, very few true (statistically significant) analogues were found for the LPG pollen assemblages from the CB (Fig. 9). Statistically significant analogues were most often dry steppe, wet and mesic grassland and meadow steppe at all the three CB/CM sites. Hemiboreal forest and taiga were rarely indicated as the first true analogue; in SZA continental taiga was identified at 23.5 and 24.7 ka cal BP as the best analogue,

and at 23.8 ka cal BP as the second best analogue (after dry steppe). The lowland site FT showed similarity with continental taiga and hemiboreal forest at 26.3 and 20 ka cal BP as the first, second or third best analogue (with <0.443 chord distance). A very similar pattern was found in NM, but at this site wooded vegetation types never appeared as the first analogue. Lake St Anne had the fewest true analogue matchings during the LGM; however, between 16.5 and 14.3 ka cal BP the pollen assemblages had true analogues with the Siberian continental taiga and dry steppe, suggesting that after Heinrich event 1 the landscape gradually became more forested with a similar character as the modern vegetation of the Altai-Sayan Region where continental taiga alternates with dry steppe.

An important feature of the modern analogue diagram (Fig. 9) is the near-total absence of true analogue vegetation between 25 and 22 ka cal BP, and in case of SZA even up to 19 ka cal BP. We assume that differential modes of pollen recruitment in modern and fossil samples (moss polsters and soil samples in the former, peat bogs and lakes in the latter) contributed only marginally to the analogue matching, as most of the surface sample sites were in large forest openings or in open landscape probably similar to the LPG landscape of the CB and CM, and pollen types with proven local origin were excluded from both the fossil and modern pollen spectra. Nonetheless, we cannot exclude that some proportion of the sample dissimilarities may derive from the different taphonomy of the sampling sites.

Fig. 6. Percentage pollen diagram of selected pollen taxa in the Late Pleniglacial profile of Lake St Anne (SZA) (950 m a.s.l., Băile Tuşnad, Eastern Carpathian Mts, Romania) plotted against calibrated BP age and depth. LPAZ: local pollen assemblage zones. Sum of mesophilous temperate deciduous trees includes *Quercus, Corylus, Ulmus, Tilia, Acer, Carpinus betulus, Ostrya/Carpinus orientalis, Fagus, Fraxinus excelsior* type and *Fraxinus ornus*.
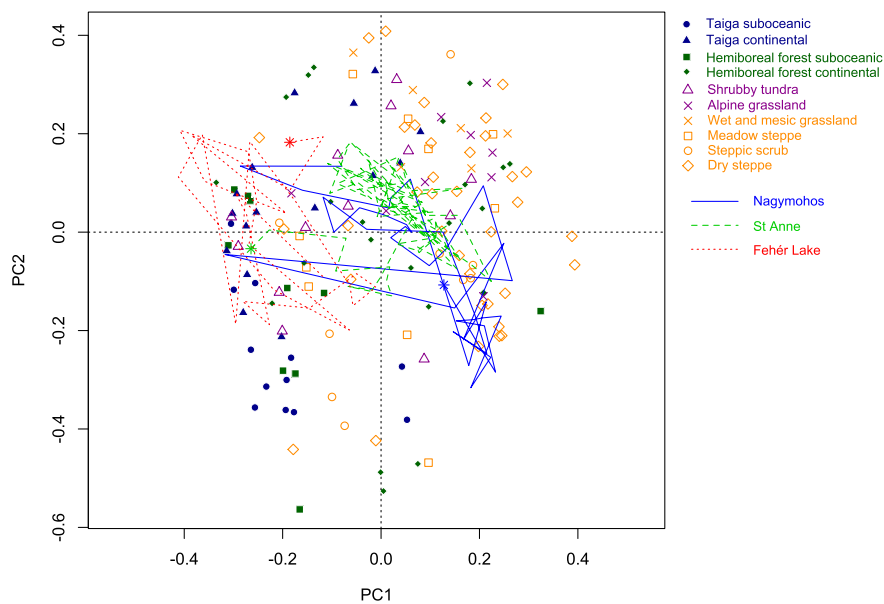
Fig. 7. Principal components analysis (PCA) ordination scatterplot of modern and fossil pollen samples analysed together. Full and empty symbols represent the modern forest and treeless vegetation types of southern Siberia, respectively. Fossil pollen spectra from eastern-central Europe are represented by lines connecting samples of each profile in their stratigraphical order. The youngest sample is marked as asterisk. Axes 1 and 2 explain 27.4% and 13.8% of the total variance, respectively.

5. Discussion

5.1. The character of the Late Pleniglacial vegetation in the Carpathian Basin and the Eastern Carpathian Mountains

Eastern—central European LPG sites are often characterized by relatively high *Pinus* pollen percentages (Gerasimenko, 2006; Andrič et al., 2009; Starnberger et al., 2009; Fletcher et al., 2010), which is often implicitly interpreted as reflecting partially wooded pine-dominated boreal forest-steppe landscapes (with *P. sylvestris* and *P. cembra*). The terms most often used are parkland forest (Willis et al., 2000), taiga forest-steppe, forest-steppe with *Pinus*, open boreal forest (Rudner and Sümegi, 2001; Gerasimenko, 2006; Fletcher et al., 2010; Sümegi et al., 2012a,b, 2013), or open forest-tundra (Müller et al., 2003).

The three LPG pollen sequences examined in this study also showed high and periodically fluctuating *Pinus* and total arboreal pollen frequencies, which we have interpreted as reflecting a partially wooded boreal forest-steppe landscape in the CB during the LPG. When we compared our fossil pollen assemblages with modern pollen spectra from southern Siberia by PCA and AM, we found that despite the high arboreal pollen frequencies, the most similar modern vegetation belongs in many cases to unforested or shrubby types (dry steppe, mesic grassland, meadow steppe), while continental hemiboreal and taiga forest types occur as second or third true analogues. Only the lowland site, Fehér Lake, overlapped frequently with the modern suboceanic and continental hemiboreal forest and continental taiga samples in the PCA biplot (Fig. 7). Therefore the first inference to be drawn from our modern-fossil data comparison is that LPG landscapes in the CB and Eastern Carpathian Mountains may have been less wooded than suggested by the AP percentage values. As demonstrated by Pelánková et al. (2008) and Pelánková and Chytrý (2009),arboreal pollen types (especially *P. sylvestris* and *P. sibirica*) are overrepresented in surface pollen assemblages in the mosaic landscape of southern Siberia where forest patches alternate with steppe and tundra due to climatic and topographic differences in relatively small areas. In the Altai and Sayan Mts dry and meadow steppes and mesic grasslands

occasionally receive 60—70% arboreal (mainly *Pinus*) pollen, even though pine forests can be within tens of kilometres distance of the surface sample locations (Pelánková et al., 2008; Pelánková and Chytrý, 2009). High values of *Pinus* pollen were also found in the Last Glacial Balkan pollen record of Lake Prespa, where the values of 40—60% of *Pinus* pollen were associated with low overall terrestrial pollen accumulation rates, suggesting overrepresentation of the rich pollen producer *Pinus* due to decreasing vegetation cover (Panagiotopoulos et al., 2013). Pollen monitoring studies at the northern distribution limit of *P. sylvestris* also show its over-representation when expressed as relative frequencies (Hicks, 2001). However, pollen accumulation rates clearly suggest that local presence is associated with values >500 grains cm^{-2} yr^{-1}. Although the age—depth model derived sediment accumulation rates may not be accurate for each level in case of our studied sediment sequences, calculation of total *Pinus* pollen accumulation rates suggest that in Fehér Lake this limit is only attained in samples older than 26.5 ka cal BP, in Nagymohos older than 25.7 ka and at 19.2 ka cal BP, while in Lake St Anne nearly all samples exceed this limit considerably; values are mostly within the range of 600—3000 grains cm^{-2} yr^{-1}, and only in a few samples fall below the local detection limit of 500 grains cm^{-2} yr^{-1} (Fig. 9). These accumulation rate data suggest that *Pinus* relative frequencies are misleading in these records, and local presence can most securely be inferred in the pre-LGM layers of NM and FT, while in the vicinity of Lake St Anne *Pinus* was present between 25.6 and 15 ka cal BP, i.e. also throughout the LGM. We must note, however, that *P. cembra* macrofossils were found in the bottom layers of NM, where total *Pinus* pollen accumulation rates either do not exceed the local detection limit (Figs. 4 and 9), or exceed it only slightly, so accumulation rates have to be treated also with caution when inferring local presence during glacial conditions when pollen production was likely affected by low CO_2 levels (Willis and Whittaker, 2000).

The predominance of steppic vegetation types as the best modern analogues is thus supported by the pollen accumulation rate data; however, this does not mean that trees or forest patches were not present in the LPG landscape. The presence of trees during the LPG has been demonstrated in the CB and in the lowlands east

Table 2
Principal component scores of selected pollen types.

	PC1	PC2
Betula	−0.258	−0.817
Larix	0.161	0.156
Picea abies	−0.151	0.132
Pinus	−0.827	0.370
Alnus viridis	−0.104	−0.075
Juniperus	0.266	0.114
Artemisia	0.631	−0.116
Caryophyllaceae undiff.	0.193	0.077
Chenopodiaceae	0.252	0.077
Poaceae	0.657	0.144
Umbelliferae undiff.	0.101	−0.058

of the Carpathians by numerous loess-charcoal records (Rudner and Sümegi, 2001; Willis and van Andel, 2004; Haesaerts et al., 2010). Rather, we infer that forest cover was less than suggested by the tree pollen values of the fossil samples. Trees were likely concentrated along water courses, in wet basins and on north-facing slopes, and less abundant on south-facing slopes and lowland exposed surfaces outside river floodplains. Supporting evidence for this interpretation comes from palaeozoological studies of cave and loess deposits in the CB (Pazonyi, 2004, 2011) that indicated the dominance of steppe-dwelling herbivores in association with typical tundra and boreal forest elements during MIS 2. Other evidence for decreasing woody cover during the LGM in Central Europe comes from Late Pleniglacial loess charcoal studies (31–17 ka cal BP according to Haesaerts et al., 2010), which show that in Moravia and Lower Austria charcoals were missing from the loess deposits after 23 ^{14}C ka (∼27.85 ka cal BP) (Damblon and Haesaerts, 2002; Willis and van Andel, 2004; Haesaerts et al., 2010). These datasets along with geomorphological features (ice-wedge casts, tundra gleys, sandy loess) were interpreted by Haesaerts et al. (2010) as evidence for steppic, deseretic or tundra character of these sites during the LPG. In contrast, *P. sylvestris*, *P. cembra*, *Larix* and *Betula* charcoal remains were still recovered in lower quantities from LPG loess deposits in Hungary (summarized by Willis and van Andel, 2004), suggesting that hemiboreal open woodlands were present in the landscape. In contrast, the only dark taiga component, *P. abies*, likely disappeared or decreased considerably in the lowlands, suggesting also decreasing moisture availability in that period. This picture agrees with the pollen record and modern analogue technique inferred LPG vegetation of our CB lowland site Fehér Lake (FT), where the few statistically significant analogues showed similarity with the south Siberian dry and mesic hemiboreal forests, where the canopy is composed of *P. sylvestris*, *B.*

pendula, *L. sibirica* and *P. sibirica* (Ermakov et al., 2000; Chytrý et al., 2008, 2012) and occasionally with continental taiga in which *P. sibirica* is mixed with *P. obovata*. We must emphasize, however, that these wooded vegetation types nearly always showed less similarity with the LPG vegetation than wet and mesic grasslands and dry steppe, likely indicating the larger share of these open vegetation types.

Loess-charcoal studies also point out an important difference between the CB and the lowlands along the Prut river valley (Fig. 1). The latter area lies in the vicinity of our East Carpathian Mountain pollen record, Lake St Anne (SZA). Although SZA showed the least similarity with any of the south Siberian modern vegetation types, the record clearly attested to the persistence of regional woody cover composed of *P. sylvestris*, *P. mugo*, *P. cembra* and *Juniperus* between 19 and 23 ka cal BP in association with increasing regional wildfires. This observation is in contrast with the global fire regime trend during the LGM, which showed decreasing biomass burning (Daniau et al., 2010). This surprising persistence of regional woody cover and biomass burning throughout the LGM coincides with the persistence of Epigravettian human populations and sustained diverse boreal tree cover in the lowlands east of the Carpathians (Fig. 1), where macrocharcoals of *Picea*, *P. cembra*, *Larix*, *Juniperus*, *Betula*, *Salix*, *Alnus*, *Populus* and *Rubus* were continuously recorded in the Prut river valley loess sequences (Willis and van Andel, 2004; Haesaerts et al., 2010)even in the tundra-gley horizons. Again, the presence of trees and shrubs does not mean that wooded vegetation types were predominant landscape components; the SZA pollen record itself shows a broader overlap with the modern steppe and alpine grassland vegetation types in the PCA plot, which despite the non-analogue vegetation suggests the partial openness of the landscape in the mid-elevation zones of the Eastern Carpathians.

Now turning to the character of the LPG vegetation of the CB and CM, several fine details become apparent when we compare the herbaceous pollen types and their affinity to various modern vegetation types in southern Siberia. Table 4 shows 1) the appearance of several herbaceous pollen types that occur jointly in dry to mesichemi boreal forests and steppe or forest-steppe meadows (e.g. *Androsace*, *Pleurospermum*, *Potentilla*, *Primula*, *Prunella*, *Sanguisorba officinalis*, *Thalictrum*); this group of herbs is the most numerous; 2) the presence of herbs typical of taiga or mesic to wet forest (*Aconitum*, *Empetrum*, *Ribesalpinum*, *Lonicera nigra*, *Vaccinium*, *Trientalis europaea*) in all three LPG pollen records, but most abundantly in Nagymohos (NM) and after 17 ka cal BP in SZA suggesting the presence of taiga habitats in the vicinity of Nagymohos; 3) the absence of typical tundra elements in the fossil pollen records, except for a few pollen grains of *Dryas octopetala* in

Table 3
Summary results from the receiver operating characteristics (ROC) curve analysis of the training pollen dataset from southern Siberia. Analysis has been applied individually to ten defined vegetation types as well as to all types combined.

ROC curves of dissimilarities:						
	No. analogue pairings	No. non-analogue pairings	Optimal dissimilarity	Area under ROC curve (AUC)	Standard error of AUC	*p*-value
Alpine grassland	9	134	0.515	0.988	0.025	0.0010
Dry steppe	36	107	0.417	0.922	0.032	<0.0001
Hemiboreal forest continental	22	121	0.448	0.951	0.032	0.0006
Hemiboreal forest suboceanic	10	133	0.416	0.987	0.025	0.0005
Meadow steppe	10	133	0.295	0.972	0.036	0.1600
Shrubby tundra	13	130	0.382	0.981	0.027	0.0003
Steppic scrub	9	134	0.474	0.986	0.028	0.0042
Taiga continental	16	127	0.349	0.985	0.021	<0.0001
Taiga suboceanic	12	131	0.353	0.992	0.017	<0.0001
Wet and mesic grassland	6	137	0.47	0.994	0.021	0.0024
Combined	143	1287	0.443	0.980	0.008	<0.0001
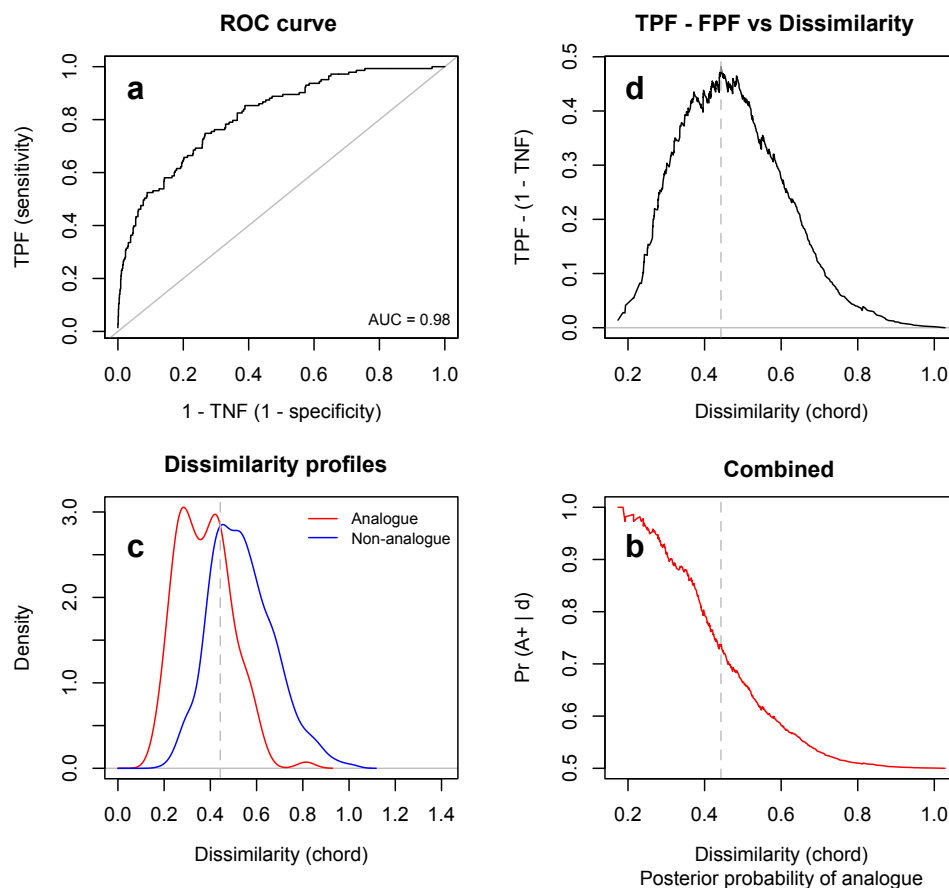
Fig. 8. Receiver operating characteristic (ROC) curve analysis applied to the Altai-Sayan modern pollen dataset using the chord distance. Clockwise from top left: (a) the ROC curve and area under curve (AUC) statistic; (b) posterior probability that two samples are analogues as a function of dissimilarity; (c) kernel density estimates of the distribution of pair-wise dissimilarities for analogue and non-analogue samples; (d) plot of True Positive Function (TPF) − False Positive Function (FPF) as a function of dissimilarity. The dotted vertical line in the plots is the optimal dissimilarity threshold indicated by the ROC curve, which is 0.443.

SZA and sporadic presence *Vaccinium* in all fossil pollen records that can indicate both tundra and taiga. This suggests that vegetation similar to modern tundra or alpine vegetation types was uncommon in the CB, but it likely occurred in wet habitats with permafrost in the crater of Lake St Anne.

Overall, our analyses suggest that vegetation of the CB and CM most resembled the forest-steppe/steppe zono-ecotone of southern Siberia with a landscape mosaic of dry steppe, wet and mesic grassland, meadow steppe and hemiboreal forest, as it has been also suggested by mollusc studies (Sümegi, 2005; Horsák et al., 2010; Sümegi et al., 2012a,b).

Further insight into the character of the LPG vegetation is offered by the bryophyte assemblages of Nagymohos that were used to reconstruct the succession of LPG mire palaeoassociations at this Western Carpathian foothill site. As shown in Fig. 4, the landslide basin of Nagymohos was paludified after its formation: the initial *P. cembra* wooded fen was followed by various flark-fen, poor-fen and rich-fen mire types in which brown mosses (e.g. *C. richardsonii*, *S. scorpioides* and *W. sarmentosa*) and occasionally *Sphagnum* species prevailed. These brown mosses have restricted distribution today in the higher mountains of Europe, in Scandinavia and in the boreal and subarctic zone of NE Europe and Siberia (Eurola et al., 1984), where they usually appear in different types of fens and other wet habitats. Together with the abundant macro-fossil findings of *P. cembra* (twig and seed fragments) this assemblage pointed to the development of a boreal wooded fen in the Nagymohos basin directly before the onset of the LGM. Such mires

in NE Europe and Siberia today are usually associated with taiga and hemiboreal forest habitats (Eurola et al., 1984), but in northern Siberia they also appear in forest-tundra, tussock and dwarf-shrub tundra (Walker et al., 2002). Although typical tundra herbs were not found in Nagymohos, several taxa, e.g. Rosaceae undifferenti-ated, *Papaver*, *Saxifraga* and *Polygonum bistorta* may derive from tundra herbs in this pollen record, suggesting that a heterogeneous environment with altitudinal and exposure-driven habitat differences likely existed there.

Such mosaic-like environment can also be traced in the present vegetation of southern Siberian mountains where the pattern of treeless and forested vegetation is strongly determined by slope aspect, with steppe regularly appearing on south-facing slopes, forest on north-facing slopes, wet and mesic grasslands on valley bottoms, and alpine grasslands and tundra restricted to high elevations (Chytrý et al., 2008, 2012; Pelánková et al., 2008; Pelánková and Chytrý, 2009). The Nagymohos site is situated in a local depression of an SE-facing gentle slope, but with cool mesoclimate because of the topographic shading by a nearby N–S running ridge. The mire was surrounded by south-facing hillslopes that likely supported dry steppes and mesic grasslands during the LPG, while boreal trees likely survived in wet microhabitats of the nearby Kelemér river valley and the western slopes of the N–S running ridge. In case of Lake St Anne slope aspect was probably also important together with elevation. Since this volcanic crater is situated at 950 m a.s.l. and has a cool mesoclimate today that is reflected in reversed vegetation zonation (Magyari et al., 2009), we
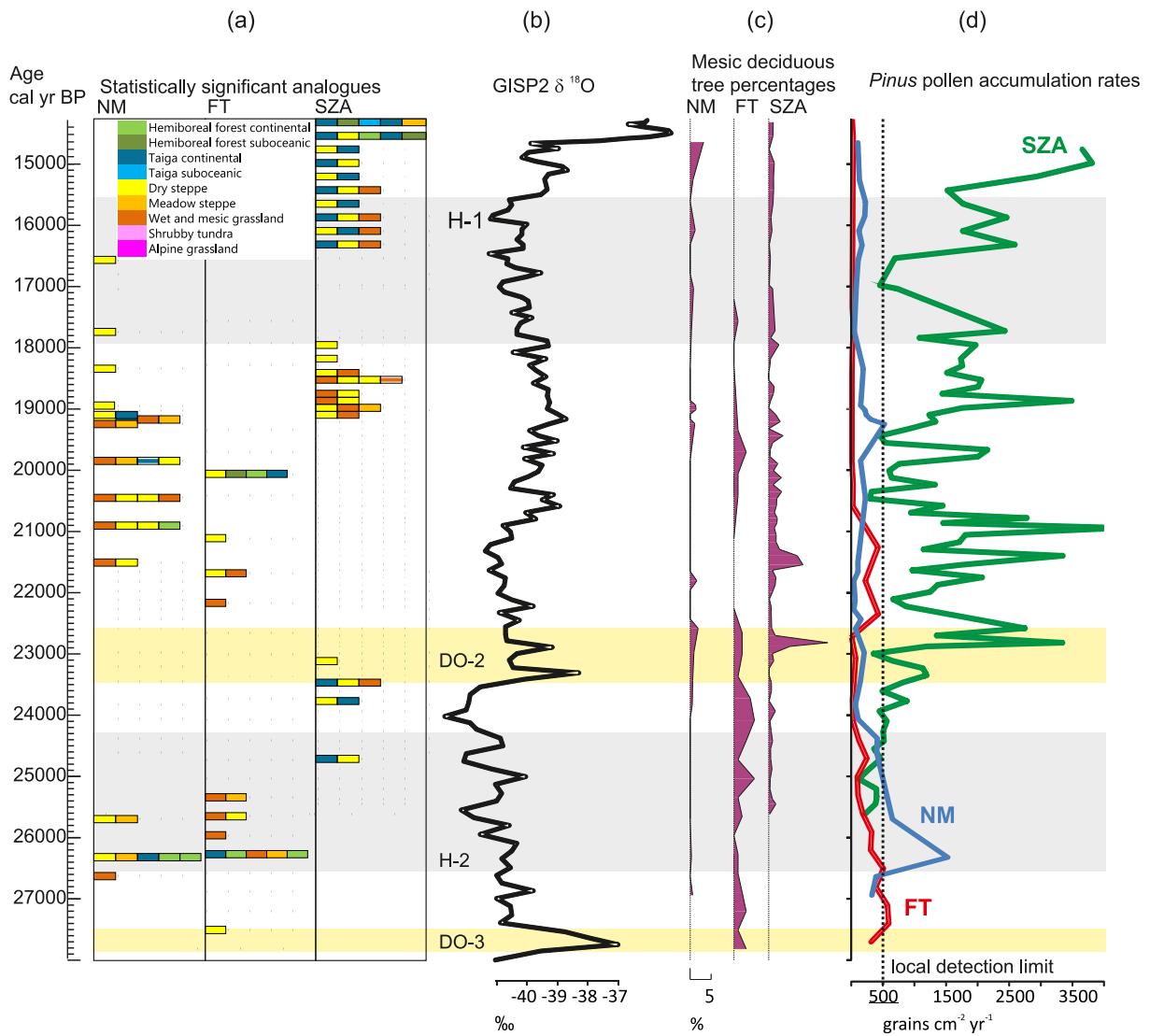
Fig. 9. Data synthesis. (a) Statistically significant analogues between the Late Pleniglacial pollen spectra of Lake St Anne (SZA), Nagymohos (NM), Fehér lake (FT) and the modern pollen assemblages of the Altai-Sayan Mountains. Statistically significant analogues are shown in ascending chord distance order; (b) GISP2 δ18O curve form Greenland (Grootes et al., 1993); (c) temperate mesophilous temperate deciduous tree pollen curves, each curve sums up the relative frequencies of *Quercus, Corylus, Ulmus, Tilia, Acer, Carpinus betulus, Fagus* and *Fraxinus excelsior* type; d) *Pinus* (subgenus *Diploxylon* & *Haploxylon*) pollen accumulation rates. DO-1, DO-2: Dansgaard-Oeschger events 1 & 2; H-1: Heinrich events 1 & 2.

suggest that boreal trees were not present in the crater during the LGM, but the moist lakeshore likely supported dwarf shrubs (e.g. *Alnu sviridis* and *B. nana*) and the crater slopes were either barren or supported patchy tundra or alpine grasslands (with *D. octopetala, Salix herbacea* and *Soldanella* species), while *P. sylvestris* and *L. decidua* dominated open forests likely prevailed in sheltered places of the north-facing slopes at lower elevation, with *Juniperus* scrub and alpine mesic grasslands developed higher up. *Juniperus* species (*J. pseudosabina, Juniperus sabina* and *J. sibirica*) do not form any distinct vegetation zones in the Altai and Sayan Mts today, and become dominant in small patches only (Kuminova, 1960). Therefore modern analogues for this vegetation have to be looked for elsewhere. The abundance of *Juniperus* in the East Carpathian Mountains during the LPG is a distinctive feature of this area in comparison with the other two CB locations. It can most likely be ascribed to the high elevation of the site and the enhanced continentality of its climate (January mean temperatures in the nearby Ciuc basin often reach −20 °C today while summers are relatively

warm). Continentality extremes must have been even more pronounced during the LGM (Strandberg et al., 2011). Similar climates today prevail in several Central Asian high mountain ranges, e.g. in the Northern Tien-Shan, where *Juniperus turkestanica* forms a wide vegetation belt on north facing slopes between 1500 and 2500 m in the Dzhungarsky Alatau above a narrow coniferous belt (Agakhanyants, 1981). Also notable is that in these mountains semi-desert and meadow-steppe occupy northern slopes at lower elevation (below 1500−1100 m) due to low available moisture at these altitudes. Although the mountains around Lake St Anne are much lower (highest peaks 1100−1200 m a.s.l.), the northern slope zonation during the LPG may have been similar to Dzhungarsky Alatau today.

Finally, the vegetation pattern of the most southerly located lowland site, Fehér Lake, can be best compared with the large intermontane basins in the southern Altai-Sayan Mountains, which are dominated by dry steppes intersected by gallery forests of *Larix* and *Picea* along the rivers (Chytrý et al., 2008; Pelánková and

Table 4
Appearance of indicator pollen types in the studied Late Pleniglacial pollen sequences: Lake St Anne (SZA), Fehér Lake (FT) and Nagymohos (NM).

	Tundra and alpine elements	Taiga and mesic-wet forest elements	Mesic-dry forest and steppe elements
SZA	*Dryas octopetala*	*Vaccinium*	*Pedicularis*
	Soldanella	*Trientalis*	*Pleurospermum*
	Pedicularis	(>17-ka cal BP)	
	Vaccinium		
	Polygonum viviparum		*Potentilla*
	Saussurea		*Prunella*
			Primula
			Sanguisorba officinalis
			Saussurea
			Thalictrum
FT	Ericaceae	*Ribes alpinum*	*Gentiana*
		Picea	*Sanguisorba officinalis*
		Ericaceae	
		Frangula	
NM	*Polygonum viviparum*	*Lonicera nigra*	*Sedum*
	Aconitum	*Ribes alpinum*	*Aconitum*
	Polemonium	*Aconitum*	*Polemonium*
	Gentiana		*Papaver*
	Androsace		*Gentiana*
			Sanguisorba officinalis
			Thalictrum
			Pleurospermum
			Androsace

Chytrý, 2009). While *Larix* was likely present in the riparian forests around Fehér Lake, the canopy composition of these open forests changed between 27 and 13 ka cal BP, as the pollen assemblages suggest a decreasing representation of *Picea*, *Larix* and *Betula* after 20ka calBP and increasing abundance (but decreasing accumulation rates) of *Pinus* subg. *Diploxylon* suggesting either decreasing tree cover on the palaeochannel shore or the spread of pines (*P. mugo* and *P. sylvestris*).

An important common feature of the CB LPG pollen records was the decrease of *Artemisia* against Poaceae. This relative frequency change broadly coincides with the onset of the maximum cooling above Greenland after Dansgaard–Oeschger event 2, around 21 ka cal BP (NGRIP members 2004). Surface pollen studies from southern Siberia, Mongolia and China help us interpret the underlying climatic and ecological changes (Wang et al., 1996; Liu et al., 2006;Pelánková et al., 2008). In southern Siberia the pollen representation of *Artemisia* is positively correlated with summer temperatures (Pelánková et al., 2008), therefore one plausible explanation is a significant decrease in summer mean temperatures that might have favoured a change in steppe vegetation composition. In the modern vegetation of southern Siberia, the highest Poaceae and lowest *Artemisia* pollen values are in wet and mesic grasslands, and despite the poor true analogue situation, this vegetation types was indeed found as the most frequent best analogue for the LPG vegetation. In southern Siberia wet and mesic grasslands occur in the river floodplains or north-facing or shaded slopes of the river valleys, which are receiving higher moisture than the surrounding landscape due to the effect of the river. Often there is a sharp transition from wet and mesic grasslands to dry steppes at the floodplain edges or between sun-exposed and shaded slopes. Similar mesic grasslands may have been developed in the floodplain or its edges or near the lakeshore at Féher Lake, although vegetation of the broader surroundings of this site may have been dry steppe.

An alternative explanation of the *Artemisia* decline and Poaceae rise is offered by changing grazing pressure after 21 ka cal BP. Surface pollen studies from the Asian steppes often find poor correlation between the representation of grasses in the vegetation and surface pollen spectra and explain this mismatch by restricted flowering of grasses due of overgrazing (Wang et al., 1996). If we assume that the herbivore population was more numerous in the CB before the LGM, we can argue that the compositional change in the herbaceous vegetation may reflect decreasing herbivore population size. This inference is seemingly supported by the mammalian faunas that show a decrease in large herbivore presence after 20 ka uncal BP (23.9 ka cal BP) (Pazonyi, 2004). However late Pleistocene faunas of the CB are mostly undated. The few radiometrically dated mammoth, rhinoceros and horse remains suggest that large herbivores were present during MIS 2 in the CB (Kovács et al., 2012), but the data are yet inconclusive regarding the LGM population size changes.

5.2. Is the south Siberian landscape a good analogue of the Late Pleniglacial vegetation of the Carpathian Basin and Carpathian Mountains?

One important result of our LPG − modern pollen assemblage comparison was a low number of statistically significant analogues with the modern vegetation types of southern Siberia. This was despite many vegetation and faunal studies argue that the most similar ecosystems to the LPG landscapes of east Central Europe exist in the Altai and Sayan Mountains (Frenzel et al., 1992; Sümegi, 2005; Jankovská and Pokorný, 2008; Kuneš et al., 2008; Horsák et al., 2010; Varga, 2010). Although we cannot exclude that better analogues to the LPG vegetation may exist in other parts of continental Asia, the apparent overlap in the herbaceous vegetation components, fossil and modern snail faunas of the CB/CM and southern Siberia are quite convincing (Varga, 2010) and no better analogues have been suggested so far. However, it would be naive to expect that current ecosystems of southern Siberia or any other region are perfect analogues of certain palaeoecosystems. Although modern analogues can help us develop understanding of past ecological processes, they are always only partial analogues, with some common features but also some differences. There are several reasons for these differences.

First, the studied fossil sites in the CB and the sites of modern pollen samples in the Altai-Sayan Mountains are separated by a distance of about 4300−5100 km. Both of these regions have different biogeographical histories and are influenced by species migration from different regions. Therefore, in addition to the shared species and similar vegetation types, there are inevitable differences in biota that would exist even if local environmental conditions were identical between the LPG CB/CM and the modern Altai-Sayan.

Second, the quality of the fossil−modern analogues is crucially dependent on the taxonomic resolution of fossil data. Here we used pollen, which cannot be determined to the species or genus level in most cases. If all fossil pollen grains could be determined to the species level, the similarity between fossil and modern samples calculated based on the species would be almost certainly lower, because several higher-level taxa are present in both fossil and modern samples (e.g. Poaceae), thus contributing to sample similarity, but if they were divided into species, they would contain several different species, contributing to dissimilarity. Thus it is important to realize that whether or not some samples are identified as 'statistically significant' analogues depends on taxonomic resolution. Therefore even 'statistically significant' analogues as identified by the modern analogue method are probably no true analogues in a strict sense.

Third, although the Altai-Sayan Mountains have several features of their continental climate similar to the modelled climate of the CB/CM, there are some differences. The most important characteristics of the European LGM climate have been discussed in detail

by several authors (Peyron et al., 1998; Jost et al., 2005; Kageyama et al., 2006; Ramstein et al., 2007; Strandberg et al., 2011). Regional climate simulations (Jost et al., 2005; Strandberg et al., 2011) suggest that the mean temperature of the coldest month (MTCO) in the Carpathian Basin (East Carpathian Mountains) was around −9 to −15 °C (−14 to −17 °C), while mean temperature of the warmest month (MTWA) was 12–18 °C (6–12 °C) and annual precipitation (PANN) was ~360 mm (~500 mm at 950 m a.s.l.). Model simulations furthermore suggested relatively weak MTCO decrease in the CB (6–9 °C lower than today) and some models even suggest higher than present precipitation in the Carpathian Mountains (by ~10%, Strandberg et al., 2011). Some of these climatic characteristics differ from the present climate of the Altai-Sayan region, where particularly winter temperatures are much lower (−17 to −36 °C) in a large part of the area than expected for the LGM CB by the model simulations (−9 to −15 °C). Proxy-based climatic reconstructions from the CB also confirm the model-based estimates of the mean temperature of the warmest month. Sümegi and Krolopp (2002) and Sümegi et al. (2012a,b) reconstructed 11–14 °C using LGM mollusc assemblages, while groundwater noble gas and mammoth teeth oxygen isotope studies suggested that LGM mean annual temperatures (MAT) were around 9 °C colder than today (Varsányi et al., 2011; Kovács et al., 2012). Although these two reconstructions do not fully agree with the climate model simulations, reconstructed MAT values fall within the lower limit of the modelled MAT, which is estimated to be by 3–11 °C colder than today (Strandberg et al., 2011). Proxy based rainfall reconstructions for the LPG furthermore suggest that annual rainfall in the CB was 350–400 mm/yr (Bradák et al., 2010) in the cold phases. This reconstructed value agrees well with the lower limit of the modelling results, which is 360–720 mm/yr (Strandberg et al., 2011). Most areas with dry or meadow steppe and forest-steppe covering the modern landscapes of the Altai-Sayan Mountains receive similar rainfall or less, suggesting that annual rainfall values are comparable. Overall, the non-analogue climatic and vegetation features of the Carpathian Basin during the LGM likely result from less cold winters relative to the modern climate of the areas in the Altai-Sayan Mountains dominated by cold steppe and hemiboreal forest. In these areas MTCO of the modern pollen sample locations ranges from −16 to −37 °C.

Fourth, LPG vegetation was globally limited by extremely low CO_2 levels, which affected vegetation via modifying the water and carbon uptake by plants (Cowling and Sykes, 1999). This makes the existence of true modern analogues impossible on the global scale. The LPG vegetation would probably be less productive even if all climate features were perfectly matching between the LPG CB/CM and the modern Altai-Sayan region. The change in CO_2 level explained well the shift to steppic vegetation in the Mediterranean (Wu et al., 2007), and it likely also explains the palynologically less distinctive decrease of boreal woody cover in the CB and CM, as low CO_2 specifically makes arboreal species less competitive (Harrison and Prentice, 2003).

If we examine how the analogue situation alters when we compare MIS 3 pollen assemblages with the modern pollen spectra of the Altai-Sayan Mountains, we find that two Western Carpathian mountain sites are much more similar to the south Siberian vegetation (Fig. 10). We used the pollen record of Jablůnka, dated to 44.8–39.7 ka cal BP (Jankovská et al., 2002; Jankovská and Pokorný, 2008; Kuneš et al., 2008), and Šafárka, dated to 52–16.5 ka cal BP (Jankovská and Pokorný, 2008; Kuneš et al., 2008), and found higher proportions of statistically significant analogues than in the case of the LPG pollen assemblages of the CB and CM. Dissimilarity values were lowest between the modern dry steppe and the fossil samples, but continental taiga, suboceanic hemiboreal forest and continental hemiboreal forest pollen samples also showed very low
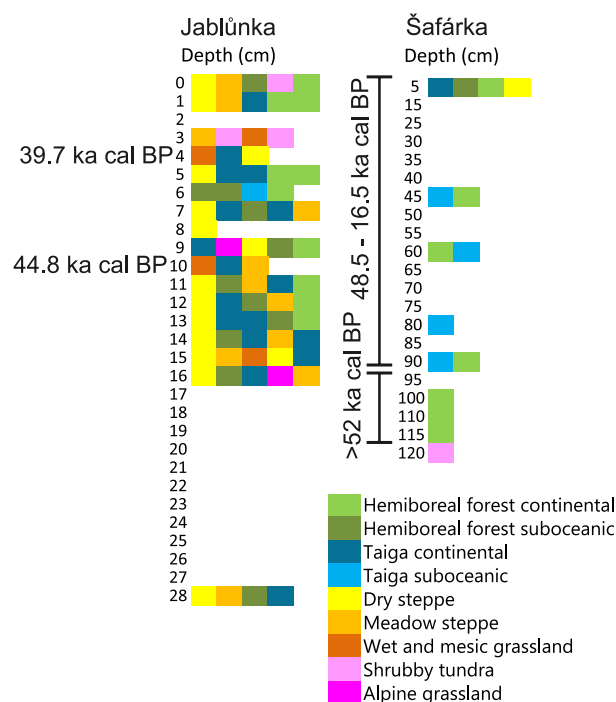
Fig. 10. Statistically significant modern analogues between the MIS 3–2 pollen spectra of Jablůnka and Šafárka (Western Carpathians, Czech Republic and Slovakia, respectively) and the modern pollen assemblages of the Altai-Sayan Mountains. Statistically significant analogues are shown in ascending chord distance order. See Fig. 9 for colour code legend and Fig. 1 for site locations. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

dissimilarities, suggesting that some regions of the Western Carpathian Mountains were characterized by a mosaic of dry steppes, meadow steppes and various taiga and hemiboreal forests during MIS 3 (Kuneš et al., 2008). The similarity with the southern Siberian mountain landscape however decreased later, as suggested by the scarcity of statistically significant analogues between the younger, MIS 3–2 Šafárka pollen record and the Siberian modern samples. The number of statistically significant analogues, on the other hand, increased again towards the Lateglacial at this site, similarly to Lake St Anne, where the records younger than 17 ka cal BP had several statistically significant analogues with the Siberian continental taiga and dry steppe samples. This comparison suggests that the most deviating vegetation types were likely formed during the LGM, when climatic settings and CO_2 levels were the most different from today's, while the MIS3 and Lateglacial landscapes have matching vegetation types in the modern vegetation of southern Siberia.

5.3. Temperate broad-leaved deciduous tree refugia in the CB during the LPG and LGM

While global or continental-scale vegetation reconstructions and biome models suggest that the major biomes were tundra and steppe in the CB and CM during the LGM (Harrison and Prentice, 2003; Jost et al., 2005; Peyron et al., 2005; Wu et al., 2007), our pollen and microcharcoal records from this area along with loess-charcoal records suggested that the LPG vegetation had a significant woody component; woody cover showed cyclic increase and decrease, and fire frequencies increased in the mid-mountain zone of the East Carpathians, where further decrease in woody cover was not detected during the LGM; instead, woody cover decreased after 19 ka cal BP (Fig. 9).

In addition to the proven LGM survival of boreal and cool-temperate trees in the CB (Willis et al., 2000; Rudner and Sümegi, 2001; Willis and van Andel, 2004; Bhagwat and Willis, 2008; Birks and Willis, 2008; Provan and Bennett, 2008), an important question remains whether the topographically diverse mountains and the humid river valleys provided shelter for some mesophilous temperate broad-leaved deciduous trees during the LGM in the CB and CM (mesophilous temperate deciduous trees are defined here as tree taxa of the modern European mesic temperate broad-leaved deciduous forests; see Olson et al., 2001). Macrofossil evidence is yet missing for LGM mesophilous temperate deciduous tree survival in the CB, CM and adjacent regions (Tzedakis et al., 2013), but several Lateglacial and MIS 3 pollen studies argue that some of these tree species likely survived in the CB and CM (Willis et al., 1995; Feurdean et al., 2007, 2012; Jankovská and Pokorny, 2008;Magyari et al., 2010). As shown in Fig. 9 and Supplementary Fig. 2 the composite percentage pollen curve of mesophilous temperate deciduous tree taxa is continuous at our East Carpathian mid-mountain site (Lake St Anne, SZA) during the LPG, while the low-altitude Fehér Lake (FT)and Nagymohos (NM) records show only sporadic presence of mesophilous temperate deciduous trees after 22 ka cal BP. At Lake St Anne we demonstrated the near-continuous presence of *Quercus*, *Ulmus*, *Corylus*, *Fagus*, *F. excelsior*, intermittent presence of *C. betulus* and sporadic presence of *Tilia*, *Acer* and *C. orientalis* pollen even after 22 ka cal BP suggesting likely regional persistence of *Quercus*, *Ulmus*, *Corylus*, *Fagus*, *F. excelsior* at 46° N in the CM during the LGM. Although long-distance pollen transport and redeposition cannot be excluded in case of low pollen abundances, similar low values (usually less than or around 1–2%) are recorded in the Balkan sites during the LGM, with the exception of *Quercus* and *Corylus* (e.g. Allen et al., 1999; Tzedakis et al., 2002; Tzedakis, 2004; Panagiotopoulos et al., 2013). In the Balkans the presence of the mesophilous temperate deciduous tree refugia is also supported by high genetic diversity and area specific haplotypes in the genetic records (Hewitt, 2000; Palmé and Vendramin, 2002; Petit et al., 2002; Heuertz et al., 2004; Magri et al., 2006). Moreover, northerly glacial refugia have also been proposed for *Corylus avellana*, *F. sylvatica*, *F. excelsior* and *Fraxinus angustifolia* (*F. excelsior* type pollen) based on the results of phylogeographic studies (Palmé and Vendramin, 2002; Magri et al., 2006, 2008; Temunović et al., 2012), which supports survival of these taxa north of the Balkan Peninsula, in concert with our pollen data. Although this question has to be studied thoroughly via systematic mapping of the postglacial first detection and expansion times of each mesophilous temperate deciduous tree pollen type in this area, the available pollen and genetic data seem to support that some species belonging to the genera *Quercus*, *Ulmus*, *Corylus*, *Fagus* and *Fraxinus* survived the LPG including the LGM in the CM, but did not contribute to the mainstream of postglacial mass expansions, and thus have remained invisible or hardly detectable in the phylogeographic records. Some chloroplast and PCR-RFLP haplotype maps indicate area-specific haplotypes in the CM that are either not interpreted in the publications or interpreted as possible proofs of eastern refuges without colonization from these sources (Palmé and Vendramin, 2002; Heuertz et al., 2004; Magri et al., 2006).

In a recent review based on a comprehensive number of LPG pollen and plant macrofossil records from Europe, Tzedakis et al. (2013) concluded that mesophilous temperate deciduous trees were absent north of 45° N during the LGM, i.e. these species reached only the SW fringe of the Carpathians and the Pannonian Basin, but not our study sites (Fig. 1). This inference is in apparent contradiction with the evidence based on pollen data in this study. One condition mentioned by Tzedakis et al. (2013) as convincing evidence for LGM survival of mesophilous temperate deciduous trees was the quasi-continuous pollen percentage curves through the LPG followed by increases at the onset of the Lateglacial interstadial. Although pollen data are not shown in this study for the Lateglacial interstadial (FT and NM do not reach into this interval), Lake St Anne (Magyari et al., 2014) and several other Lateglacial pollen records from the CB and CM do indeed show increases in mesophilous temperate deciduous tree pollen frequencies (e.g. *Ulmus*, *Quercus*, *Corylus*, *Tilia*) at the onset of the Lateglacial supporting the notion of general LPG presence in the region.

LGM niche models that use the LMDZHR climate simulation infer presence of several mesophilous temperate deciduous taxa in the CB (e.g. *T. cordata*, *U. laevis*, *U. glabra*, *Q. robur*; Svenning et al., 2008), in the southern foothills of the CM, but not in the CM. These data first of all suggest that LGM climate alone was not limiting mesophilous temperate deciduous tree growth in the CB. Second, the simulation results are in apparent contradiction with our pollen data that generally indicate higher pollen representation of the mesophilous temperate deciduous tree taxa in the CM during the LGM, while our pollen records suggest regional presence of some mesophilous deciduous trees or shrubs (mainly *Corylus*) in the lowland river valleys until 22 ka cal BP, but less likely after 22 ka cal BP. One plausible explanation of this mismatch is the strong impact of low CO_2 levels via evaporative water loss, which was likely limiting mesophilous deciduous tree growth in the lowlands that received around 360 mm of annual precipitation against the more humid mid-mountains, where annual precipitation was ~500 mm (based on the LMDZHR and CCSM3 simulations, Jost et al., 2005; Strandberg et al., 2011).

The fact that mesophilous deciduous tree pollen types were more frequent in the topographically diverse East Carpathians than in the lowland sites of the Carpathian Basin supports the original idea of Bennett et al. (1991) that mid-altitude sites were better suited in sustaining refugial temperate tree populations due to the effect of orographic precipitation.

6. Conclusions

In this study we presented three LPG pollen records from the Carpathian Basin and adjoining East Carpathian Mountains. We compared the fossil pollen assemblages with surface pollen spectra from the Altai-Sayan Mountains in southern Siberia using ordination and modern analogue techniques combined with ROC analysis in order to characterize LPG vegetation composition and find the best analogues of the LPG vegetation. The most important conclusions can be summarized as follows:

1) Although we found several statistically significant analogues, a large amount of non-analogue samples suggest that LPG vegetation and landscape is only marginally similar to modern vegetation and landscape in southern Siberia. This non-analogue situation has to be taken into account when Siberian surface pollen data are used for quantitative climate reconstruction, because non-analogue vegetation may lead to biases in the inferred climate.

2) A comparison with Siberian pollen samples indicates that trees are overrepresented in surface pollen samples of the steppe and forest-steppe landscapes, and they are likely also over-represented in the fossil pollen spectra from the Late Pleniglacial.

3) LPG landscapes in the Carpathian Basin lowlands were likely dominated by dry steppe that occurred outside the river flood-plains, while wet and mesic grasslands occurred in the river floodplains and other sites influenced by ground water. This mosaic of different grassland types was potentially productive enough to sustain a large herbivore fauna even during the LGM.

Forest patches or scattered trees probably also occurred in the Carpathian Basin in river valleys, on north-facing hillslopes, and at moister sites of the loess plateaus. These forest stands were dominated by boreal and cool temperate tree and shrub species (*Larix*, *P. sylvestris*, *P. mugo*, *P. cembra*, *P. abies*, *B. pendula/pubescens*, *B. nana*, *Juniperus*, *H. rhamnoides*, *Populus*, *Salix* and *Alnus*).

4) The LGM climatic models for the Carpathian Basin do not explain the absence of mesophilous temperate trees; proxy-derived and modelled LGM climatic parameters are within the climatic range of several mesophilous trees. Despite the potential habitat suitability in the CB, the pollen records suggested uninterrupted regional presence of mesophilous temperate deciduous trees only in the Carpathian Mountains, where persistence of *Quercus*, *Ulmus*, *Corylus*, *Fagus*, *F. excelsior* was inferred throughout the LPG. However, these findings can only be interpreted in terms of local survival if confirmed by plant macrofossils dated to the LGM, which are still missing. Nonetheless, most likely areas of mesophilous temperate deciduous tree survival are expected in moist mesoclimate of mid-elevation slopes in the Carpathians.

5) The character of the LGM landscape fundamentally differed from the MIS 3 and Lateglacial landscapes. The most characteristic features of the LGM ecosystems were the increasing cover of grasses against other herbs.

Acknowledgements

Appendix A. Supplementary data

Supplementary data related to this article can be found at http://dx.doi.org/10.1016/j.quascirev.2014.04.020.

References

Agakhanyants, O.Ye, 1981. Aridnye Gory SSSR (Arid Mountains of the USSR). Mysl, Moscow, p. 270 (in Russian).

Allen, J.R.M., Brandt, U. Brauer, A., Hubberten, H.W., Huntley, B., 1999. Rapid environmental changes in southern Europe during the last glacial period. Nature 400, 740–743.

Allen, J.R.M., Hickler, T., Singarayer, J.S., Sykes, M.T., Valdes, P.J., Huntley, B., 2010. Last glacial vegetation of northern Eurasia. Quat. Sci. Rev. 29, 2604–2618.

Andrič, M., Massaferro, J., Eicher, U., Ammann, B., Leuenberger, M.C., Martinčič, A., Marinova, E., Brancelj, A., 2009. A multi-proxy Late-glacial palaeoenvironmental record from Lake Bled, Slovenia. Hydrobiologia 631, 121–141.

Barati, S., Hudák, K., Nagy, D., Boldogh, S., Szmorad, F., 1999. A Keleméri Mohostavak TT természetvédelmi kezelési terve. Aggteleki Nemzeti Park igazgatóság, Jósvafő, p. 63.

Bennett, K.D., Tzedakis, P.C., Willis, K.J., 1991. Quaternary refugia of north European trees. J. Biogeogr. 18, 103–115.

Bennett, K.D., 2007. Psimpoll Manual. http://www.chrono.qub.ac.uk/psimpoll/psimpoll-faq.html (accessed 12.11.13).

Bennett, K.D., Willis, K.J., 2001. Pollen. In: Smol, J.P., Birks, H.J.B., Last, W.M. (Eds.), Tracking Environmental Change Using Lake Sediments, Terrestrial, Algal and Siliceous Indicators, vol. 3. Kluwer Academic Publishers, Dordrecht, The Netherlands, pp. 5–32.

Beug, H.-J., 2004. Leitfaden der Pollenbestimmung für Mitteleuropa und angrenzende Gebiete. Verlag Dr. Friedrich Pfeil, München, p. 542.

Bhagwat, S.A., Willis, K.J., 2008. Species persistence in northerly glacial refugia of Europe: a matter of chance or biogeographical traits? J. Biogeogr. 35, 464–482.

Birks, H.J.B., Willis, K.J., 2008. Alpines, trees, and refugia in Europe. Plant Ecol. Divers. 1, 147–160.

Borhidi, A., Kevey, B., Lendvai, G., 2012. Plant Communities of Hungary. Akadémiai Kiadó, Budapest, p. 544.

Bradák, B., Thamó-Bozsó, E., Kovács, J., Márton, E., Csillag, G., Horváth, E., 2010. Characteristics of Pleistocene climate cycles identified in Cérna Valley loess-paleosol section (Vértesacsa, Hungary). Quat. Int. 234, 86–97.

Buczkó, K., Magyari, E., Bitušík, P., Wacnik, A., 2009. Review of dated Late Quaternary palaeolimnological records in the Carpathian region, East Central Europe. Hydrobiologia 631, 3–28.

Chytrý, M., Danihelka, J., Kubešová, S., Lustyk, P., Ermakov, N., Hájek, M., Hájková, P., Kočí, M., Otýpková, Z., Roleček, J., Řezníčková, M., Šmarda, P., Valachovič, M., Popov, D., Pišút, I., 2008. Diversity of forest vegetation across a strong gradient of climatic continentality: Western Sayan Mountains, southern Siberia. Plant Ecol. 196, 61–83.

Chytrý, M., Ermakov, N., Danihelka, J., Hájek, M., Hájková, P., Horsák, M., Kočí, M., Kubešová, S., Lustyk, P., Otýpková, Z., Pelánková, B., Valachovič, M., Zelený, D., 2012. High species richness in hemiboreal forests of the northern Russian Altai, southern Siberia. J. Veg. Sci. 23, 605–616.

Clark, R.L., 1982. Point count estimation of charcoal in pollen preparations and thin sections in sediments. Pollen Spores 24, 523–535.

Clark, P.U., Dyke, A.S., Shakun, J.D., Carlson, A.E., Clark, J., Wohlfarth, B., Mitrovica, J.X., Hostetler, S.W., McCabe, A.M., 2009. The Last Glacial Maximum. Science 325 (5941), 710–714.

Cowling, S.A., Sykes, M.T., 1999. Physiological significance of low atmospheric CO_2 for plant-climate interactions. Quat. Res. 52, 237–242.

Damblon, F., Haesaerts, P., 2002. Anthracology and radiochronology of the Upper Pleistocene in the loessic areas of Eurasia. In: Thiébault, S. (Ed.), Charcoal Analysis. Methodological Approaches, Palaeoecological Results and Wood Uses. Proc. 2nd International Meeting of Anthracologists, Paris, September 2000, BAR International Series 1063, pp. 65–71.

Daniau, A.L., Harrison, S.P., Bartlein, P.J., 2010. Fire regimes during the last glacial. Quat. Sci. Rev. 29, 2918–2930.

Davis, B.A.S., Zanon, M., Collins, P., Mauri, A., Bakker, J., Barboni, D., Barthelmes, A., Beaudouin, C., Bjune, A.E., Bozilova, E., Bradshaw, R.H.W., Brayshay, B.A., Brewer, S., Brugiapaglia, E., Bunting, J., Connor, S.E., de Beaulieu, J.L., Edwards, K., Ejarque, A., Fall, P., Florenzano, A., Fyfe, R., Galop, D., Giardini, M., Giesecke, T., Grant, M.J., Guiot, J., Jahns, S., Jankovska, V., Juggins, S., Kahrmann, M., Karpinska-Kołaczek, M., Kołaczek, P., Kühl, N., Kuneš, P., Lapteva, E.G., Leroy, S.A.G., Leydet, M., Lopez Saez, J.A., Masi, A., Matthias, I., Mazier, F., Meltsov, V., Mercuri, A.M., Miras, Y., Mitchell, F.J.G., Morris, J.L., Naughton, F., Nielsen, A.B., Novenko, E., Odgaard, B., Ortu, E., Overballe-Petersen, M.V., Pardoe, H.S., Peglar, S.M., Pidek, I.A., Sadori, L., Seppä, H., Severova, E., Shaw, H., Swięta-Musznicka, J., Theuerkauf, M., Tonkov, S., Veski, S., van der Knaap, W.O., van Leeuwen, J.F.N., Woodbridge, J., Zimny, M., Kaplan, J.O., 2013. The European modern pollen database (EMPD) project. Veg. Hist. Archaeobot. 22, 521–530.

Ermakov, N., Dring, J., Rodwell, J., 2000. Classification of continental hemiboreal forests of North Asia. Braun-Blanquetia 28, 1–131.

Eurola, S., Hicks, S., Kaakinen, E., 1984. Key to Finnish mire types. In: Moore, P.D. (Ed.), European Mires. Academic Press, London, pp. 11–117.

Faegri, K., Iversen, J., 1989. Textbook of Pollen Analysis. John Wiley & Sons, Chichester, p. 237.

Feurdean, A., Wohlfarth, B., Björkman, L., Tantau, I., Bennike, O., Willis, K.J., Farcas, S., Robertsson, A.M., 2007. The influence of refugial population on Lateglacial and early Holocene vegetational changes in Romania. Rev. Palaeobot. Palynol. 145, 305–320.

Feurdean, A., Tămaş, T., Tanţău, I., Fărcaş, S., 2012. Elevational variation in regional vegetation responses to late-glacial climate changes in the Carpathians. J. Biogeogr. 39, 258–271.

Fletcher, W.J., Sánchez Goñi, M.F., Allen, J.R.M., Cheddadi, R., Coumbourieu-Nebout, N., Huntley, B., Lawson, I.T., Londeix, L., Magri, D., Margari, V., Müller, U.C., Naughton, F., Novenko, E., Roucoux, K.H., Tzedakis, P.C., 2010. Millennial-scale variability during the last glacial in vegetation records from Europe. Quat. Sci. Rev. 29, 2839–2864.

Frenzel, B., Pécsi, M., Velichko, A.A., 1992. Atlas of Paleoclimates and Paleoenvironments of the Northern Hemisphere. Geographical Research Institute and Gustav Fischer Verlag, p. 153.

Gerasimenko, N., 2006. Upper Pleistocene loess-palaeosol and vegetational successions in the Middle Dnieper Area, Ukraine. Quat. Int. 149, 55–66.

Grootes, P.M., Stuiver, M., White, J.W.C., Johnsen, S.J., Jouzel, J., 1993. Comparison of oxygen isotope records from the GISP2 and GRIP Greenland ice cores. Nature 366, 552–554.

Haesaerts, P., Borziac, I., Chekha, V.P., Chirica, V., Drozdov, N.I., Koulakovska, L., Orlova, L.A., van der Plicht, J., Damblon, F., 2010. Charcoal and wood remains for radiocarbon dating Upper Pleistocene loess sequences in Eastern Europe and Central Siberia. Palaeogeogr. Palaeoclimatol. Palaeoecol. 291, 106–127.

Harrison, S.P., Prentice, I.C., 2003. Climate and CO_2 controls on global vegetation distribution at the last glacial maximum: analysis based on palaeovegetation data, biome modelling and palaeoclimate simulations. Glob. Change Biol. 9, 983–1004.

Harrison, S.P., Bartlein, P.J., 2012. Records from the past, lessons for the future: what the palaeorecord implies about mechanisms of global change. In: Henderson-Sellers, A., McGuffie, K. (Eds.), The Future of the World's Climates. Elsevier, Amsterdam, Oxford, pp. 403–436.

Heuertz, M., Fineschi, S., Anzidei, M., Pastorelli, R., Salvini, D., Paule, L., Frascaria-Lacoste, N., Hardy, O.J., Vekemans, X., Vendramin, G.G., 2004. Chloroplast DNA variation and postglacial recolonization of common ash (*Fraxinus excelsior* L.) in Europe. Mol. Ecol. 13, 3437–3452.

Hewitt, G., 2000. The genetic legacy of the Quaternary ice ages. Nature 405, 907–913.

Hicks, S., 2001. The use of annual arboreal pollen deposition values for delimiting tree-lines in the landscape and exploring models of pollen dispersal. Rev. Palaeobot. Palynol. 117, 1–29.

Horsák, M., Chytrý, M., Pokryszko, B.M., Danihelka, J., Ermakov, N., Hájek, M., Hájková, P., Kintrová, K., Kočí, M., Kubešová, S., Lustyk, P., Otýpková, Z., Pelánková, B., Valachovič, M., 2010. Habitats of relict terrestrial snails in southern Siberia: lessons for the reconstruction of palaeoenvironments of full-glacial Europe. J. Biogeogr. 37, 1450–1462.

Höhn, M., Gugerli, F., Abran, P., Bisztray, Gy, Buonamici, A., Cseke, K., Hufnagel, L., Quintela-Sabarís, C., Sebastiani, F., Vendramin, G.G., 2009. Variation in the chloroplast DNA of Swiss stone pine (*Pinus cembra* L.) reflects contrasting post-glacial history of populations from the Carpathians and the Alps. J. Biogeogr. 36, 1798–1806.

Hudák, K., 2008. A keleméri Mohos-tavak vízgyüjtő területének vegetációja és edényes flórája (Vegetation and vascular plants in the water catchment area of the Mohos lakes and Kelemér). In: Boldogh, S.G., Farkas, T. (Eds.), A keleméri Mohos-tavak: Kutatás, kezelés, védelem (The Mohos Peat Bogs in Kelemér: Research, Conservation, Management). Aggteleki Nemzeti Park Igazgatóság, Jósvafő, pp. 111–126.

Huntley, B., 1993. Rapid early-Holocene migration and high abundance of hazel (*Corylusavellana* L.): alternative hypotheses. In: Chambers, F.M. (Ed.), Climate Change and Human Impact on the Landscape. Chapman & Hall, London, pp. 205–215.

Huntley, B., Birks, H.J.B., 1983. An Atlas of Past and Present Pollen Maps for Europe 0–13000 Years Ago. Cambridge University Press, Cambridge, p. 667.

Jakab, G. (Ed.), 2012. A Körös-Maros Nemzeti Park növényvilága (The Flora of the Körös-Maros National Park). Szarvas, Körös-Maros Nemzeti Park Igazgatóság, p. 416 (in Hungarian).

Jakab, G., Magyari, E., Rudner, Z.E., Sümegi, P., 1998. A keleméri Nagy-Mohos tó fosszilis mohaflórája. Kitaibelia 3 (2), 353–354 (in Hungarian).

Jankovská, V., Chromý, P., Nižnianská, M., 2002. Šafárka – first palaeobotanical data of the character of Last Glacial vegetation and landscape in the West Carpathians (Slovakia). Acta Palaeobot. 42, 39–50.

Jankovská, V., Pokorný, P., 2008. Forest vegetation of the last full-glacial period in the Western Carpathians (Slovakia and Czech Republic). Preslia 80, 307–324.

Jánossy, D., 1986. Pleistocene Vertebrate Faunas of Hungary. Elsevier, Amsterdam, p. 206.

Járai-Komlódi, M., 1991. Late Pleistocene vegetation history in Hungary since the last interglacial. In: Pécsi, M., Schweitzer, F. (Eds.), Quaternary Environments in Hungary, Studies in Geography in Hungary, vol. 26. Akadémiai Kiadó, Budapest, pp. 35–46.

Jost, A., Lunt, D., Kageyama, M., Abe-Ouchi, A., Peyron, O., Valdes, P.J., Ramstein, G., 2005. High-resolution simulations of the last glacial maximum climate over Europe: a solution to discrepancies with continental palaeoclimatic reconstructions. Clim. Dyn. 24, 577–590.

Kageyama, M., Laîné, A., Abe-Ouchi, A., Braconnot, P., Cortijo, E., Crucifix, M., de Vernal, A., Guiot, J., Hewitt, C.D., Kitoh, A., Kucera, M., Marti, O., Ohgaito, R., Otto-Bliesner, B., Peltier, W.R., Rosell-Melé, A., Vettoretti, G., Weber, S.L., Yu, Y., MARGO Project Members, 2006. Last Glacial Maximum temperatures over the North Atlantic, Europe and western Siberia: a comparison between PMIP models, MARGO sea-surface temperatures and pollen-based reconstructions. Quat. Sci. Rev. 25, 2082–2102.

Kakas, J., 1960. Magyarország éghajlati atlasza (Climatological Map of Hungary). Akadémiai Kiadó, Budapest.

Karátson, D., Telbisz, T., Harangi, Sz., Magyari, E., Dunkl, I., Kiss, B., Jánosi, Cs., Veres, D., Braun, M., Fodor, E., Biró, T., Kósik, Sz., von Eynatten, H., Lin, D., 2013. Morphometrical and geochronological constraints on the youngest eruptive activity in East-Central Europe at the Ciomadul (Csomád) lava dome complex, East Carpathians. J. Volcanol. Geotherm. Res. 255, 43–56.

Kovács, J., Moravcová, M., Újvári, G., Pintér, A.G., 2012. Reconstructing the paleoenvironment of East Central Europe in the Late Pleistocene using the oxygen and carbon isotopic signal of tooth in large mammal remains. Quat. Int. 276–277, 145–154.

Kotlík, P., Deffontaine, V., Mascheretti, S., Zima, J., Michaux, J.R., Searle, J.B., 2006. A northern glacial refugium for bank voles (Clethrionomys glareolus). Proc. Natl. Acad. Sci. U. S. A. 103, 14860–14864.

Kristó, A., 1995. A Csomád hegycsoport. A Szent Anna-tó természetvédelmi területe (The Ciomadul Mountains. The Nature Conservation Area of Lake St Anne). In: Papp, Á., Szíjártó, I. (Eds.), Kristó András emlékére (In Memorian András Kristó). Balaton Akadémia Könyvek 13, Vörösberény, Budapest, pp. 1–17.

Kuneš, P., Pelánková, B., Chytrý, M., Jankovská, V., Pokorný, P., Petr, L., 2008. Interpretation of the last-glacial vegetation of eastern-central Europe using modern analogues from southern Siberia. J. Biogeogr. 35, 2223–2236.

Kuminova, A.V., 1960. Rastitel'nyi pokrov Altaya (Plant Cover of the Altai). SO AN SSSR, Novosibirsk, p. 450 (in Russian).

Liu, H., Wang, Y., Tian, Y., Zhu, J., Wang, H., 2006. Climatic and anthropogenic control of surface pollen assemblages in East Asian steppes. Rev. Palaeobot. Palynol 138, 281–289.

Magri, D., Vendramin, G.G., Comps, B., Dupanloup, I., Geburek, T., Gomory, D., Latalowa, M., Litt, T., Paule, L., Roure, J.M., Tantau, I., Van Der Knaap, W.O.,

Petit, R.J., De Beaulieu, J.L., 2006. A new scenario for the Quaternary history of European beech populations: palaeobotanical evidence and genetic consequences. New. Phytol. 171, 199–221.

Magyari, E., Jakab, G., Rudner, E., Sümegi, P., 1999. Palynological and plant macrofossil data on Late Pleistocene short-term climatic oscillations in NE-Hungary. Acta Palaeobot. (Suppl. 2), 491–502.

Magyari, E., Jakab, G., Sümegi, P., Rudner, E., Molnár, M., 2000. Paleoökológiai vizsgálatok a keleméri Mohos-tavakon (Palaeoecological examinations at Kelemér Mohos lakes). In: Szurdoki, E. (Ed.), Tőzegmohás élőhelyek Magyarországon: kutatás, kezelés, védelem, (Peat Bog Habitats in Hungary: Research, Conservation, Management) CEEWEB Munkacsoport (Workshop), Miskolc, pp. 101–131.

Magyari, E., Sümegi, P., Braun, M., Jakab, G., Molnár, M., 2001. Retarded wetland succession: anthropogenic and climatic signals in a Holocene peat bog profile from the NE Carpathian Basin. J. Ecol. 89, 1019–1032.

Magyari, E.K., Buczkó, K., Jakab, G., Braun, M., Pál, Z., Karátson, D., 2009. Palaeolimnology of the last crater lake in the Eastern Carpathian Mountains - a multiproxy study of Holocene hydrological changes. Hydrobiologia 631, 29–63.

Magyari, E.K., Chapman, J.C., Passmore, D.G., Allen, J.R.M., Huntley, J.P., Huntley, B., 2010. Holocene persistence of wooded steppe in the Great Hungarian Plain. J. Biogeogr. 37, 915–935.

Magyari, E.K., Veres, D., Wennrich, V., Wagner, B., Braun, M., Karátson, D., Pál, Z., Ferenczy, Gy, St-Ogne, G., Rethmayer, J., Francois, J.-P., von Reumont, F., Schäbitz, F., 2014. Vegetation and environmental responses to climate forcing during the last glacial maximum and deglaciation in the East Carpathians: attenuated response to maximum cooling and increased biomass burning. Quat. Sci. Rev. (submitted for publication).

Matus, G., Molnár, A., Vidéki, R., Less, N., 2000. A Keleméri Mohosok flórája és vegetációja (Flora and Vegetation of the Kelemér Mohos-mires). In: Szurdoki, E. (Ed.), Tőzegmohás élőhelyek hazánkban: kutatás, kezelés, védelem CEEWEB Munkacsoport, Miskolc, pp. 69–87.

Monin, E., Indermuhle, A., Dallenbach, A., Fluckiger, J., Stauffer, B., Stocker, T.F., Raynaud, D., Barnola, J.-M., 2001. Atmospheric CO_2 concentrations over the last glacial termination. Science 291, 112–114.

Moore, P.D., Webb, J.A., Collinson, M.E., 1992. Pollen Analysis, second ed. Blackwell Scientific Publications, Oxford, p. 216.

Müller, U.C., Pross, J., Bibus, E., 2003. Vegetation response to rapid climate change in Central Europe during the past 140,000 yr based on evidence from the Füramoos pollen record. Quat. Res. 59, 235–245.

Oksanen, J., Blanchett, F.G., Kindt, R., Legendre, P., Minchin, P.R., O'Hara, R.B., Simpson, G.L., Sólymos, P., Stevens, M.H.M., Wagner, H., 2012. Vegan: Community Ecology Package. R Package 2.0.3 Downloaded from. http://CRAN.R-project.org/package=vegan on 9 May 2012.

Olson, D.M., Dinerstein, E., Wikramanayake, E.D., Burgess, N.D., Powell, G.V.N., Underwood, E.C., D'Amico, J.A., Itoua, I., Strand, H.E., Morrison, J.C., Loucks, C.J., Allnutt, T.F., Ricketts, T.H., Kura, Y., Lamoreux, J.F., Wettengel, W.W., Hedao, P., Kassem, K.R., 2001. Terrestrial ecoregions of the world: a new map of life on Earth. Bioscience 51 (11), 933–938.

Pál, Z., 2000. A Szent Anna Tó: következtetések a tó mélységét és feltöltodését illetoen (Lake St Anne: inferences regarding water depth and sediment accummulation rates). Coll. Geogr 1, 65–74.

Palmé, A.E., Vendramin, G.G., 2002. Chloroplast DNA variation, postglacial recolonization and hybridization in hazel, Corylusavellana. Mol. Ecol. 11 (9), 1769–1779.

Palmé, A.E., Su, Q., Rautenberg, A., Manni, F., Lascoux, M., 2003. Postglacial recolonization and cpDNA variation of silver birch, *Betula pendula*. Mol. Ecol. 12, 201–212.

Panagiotopoulos, K., Böhm, A., Leng, M.J., Wagner, B., Schäbitz, F., 2013. Climate variability since MIS 5 in SW Balkans inferred from multiproxy analysis of Lake Prespa sediments. Clim. Past Discuss. 9, 1321–1362.

Pazonyi, P., 2004. Mammalian ecosystem dynamics in the Carpathian Basin during the last 27,000 years. Palaeogeogr. Palaeoclimatol. Palaeoecol. 212 (3–4), 295–314.

Pazonyi, P., 2011. Palaeoecology of Late Pliocene and Quaternary mammalian communities in the Carpathian Basin. Acta Zool. Cracoviensia Ser. A Vertebr. 54 (1–2), 1–32.

Pelánková, B., Kuneš, P., Chytrý, M., Jankovská, V., Ermakov, N., Svobodová-Svitavská, H., 2008. The relationships of modern pollen spectra to vegetation and climate along a steppe–forest–tundra transition in southern Siberia, explored by decision trees. Holocene 18, 1259–1271.

Pelánková, B., Chytrý, M., 2009. Surface pollen-vegetation relationships in the forest-steppe, taiga and tundra landscapes of the Russian Altai Mountains. Rev. Palaeobot. Palynol. 157, 253–265.

Peltier, W.R., Fairbanks, R.G., 2006. Global glacial ice volume and Last Glacial Maximum duration from an extended Barbados sea level record. Quat. Sci. Rev. 25, 3322–3337.

Petit, R.J., Brewer, S., Bordács, S., Burg, K., Cheddadi, R., Coart, E., Cottrell, J., Csaikl, U.M., van Dam, B.C., Deans, J.D., Espinel, S., Fineschi, S., Finkeldey, R., Glaz, I., Goicoechea, P.G., Jensen, J.S., König, A.O., Lowe, A.J., Madsen, S.F., Mátyás, G., Munro, R.C., Popescu, F., Slade, D., Tabbener, H., de Vries, S.M.G., Ziegenhagen, B., de Beaulieu, J.-L., Kremer, A., 2002. Identification of refugia and postglacial colonization routes of European white oaks based on chloroplast DNA and fossil pollen evidence. For. Ecol. Manag. 156, 49–74.

Peyron, O., Guiot, J., Cheddadi, R., Tarasov, P., Reille, M., Beaulieu, J.L., Bottema, S., Andrieu, V., 1998. Climatic reconstruction in Europe for 18,000 yr B.P. from pollen data. Quat. Res. 49, 183–196.

Peyron, O., Bégeot, C., Brewer, S., Heiri, O., Magny, M., Millet, L., Ruffaldi, P., Van Campo, E., Yu, G., 2005. Late-Glacial climatic changes in Eastern France (Lake Lautrey) from pollen, lake-levels, and chironomids. Quat. Res. 64, 197–211.

Provan, J., Bennett, K.D., 2008. Phylogeographic insights into cryptic glacial refugia. Trends Ecol. Evol. 23, 564–571.

R Core Team, 2012. R: a Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL. http://www.R-project.org/.

Ramstein, G., Kageyama, M., Guiot, J., Wu, H., Hély, C., Krinner, G., Brewer, S., 2007. How cold was Europe at the Last Glacial Maximum? A synthesis of the progress achieved since the first PMIP model-data comparison. Clim. Past 3, 331–339.

Reille, M., 1992. Pollen et spore D'Europe et D'Afrique du Nord. Laboratorie de Botanique Historique et Palynologie Marseille, France, p. 520.

Reille, M., 1995. Pollen et spore D'Europe et D'Afrique du Nord. Supplement 1. Laboratorie de Botanique Historique et Palynologie Marseille, France, p. 327.

Reille, M., 1998. Pollen et spore D'Europe et D'Afrique du Nord. Supplement 2. Laboratorie de Botanique Historique et Palynologie Marseille, France, p. 521.

Rudner, Z.E., Sümegi, P., 2001. Recurring taiga forest-steppe habitats in the Carpathian Basin in the Upper Weichselian. Quat. Int. 76/77, 177–189.

Schmitt, T., 2007. Molecular biogeography of Europe: Pleistocene cycles and Postglacial trends. Front. Zool. 4, 11.

Schmitt, T., 2009. Biogeographical and evolutionary importance of the European high mountain systems. Front. Zool. 6, 9.

Schmitt, T., Varga, Z., 2012. Extra-Mediterranean refugia: the rule and not the exception? Front. Zool. 9, 22.

Simpson, G., 2007. Analogue methods in palaeoecology: using the analogue package. J. Stat. Softw. 22, 1–29.

Simpson, G.L., 2012. Analogue methods in palaeolimnology. In: Birks, H.J.B., Lotter, A.F., Juggins, S., Smol, J.P. (Eds.), Tracking Environmental Change Using Lake Sediments, Data Handling and Numerical Techniques, vol. 5. Springer, Dordrecht, pp. 495–522.

Sommer, R.S., Nadachowski, A., 2006. Glacial refugia of mammals in Europe: evidence from fossil records. Mammal. Rev. 36, 251–265.

Starnberger, R., Terhorst, B., Rähle, W., Peticzka, R., Haas, J.N., 2009. Palaeoecology of Quaternary periglacial environments during OIS-2 in the forefields of the Salzach Glacier (Upper Austria). Quat. Int. 198, 51–61.

Stieber, J., 1967. A magyarországi felsőpleisztocén vegetációtörténete anthrakotómiai eredmények (1957-ig) tükrében. Földtani Közlöny 97 (3), 305–317 (in Hungarian).

Stockmarr, J., 1971. Tablets with spores used in absolute pollen analysis. Pollen Spores 13, 614–621.

Strandberg, G., Brandefelt, J., Kjellström, E., Smith, B., 2011. High-resolution regional simulation of last glacial maximum climate in Europe. Tellus 63A, 107–125.

Sugita, S., 2007. Theory of quantitative reconstruction of vegetation I. Pollen from large sites REVEALS regional vegetation composition. Holocene 17, 229–241.

Sümegi, P., 2005. Loess and Upper Paleolithic Environment in Hungary. Aurea Kiadó, Nagykovácsi, p. 312.

Sümegi, P., Magyari, E., Dániel, P., Hertelendi, E., Rudner, E., 1999. A kardoskúti Fehér-tó negyedidőszaki fejlődéstörténetének rekonstrukciója (A reconstruction of the Quaternary geohistory of Fehér lake at Kardoskút). Földtani Közlöny 129 (4), 479–519.

Sümegi, P., Krolopp, E., 2002. Quarter malacological analyses for modeling of the Upper Weichselian palaeoenvironmental changes in the Carpathian Basin. Quat. Int. 91, 53–63.

Sümegi, P., Gulyás, S., Persaits, G., Szelepcsényi, Z., 2012a. Long environment change in the forest steppe habitat of the Great Hungarian Plain based on paleoecological data. In: Rakonczai, J., Ladányi, Zs (Eds.), Review of Climate Change Research Program at the University of Szeged (2010–2012). Institute of Geography and Geology, University of Szeged, pp. 7–24.

Sümegi, P., Persaits, G., Gulyás, S., 2012b. Woodland-grassland ecotonal shifts in environmental mosaics: lessons learnt from the environmental history of the Carpathian Basin (Central Europe) during the Holocene and the last ice age based on investigation of paleobotanical and mollusk remains. In: Myster, R.W. (Ed.), Ecotones between Forest and Grassland. Springer-Verlag, New York, pp. 13–37.

Sümegi, P., Magyari, E., Dániel, P., Molnár, M., Törőcsik, T., 2013. Responses of terrestrial ecosystems to Dansgaard-Oeshger cycles and Heinrich-events: a 28,000-year record of environmental changes from SE Hungary. Quat. Int. 293, 34–50.

Svenning, J.-C., Normand, S., Kageyama, M., 2008. Glacial refugia of temperate trees in Europe: insights from species distribution modelling. J. Ecol. 96, 1117–1127.

Szász, G., Tőkei, L., 1997. Meteorológia mezőgazdáknak, kertészeknek, erdészeknek. Mezőgazda Kiadó, Budapest, p. 722 (in Hungarian).

Temunović, M., Franjić, J., Satovic, Z., Grgurev, M., Frascaria-Lacoste, N., Fernández-Manjarrés, J.F., 2012. Environmental Heterogeneity explains the genetic structure of Continental and mediterranean populations of *Fraxinus angustifolia* Vahl. PLoS ONE 7 (8), e42764.

Tzedakis, P.C., 2004. The Balkans as prime glacial refugial territory of European temperate trees. In: Griffiths, H.I., Krystufek, B., Reed, J.M. (Eds.), Balkan Biodiversity. Pattern and Process in the European Hotspot. Kluwer, Dordrecht, pp. 49–68.

Tzedakis, P.C., Lawson, I.T., Frogley, M.R., Hewitt, G.M., Preece, R.C., 2002. Buffered tree population changes in a quaternary refugium: evolutionary implications. Science 297, 2044–2047.

Tzedakis, P.C., Emerson, B.C., Hewitt, G.M., 2013. Cryptic or mystic? Glacial tree refugia in northern Europe. Trends Ecol. Evol. 28, 696–704.

Varga, Z., 2010. Extra-Mediterranean refugia, post-glacial vegetation history and area dynamics in Eastern Central Europe. In: Habel, J.C., Assmann, T. (Eds.), Relict Species: Phylogeography and Conservation Biology. Springer, Heidelberg, pp. 57–87.

Varsányi, I., Palcsu, L., Kovács, LÓ., 2011. Groundwater flow system as an archive of palaeotemperature: noble gas, radiocarbon, stable isotope and geochemical study in the Pannonian Basin, Hungary. Appl. Geochem. 26, 91–104.

Walker, D.A., Gould, W.A., Maier, H.A., Raynolds, M.K., 2002. The Circumpolar Arctic vegetation map: AVHRR-derived base maps, environmental controls, and integrated mapping procedures. Int. J. Remote Sens. 23 (21), 4551–4570.

Wang, B.Y., Song, C.Q., Sun, X.J., 1996. Study on surface pollen in middle Inner Mongolia, China. Acta Bot. Sin. 38, 902–909 (in Chinese).

Willis, K.J., 1994. The vegetational history of the Balkans. Quat. Sci. Rev. 13, 769–788.

Willis, K.J., Sümegi, P., Braun, M., Tóth, A., 1995. The Late Quaternary environmental history of Bátorliget, NE-Hungary. Palaleoclimatol. Palaeoecol. Palaeogeogr. 118, 25–47.

Willis, K.J., Rudner, E., Sümegi, P., 2000. The full-glacial forests of Central and Southeastern Europe. Quat. Res. 53, 203–213.

Willis, K.J., Whittaker, R.J., 2000. Paleoecology – the refugial debate. Science 287, 1406–1407.

Willis, K.J., van Andel, T.H., 2004. Trees or no trees? The environments of central and eastern Europe during the Last Glaciation. Quat. Sci. Rev. 23, 2369–2387.

Wu, H., Guiot, J., Brewer, S., Guo, Z., 2007. Climatic changes in Eurasia and Africa at the last glacial maximum and mid-Holocene: reconstruction from pollen data using inverse vegetation modeling. Clim. Dyn. 29, 211–229.

Zech, M., Buggle, B., Leiber, K., Markovic, S., Glaser, B., Hambach, U., Huwe, B., Stevens, T., Sümegi, P., Wiesenberg, G., 2009. Reconstructing Quaternary vegetation history in the Carpathian Basin, SE Europe, using n-alkane biomarkers as molecular fossils: problems and possible solutions, potential and limitations. Eiszeitalt. Ggw. 58, 148–155.

Zech, R., Zech, M., Marković, S., Hambach, U., Huang, Y., 2013. Humid glacials, arid interglacials? Critical thoughts on pedogenesis and paleoclimate based on multi-proxy analyses of the loess–paleosol sequence Crvenka, Northern Serbia. Palaeogeogr. Palaeoclimatol. Palaeoecol. 387, 165–175.

Zólyomi, B., 1952. Magyarország növénytakarójának fejlődéstörténete az utolsó jégkorszaktól. Magyar Tudományos Akadémia Biológiai Osztályának Közleményei 1, pp. 491–544 (in Hungarian).

Zólyomi, B., Kéri, M., Horváth, F., 1992. A szubmediterrán éghajlati hatások jelentősége a Kárpát-medence klimazonális növénytársulásainak összetételére (Importance of Submediterranean climatic effects to the composition of the climazonale plant associations of the Carpathian basin). In: Hegyfoky Kabos klimatológus születésének. évfordulója alkalmából rendezett tudományos emlékülés előadásai, vol. 145. MTA Debreceni Területi Bizottságának kiadványa, pp. 60–74.