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Abstract: Records of past climate variability and associated vegetation response exist in various regions throughout Central and Eastern Europe (CEE). To date, there has been no coherent synthesis of the existing palaeo-records. During an INTIMATE meeting (Cluj Napoca, Romania) focused on identifying CEE paleo-records, it was decided to address this gap by presenting the palaeo-community with a compilation of high-quality climatic and vegetation records for the past 60-8 kyrs. The compilation should also serve as a reference point for the use in the modelling community working towards the INTIMATE project goals, and in data-model inter-comparison studies. This paper is therefore a compilation of up to date, best available quantitative and semi-quantitative records of past climate and biotic response from CEE covering this period. It first presents the proxy and archive used. Speleothems and loess mainly provide the evidences available for the 60-20 ka interval, whereas pollen records provide the main source of information for the Lateglacial and Holocene. It then examines the temporal and spatial patterns of climate variability inferred from different proxies, the temporal and spatial magnitude of the vegetation responses inferred from pollen records and highlights differences and similarities between proxies and sub-regions and the possible mechanisms behind this variability. Finally, it identifies weakness in the proxies and archives and their geographical distribution. This exercise also provides an opportunity to reflect on the status of research in the area and to identify future critical areas and subjects of research.

Highlights

- A comprehensive review of climate change and impacts on vegetation in Central and Eastern Europe
- Synchronous climate shifts in CEE and the wider North Atlantic region between 14.7-8 ka
- Reduced magnitude of these climatic shifts in the continental part of Europe
- Cooling intervals between 14.7 and 11.7 ka cal BP strongly expressed during winters
- Vegetation in CEE responded less drastically to the climate shifts compared to Western Europe

Climate variability and associated vegetation response throughout Central and Eastern Europe (CEE) between 60 and 8 ka

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Abstract

Records of past climate variability and associated vegetation response exist in various regions throughout Central and Eastern Europe (CEE). To date, there has been no coherent synthesis of the existing palaeo-records. During an INTIMATE meeting (Cluj Napoca, Romania) focused on identifying CEE paleo-records, it was decided to address this gap by presenting the palaeo-community with a compilation of high-quality climatic and vegetation records for the past 60-8 kyrs. The compilation should also serve as a reference point for the use in the modelling community working towards the INTIMATE project goals, and in data-model inter-comparison studies. This paper is therefore a compilation of up to date, best available quantitative and semi-quantitative records of past climate and biotic response from CEE covering this period. It first presents the proxy and archive used. Speleothems and loess mainly provide the evidences available for the 60-20 ka interval, whereas pollen records provide the main source of information for the Lateglacial and Holocene. It then examines the temporal and spatial patterns of climate variability inferred from different proxies, the temporal and spatial magnitude of the vegetation responses inferred from pollen records and highlights differences and similarities between proxies and sub-regions and the possible mechanisms behind this variability. Finally, it identifies weakness in the proxies and archives and their geographical distribution. This exercise also provides an opportunity to reflect on the status of research in the area and to identify future critical areas and subjects of research.

Keywords: terrestrial records, climate, pollen, vegetation response, INTIMATE, latitudinal gradients, glacial, Holocene

1. Introduction

One of the main aims of the INTegration of Ice-core, MArine, and TErrestrial records (INTIMATE group) is to reconstruct past climatic changes and their impact on the biotic and abiotic environment for the period between 60 and 8 ka. The main mechanisms used to achieve this aim are the refinement of dating methods and resulting chronologies of past changes, quantification of past climatic changes and related impacts, testing for leads and lags in the climatic system and improvement of all the above by modelling the mechanisms driving these changes (Björck et al., 1998, Walker et al., 1999; Blockley et al., 2012a). Initially, the main area of interest was the immediate vicinity of the North Atlantic, later expanding to Eastern Europe (Blockley et al., 2012b) and even farther afield (Petherick et al., 2013). However, discrepancies between regions in terms of data availability and quality have lead to a marked dichotomy between Western and Eastern Europe, which strongly hampers, *inter alia*, testing synchronicity of climatic events, analysis of possible lags in the transfer of climatic influences from the North Atlantic towards the east, and analysis of the response of vegetation to climate changes. Further, while records of past climate variability exist in various regions throughout Central and Eastern Europe, to date there has been no thorough review paper that synthesizes the available high-resolution climate records and data on the biotic responses to the climatic changes.

Present-day climatic differences between Eastern and Western Europe very likely translate into different climatic histories between the two regions in terms of the timing and/or amplitude of palaeoclimatic events. The proximity of Western Europe to the North Atlantic leads to a strong oceanic influence on terrestrial ecosystems, likely overwhelming other possible, distant influences. In contrast, the reduced Atlantic influence in CEE allows for a stronger input from other centers of climatic variability (*e.g.*, the Mediterranean Sea, NW Russia and the Black Sea). These influences result in the northern part (in the vicinity of the Baltic Sea) having cold winters and short, wet summers, while the southern (closer to the Mediterranean Sea) part has relatively warm, wet winters and dry, hot summers. The differences between the two regions were likely enhanced during the last glacial period by the strong influence of the Fennoscandian Ice Sheet and Alpine glaciers on air mass circulation (direction and intensity) and temperatures.

During an INTIMATE meeting held in Cluj-Napoca (Romania) in March 2013, it was decided to address this gap and summarize the existing high-resolution records of climate change and related impacts on vegetation in Central and Eastern Europe (CEE) for the period between 60 and 8 ka. CEE is here loosely defined as the region between the Alps and the Baltic Sea to the west, the Scandinavian Peninsula to the north, the Rhodope Mountains and Thracian Plain to the south and the Russian Plain to the east. The 60 and 8 ka interval covers the second half of the last glacial, the Last Glacial Maximum (LGM, ca 22-18 ka BP), the Lateglacial period (ca. 14.7-11.7 ka BP), and the early Holocene (ca 11.7-8 ka BP). The period before the Lateglacial is divided into Marine Isotope Stage 3 (MIS 3, ca 60-28 ka BP) and MIS 2 (ca 28-14.7 ka BP). As in Moreno et al. (this volume), the Greenland ice core stratigraphy has been applied as a template for CEE climate variability during the 60-8 ka time period (Blockley et al., 2012). This review also serves as a reference point for high-resolution palaeo-data for use in the modelling community working towards the INTIMATE project goals, and in data-model inter-comparison studies. However, this is not intended to be an exhaustive review of all palaeo-records from the CEE region. This paper should be seen as a companion to a similar compilation of Western European quantitative terrestrial palaeoclimate reconstructions for the same period (Moreno et al., this volume). By compiling the best available data from CEE, we aim to: i) present the palaeo-community with a concise compilation of high-quality climatic and vegetation records for the 60-8 ka period; ii) decipher the temporal and spatial patterns of climate variability inferred from different proxies and the magnitude of the vegetation responses; iii) offer a quantitative (*e.g.*, temperature or precipitation) and qualitative (*e.g.*, colder/warmer, wetter/drier) visual representation of past variability in climatic conditions, highlighting differences and similarities between proxies and regions; iv) (partly) understand the mechanisms behind these changes and variability.

2. Data compilation and selection criteria

The selection of best available records was guided, as much as possible, by the following criteria: i) the record should cover a fraction of the INTIMATE 60-8 ka time frame; ii) the record should include at least one quantitative or semi-quantitative parameter (proxy or reconstruction); iii) the records should be independently dated or tightly linked to a well-dated record age model. However, during the INTIMATE workshop it emerged that the Lateglacial and early Holocene was the most intensively studied period in CEE and that most records include pollen data. Abiotic proxies (geomorphology, fluvial sediments, stable isotopes, geochemistry, etc) were less used, and usually with a generalised or even contradictory explanation of the mechanisms linking them to climatic parameters. Loess, on the other hand, appeared as the most complete palaeo-archive for the period beyond the Lateglacial, albeit with a lower resolution and less precise chronology.

We first identified *non-pollen records* in order to eliminate the problem of discriminating between the forcing (*i.e.*, climate change) and the response (*i.e.*, vegetation change). In the second step, we eliminated those records where it was not clear how a measured variable registered the climatic signal or what the mechanism was by which changes in measured values were assigned to a given climate change. However, due to the extremely low number of suitable records, we have also included the pollen-based annual, summer and winter temperature reconstructions from Romania as these are among the very few quantitative climate estimates, are well dated and represent the longest quantitative records from the region. The resulting quantitative and semi-quantitative temperature reconstructions are based on two chironomid records, from Poland (Płóciennik et al., 2011) and Romania, respectively (Tóth et al., 2012); a $\delta^{18}O$ record from speleothems in Romania (Tămaş et al., 2005), a $\delta^{18}O$ record from bulk carbonates in lake sediments from Slovenia (Andrič et al., 2009), and a pollen-based quantitative reconstruction of summer, winter and mean annual temperature (MAT), as well annual precipitation from NW Romania (Feurdean et al., 2008 a, b). The climate data are presented in two distinct time frames: MIS 3 (60-28 cal BP) and MIS 2 (28-14.7 cal BP), and Lateglacial to early Holocene (14.7-8 ka). Discussions follow a north to south gradient.

We have used the ages and depth-age models as provided by the authors (see Table 1) for the number of dated points and temporal resolution for each record. All data were plotted on their own depth-age model against the NGRIP stable isotope record (Rasmussen et al., 2006) and INTIMATE event stratigraphy (Blockley et al., 2012b) for the 14.7-8 ka period (Fig. 2), and subsequently used to make a semi-quantitative assessment of the climate characteristics in the region (Table 2). A complete description of the general mechanisms by which these proxies are recording the climatic variables, the methods used to date and extract the climatic signal and the associated problems are found in a companion paper by Moreno et al. (this issue) on Western European climate changes between 60 and 8 ka.

To examine the vegetation response to the climate fluctuations we selected a total of 13 pollen sequences with good temporal and spatial coverage in CEE as follows: for small countries only a single pollen sequence was included, whereas for larger countries, or those with significant elevation gradients, the two most complete continuous records per country were selected. The pollen taxa in these sequences were then grouped into ecological types that largely follow the protocol for assigning pollen taxa to plant functional types and subsequently biomes (Fletcher et al., 2010; Moreno et al., this volume). The 5 main types were: coniferous, cold deciduous trees, temperate deciduous taxa, warm temperate taxa, warm /dry steppe, and other grassland and dry shrubland (Table 2). In addition, pollen and plant macrofossil maps were created for the following time slices: 17, 14.7 13.5, 12.7, 11.7, 10.5, 9.3, 8.2 ka cal BP for each record, to aid better geographical visualization of the vegetation dynamics in the CEE.

Quantitative reconstruction of climatic conditions during 60-8 ka in the CEE region poses a series of challenges, including: 1) a lack of investigated records for most of the period extending beyond the Lateglacial, or extremely fragmentary and low-temporal resolution records (the notable exceptions are loess deposits, see below); 2) imprecise age control (up to 10% dating uncertainties), which prevents accurate identification of the “short”-lived (less than 500 yrs) events; 3) difficulties in constraining the significance of the various measured variables in terms of climatic parameter or how the measured values were quantified. Insufficient temporal resolution and chronological control of the records also prevented: 1) the assignment of accurate dates for the timing of the short climatic events, and 2) a precise correlation, in terms of "synchronicity" or "lags", between the local climatic shifts and the INTIMATE event stratigraphy. However, within the dating uncertainties, possible correlations have been proposed.

3. Climate changes in CEE

Our analysis is based on stable isotope variations in lake sediments, speleothems, loess and chironomid assemblages (Fig. 2), but is restricted to loess and speleothem records for the interval between 60 and 14.7 ka.

3.1. 60-8 ka

3.1.1. Loess records

Loess covers large parts of CEE, especially in areas south of the previous maximal extent of the former Fenoscandian Ice Sheet. Its distribution widens eastward, towards the Ukrainian and Russian lowlands. The province can further be subdivided into 5 subprovinces, each experiencing contrasting palaeoclimate: 1. between the Alps and the Carpathians; 2. north of the Carpathians; 3. the middle Danube Basin; 4. the lower Danube Basin and the northern coast of the Black Sea; and 5. Ukrainian and Russian continental lowlands (Table 4). The source and transport directions of loess in these areas are diverse, with material in the N and E parts of the CEE loess belt likely a large deflation area south of former ice margins. By contrast, the central Danube Basin loess is probably initially eroded from high mountain regions and then transported and deposited in floodplains of the Danube and tributaries (Buggle et al., 2008; Ujvári et al., 2013). Based on grain size investigations at three loess sections west and another five east of the Carpathian Mountains, Bokhorst et al. (2011) suggested a prevailing westerly wind over CEE during the MIS 3, and a dominant north-westerly wind during the GS-2.

Generally, this interpretation corresponds well with the major wind directions previously reconstructed by Rozycki (1991) and Marković et al. (2008) based on loess landform orientation and modeling results (Rousseau et al., 2011; Sima et al., 2013).

The Eastern European loess belt provides a unique opportunity for almost continuous climatic reconstructions over this part of Europe between 60 and 14.7 ka. However each subprovince experienced quite different palaeoclimatic conditions over the time period investigated and recovering climatic information is therefore complicated due to the changing influence of specific controls on the preserved proxies. One of the earliest attempts used soil types as indicators of past climatic conditions. However, the significant palaeoenvironmental diversity over the region controls the intensity and type of pedogenesis, meaning the resultant palaeosols represent a wide variety of habitats, from tundra gley layers (Rousseau et al., 2011; Antoine et al., 2013), parklands and grasslands soils in the Middle Danube and Ukraine (Gerasimenko and Rousseau, 2008; Marković et al., 2008; Schatz et al., 2011; Kovács et al., 2012), to dry steppic soils in the Lower Danube lowland and around the Black Sea coast (Buggle et al., 2009). Furthermore, uncertainties in loess age models (see Timar-Gabor et al., 2011; Timar-Gabor and Wintle, 2013 for the Romanian loess) prevent confident correlation of palaeopedological horizons in the CEE with individual NW European interstadials such as: Denekamp, Hengelo, Moershoofd or Glinde, or to specific Greenland interstadials. Refining these correlations represents a significant avenue of future research.

Despite this, attempts have been made to correlate multiple episodes of abrupt climatic fluctuations recorded in loess grain-size from Moravian Czech Republic and Central Ukrainian deposits, with cooling in the North Atlantic, partly associated with Heinrich events as well as with cold phases of Dansgaard-Oeschger cycles recorded in Greenland ice (Antoine et al., 2009, 2013; Rousseau et al., 2011). However, investigations in N Serbia using a similar chronological framework and level of uncertainty suggest that it is only possible to establish relationships between grain-size peaks in loess and some Heinrich Events, rather than Greenland stadial events, which require greater precision in age-dating (Stevens et al., 2011) and depending on their magnitude may not show a grain-size response. In any case, Hatté et al. (2013) suggest that these coarse-grain depositional phases are usually associated with the appearance of dry and probably cold climatic events. More frequent periods of coarser grain deposition occurred during the MIS 3 under dominant westerly air circulation (Bokhorst et al., 2011). This greater deposition of coarser material during the relatively cold early last glacial (loosely 74 to 50 ka) compared to during the period around the last glacial maximum is likely to be a consequence of reorganization of atmospheric circulation due to initial ice sheet growth and sediment mobilization, as well as changes in depositional regime of the Danube fluvial system. By contrast, during the MIS 2 although ice sheet growth was significantly greater (Wolfarth, 2010), maximal extension of northern European ice may have partially blocked penetration of the Atlantic air masses to the east (Dodonov and Baiguzina, 1995). Model results of Van Huissteden and Pollard (2003) indicate a strong anticyclonal circulation over the Fennoscandian Ice Sheet around the last glacial maximum. At the same time, the Alpine ice cap played an important role in the hydrological regime of the Danube River through controlling the considerable melt-water driven flow of the system, as well as in the production and transport of source material for later aeolian deposition (Marković et al., 2008). The shift to finer depositional modes is also likely to have been associated with changes to more dense vegetation cover during MIS 2 in Serbia (Marković et al., 2005; Zech et al., 2009, 2013).

The relatively sparse quantitative climatic reconstructions from loess subprovinces north of the Carpathians and in the middle Danube Basin generally suggest that the Carpathians significantly modified last glacial climatic gradients. Based on the spatial distribution of ice wedge casts recorded in last glacial loess, Jary (2009) suggested that in the central and E parts of Poland and W Ukraine, permafrost developed twice; in the latest part of early last glacial (potentially equivalent to Heinrich Event (HE) 6) and the late last glacial (approximately from HE2 to YD). Mean annual air temperature (MAAT) has been estimated as between -2 and -6 °C during the older phase (Vandenberghe et al., 1998; Renssen and Vandenberghe, 2003; Vandenberghe et al., 2004), while the common occurrence and large size of the younger phase of cryogenic structures indicates continuous areas of permafrost existed in the central and E parts of Poland and W Ukraine. Assuming this interpretation is correct, the MAAT of the coldest phase of the late last glacial was most likely 10 to 15 °C lower than present. Similar environmental conditions are suggested from loess in the N parts of the Ukrainian and Russian lowlands (Little et al., 2002). However, significantly drier and warmer conditions are indicated by the general absence of cryo features (Marković et al., 2008) and the relatively high July palaeotemperatures reconstructed from malacofauna (Sümegi and Krolopp, 2002; Marković et al., 2007; Molnár et al., 2010) in the Danubian loess south of the Carpathian Basin, reinforcing the suggestion of diverse climates found in this region. Cold spells related to Heinrich Events, the LGM and YD were inferred from a biomarker record from the NW Black Sea region (40-9 ka), but the amplitude of these cold phases was apparently smaller than lake temperature records in the region or other records from central Europe would suggest (Sanchi et al., 2014). Dansgaard-Oeschger variability was not detected in this record.

3.1.2. Speleothem records

The deposition of speleothems in caves of CEE during this time span is discontinuous, showing intervals (with variable length) of enhanced and decreased (or even ceased) growth. Such periods are traditionally associated with either warm or cold intervals, respectively. The cumulative growth frequency record of 62 U/Th-dated speleothems from different karst regions in NW Romania situated between 450 and 1150 m asl, show more continuous growth during the past 60 ka yrs (Onac, 1996, 2001; Onac and Lauritzen, 1996; Lauritzen and Onac, 1999) compared to those at higher latitudes, although the Scandinavian Ice Sheet was only 500 km away (Ehlers et al., 2011). This confirms that NW Romania was neither covered by alpine glaciers nor experienced enough severe permafrost conditions to suppress water percolation into the caves and hence speleothem growth. Further, the growth of a stalagmite in NW Romania between 59 and 46 ka indicates a warm/wet period (Tămaş and Causse, 2001). In contrast, the palaeoclimate records from alpine caves in Central and Western Europe are sparse over this time period (Spötl et al., 2006) are sparse over this time period because the presence of ice caps caused a significant temperature drop, prompting permafrost development, thus preventing the continuous growth of speleothems.

An almost continuous isotope record covering the period between 60 and 8 ka was documented by Constantin et al. (2007) from a cave in SW Romania (stalagmite PP10 in Poleva Cave). Its $\delta^{18}O$ isotopic values show an increase from 60 to 57 ka when they reach a maximum of -7.7 ‰. This interval was interpreted as representing warming at the onset of Marine Isotope Stage 3 (MIS 3). After this event, the oxygen isotopic profile suggests an overall cooling trend emphasized by the gradual $\delta^{18}O$ decrease to -9.0 ‰ at ~42 ka when the stalagmite ceased to grow for a short period of time. Beyond this hiatus, the $\delta^{18}O$ values decrease abruptly to -10.5 ‰ indicating an extreme cold phase between 38 and 35 ka. The gradual increase of $\delta^{18}O$ values by ca. 2 ‰ after 38 ka and until 25 ka points toward a moderate warming, which was followed by rapid cooling at the beginning of the Last Glacial Maximum when the speleothem ceased to grow until the end of the Younger Dryas (Constantin et al., 2007). The cold interval recorded in the PP10 stalagmite between 38 and 35 ka was also documented from central Romania, where archaeological findings in Gura Cheii – Râșnov Cave suggest a cold phase prior to 40 and until at least 34 ka cal BP (Cârciumaru et al., 2012).

A new study by Dragusin et al. (2014) demonstrates that $\delta^{18}O$ record does not show significant variations (-9.2±0.3 ‰) across the 8.2 ka event in the POM2 stalagmite (Ascunsa Cave, SW Romania). The low isotopic variability during the 8.2 ka event apparently reflect only temperature variations, but hydrologic conditions such as relatively more summer vs. winter rainfall cannot be ruled out. One clear indication that environmental conditions changed is the growth rate, which increased 8 times during this event compared to the rest of the Holocene.

3.2. GI-1e

The beginning of GI-1 in the Greenland Ice Core record is centred at 14,692 b2k and shows a temperature amplitude increase of 10 °C over just a few years (Blockley et al., 2012b). A warming trend was noticed throughout CEE about the same time (Table 2); however, the timing and magnitude of this warming can only be roughly estimated (Fig. 2). For example in Slovenia, the $\delta^{18}O$ on bulk carbonates from lake sediments indicates a sharp increase in summer temperatures at 14.8 ka cal BP, followed by relatively stable conditions (Andrič et al., 2009). Similarly, a rapid warming phase initiated at ~14.8 ka cal BP is revealed by the $\delta^{18}O$ values of a speleothem from NW Romania (Tămaş et al., 2005) and was also inferred from the growth intervals of another speleothem in Scărişoara Ice Cave (Onac, 2001). For the same region, Feurdean et al. (2008) used pollen to document a 2 °C increase (from 2 to 4 °C) in annual temperatures that correlate well with the timing of the GS-2/GI-1e transition in Greenland, increase generated by winter temperatures only (summer temperatures remained unchanged). A chironomid-based reconstruction of summer temperatures in the S Romanian Carpathians indicates an increase of ~2.8 °C in summer air temperature during the same transition, reaching a maximum of ~8.1 °C (Tóth et al., 2012). Further to the NE during the same period, July temperatures fluctuated between 12 and 16 °C in central Poland (Ralska-Jasiewiczowa et al., 1998, pollen data), 13-16.5 °C at Żabieniec bog, central Poland (Płóciennik et al., 2011, chironomid assemblages) and 15.5-16.5 °C at Lake Okunin, in NW Ukraine (Dobrowolski et al., 2001, ostracod assemblages). In the eastern Baltic area, July temperatures below 12 °C (Kirilova et al., 2011 - chironomid data; Veski et al., 2012, pollen data) were characteristic during the early phase of the Lateglacial (roughly overlapping with GI-1e in Greenland).

3.3. G1-1d through GI-1a

The climatic conditions during this time interval are seen as relatively stable in most of the records, with only two small-leaved decline in annual temperatures, that could be tentatively correlated with GI-1d and GI-1b in Greenland (Fig. 2). Based on the $\delta^{18}O$ record, Tămaş et al. (2005) report a decline (~1 ‰ in the $\delta^{18}O$ values) in mean annual temperatures, punctuated by rapid and strongly expressed cooling events that could correlate with GI-1d and GI-1b. Chironomid-based July temperatures in S Romania (Tóth et al., 2012) and central Poland (Płóciennik et al., 2011) were relatively stable with values slightly lower than those during GI-1e (*e.g.,* a weak increase to 8.1-8.6 °C between 13,700 and 11,480 cal BP in Romania). Instead, pollen-based quantitative reconstructions from NW Romania (Feurdean et al., 2008a) indicate that between 13,800 and 12,700 cal BP (*i.e.*, during GI-1a-c in Greenland), summer temperatures rose close to modern values (13 to 17 °C), whereas winter (ca. -6 to -12 °C) and annual temperatures (0.5 to 6 °C) as well as precipitation (550 to 700 mm) were still lower (Fig. 2), indicating stronger inter-seasonal variability and enhanced continental conditions compared to the present-day climate. The $\delta^{18}O$ based climate reconstruction at Lake Bled (Slovenia) shows warmer conditions after 13,800 cal BP (Andrič et al., 2009; Lane et al., 2011), whereas the chironomid assemblages indicate a lowering of the lake level connected to warmer and drier environment (Andrič et al., 2009). Another line of evidence for warmer summer temperatures comes from fire activity, which increased between 13,800 and 12,700 cal BP in the Carpathian Mountains and lowlands of Hungary and Slovenia (Willis et al., 1997; Andrič et al., 2009; Feurdean et al., 2012a).

3.4. GS-1

A decline in average temperatures occurred throughout the region after 12,800 cal BP, correlating, within dating uncertainties, with the onset of GS-1 in Greenland. July temperatures registered a decline of 1 °C in Poland and S Romania (chironomids-based; Płóciennik et al., 2011; Tóth et al., 2012), and 2 °C in NW Romania (pollen estimate; Feurdean et al., 2008a).

However, pollen-based estimated winter temperatures drop ~ 9 °C (Feurdean et al., 2008a), whereas precipitation declines by ca. 250 mm (Fig. 2). Similarly, diatom inferred winter ice cover in the southern Carpathians suggests that cooling associated to the GS-1 was mainly expressed during winter (Buczkó et al. 2012). Drier and cooler conditions for the stadial are indicated by δ^{13}C and δ^{18}O in speleothems from Romania (Tămaş et al., 2005, Romania); δ^{13}O (Lane et al., 2011), chironomid assemblages and lake level in a lacustrine sequence from Slovenia (Andrič et al., 2009), and ostracod assemblages from Poland (Dobrowolski et al., 2001). A drop in precipitation at the onset of GS-1 is also shown by the decreased fluvial activity from Poland (Starkel et al., 2013). Although the GS-1 was generally dry, the record from Northern Poland shows that the onset of lacustrine sedimentation occurred during this period, but was most intensive during the first half of the GS-1 (Michczyńska et al. 2013). Further, Goslar et al. (1995) have ascribed rapid fluctuations in δ^{18}O of authigenic carbonates in Lake Gościaż (central Poland) to changes in air temperature, synchronous (within dating uncertainiy) with those seen in the Greenland ice cores. The rapid (within 170 years) cooling at the onset of the Younger Dryas was foolowed by an even rapid warming (at 11,440 cal BP), seen as a 2 ‰ increase in δ^{18}O values within ~70 years.

Summarizing the records above, it appears that the decline in temperatures between 12,800 and 11,700 cal BP (corresponding to GS-1) in CEE was more pronounced for winter than for summer, which, along with evidence for a marked drop in precipitation, indicates a progression transition towards more continental, arid or seasonally variable climatic conditions (Table 2).

3.5. Early Holocene

Independent palaeoclimatological evidence from CEE suggests that transition to markedly warmer and drier conditions (summers) occurred at 40-50 °N approximately between 11.7 and 8 ka cal BP. In the northern part of Central Europe (above 47 °N), the temperature increase was significantly slower and with smaller magnitudes compared to more southern locations (Table 2). Higher (by 1 - 1.5 ºC) than today summer temperatures have been both reconstructed (Seppä and Poska, 2004; Feurdean et al., 2008b; Seppä et al., 2009) and modelled (Renssen et al., 2009) for the region during the Early Holocene. Higher summer temperature and lower moisture availability is also demonstrated by the increase in fire activity over large areas and elevations of CEE (Andrič et al., 2008; 2009; Magyari et al., 2010; Feurdean et al., 2012; 2013; Connor et al., 2013; Hájková et al., 2013). Climate simulation of the early Holocene for the lowlands of NW Romania (Transylvania) shows, higher summer temperatures (by about 4 °C) and lower precipitation values (by about ~33%) but only moderately higher annual temperatures compared to present-day values (Feurdean et al., 2013). In the southern part of the region (Poleva Cave in SW Romania), the steady increase of the δ^{18}O values (up to 2‰) in speleothems PP 9 and 10 indicates a gradual warming trend from ~11.5 ka, continuing well into the Holocene (Constantin et al., 2007), with similar warming trends seen west (Slovenia, Andrič et al, 2009) and north (Romania, Tămaş et al., 2005) of this site, while more northern regions experienced a less pronounced warming. There is also evidence for a decrease in peat surface moisture and lake levels in NW and E Romania at the beginning of the Holocene (Magyari et al., 2009; Buzcko et al., 2012; Feurdean et al., 2013) and in northeastern Polish lakes (Gałka and Tobolski, 2013; Gałka et al., 2014; Gałka and Sznel, 2013), while rivers in NW Romania changed their behaviour from braided to meandering, indicating lower discharge and related lower amounts of precipitation (Perşoiu, 2010). Simultaneously, kettle hole peatland in N Poland reveals a fen-bog transition, suggesting a decrease in the ground water table, likely related to the complete disappearance of permafrost (Lamentowicz et al., 2008; Słowiński, 2010). The Lake Gościąż record, a lacustrine sequence with the highest temporal resolution in the region (1-4 yr/cm), shows an overall warming and drying trend at the Lateglacial/Holocene transition, but with three sub-phases: a phase of dry winter conditions (11.55-11.52 cal BP); a second phase with warm, moist summer conditions

(11.52-11.46 cal BP) and a third phase with dry summers (11.46-11.39 cal BP), which caused a lowering of the lake level. In central Poland, only a small (if any) summer temperature increase is observed in chironomid assemblages during the Early Holocene, compared to the late GS-1 (Płóciennik et al., 2011).

4. Biotic response

4.1. Vegetation response to climatic oscillations from 60-20 ka

Unlike in S Europe (Fletcher et al., 2010), continuous last glacial lake or mire sediments are very rare and the chronology uncertain in CEE (Šercelj, 1966). Nonetheless, several shorter middle last glacial (60-27 ka) loess and solifluction clay sediments have been studied for pollen and plant macrofossils in this region. This, together with the numerous macrocharcoal studies from archaeological sites (Środoń, 1968, 1987; Willis and van Andel, 2004; Jankovská and Pokorný, 2008; Komar et al., 2009; Nádor et al., 2011), allow us a general characterisation of the MIS 3 and 2 vegetation in CEE, and a preliminary interpretation of region-wide vegetation responses to rapid climate change events.

In the western Carpathians, pollen and plant macrofossil analyses on peat deposits of MIS 3 provide evidence for a dense taiga forest cover until the onset of the last glacial maximum (Jankovská et al., 2002; Jankovská and Pokorný, 2008; Kuneš et al., 2008). The record of Šafárka (Fig. 3) starts at ~52 ka, ends at around 16 ka cal BP and shows a forest succession from *Larix decidua* to dense *Picea abies* taiga. Both *Picea abies* and *Larix decidua* macrofossils were abundant at the site and Jankovská et al. (2002) inferred the local presence of several other mainly boreal trees like *Betula*, *Alnus*, *Pinus cembra* and *P. sylvestris*. Pollen of temperate deciduous trees (*Corylus*, *Ulmus*, *Quercus*, *Tilia*, *Fagus* and *Carpinus*) was also recorded and the regional presence of these tree taxa was inferred in the Western Carpathians.

Solifluction clay deposits in the northern piedmont zone of the Carpathians (*e.g.*, Dobra, Sowliny) indicate that members of herb communities, typical alpine grasslands (*Callianthemum* *coriandrifolium*, *Dianthus speciosus*, *Helianthemum alpestre*, *Leontodon pseudotaraxaci*, *Linum extraaxillare*, *Minuartia sedoides*, *M. verna*, *Polygonum viviparum*, *Potentilla aurea*, *Selaginella selaginoides*, *Soldanella carpathica*), snowbed and scree communities (*Arabis alpina*, *Doronicum stiriacum*, *Cerastium lapponicum*, *Ranunculus montanus*) were found at altitudes of 300-640 m between 40 and 29 ka cal BP (MIS 3; Środoń 1987). Lowland steppe plants were also present (*e.g., Alyssum*, *Artemisia*, *Aster alpinus*, *Potentilla heptaphylla*, Chenopodiaceae, *Festuca*, *Filipendula*, *Helianthemum*). Macrofossil evidence shows that these were accompanied by cold temperate and boreal trees and tundra dwarf shrubs: *Alnus incana*, *Betula nana*, *B. pubescens*, *Larix*, *Picea excelsa*, *Pinus cembra*, *Pinus sylvestris*, *Populus* and *Salix*, altogether forming a non-analogue steppe-tundra vegetation in association with boreal forest communities. The woody component of these communities was very similar to the Šafárka flora suggesting both, open and closed boreal forests in the Western Carpathians. Loess pollen studies in S Poland and S Ukraine furthermore demonstrate that lowland areas north and east of the Carpathian Mountains hosted a vegetation mosaic of steppe tundra and boreal parkland forests, dominated by *Pinus sylvestris*, *Pinus cembra*, *Betula*, *Larix, Picea abies*, *Abies alba* and various shrubs (Komar et al., 2009). Open woodlands reached well into middle Poland during the MIS 3 (Mamakowa and Latałowa, 2003; Szczepanek et al., 2007).

Vegetation in the lowland and hill zone W, E and S of the Carpathian Mountains over the same period is mainly recorded by macrocharcoal and pollen studies of archaeological sites or loess exposures (*e.g.*, Urban, 1984; Svoboda and Svobodová, 1985; Opravil, 1994; Culiberg and Šercelj, 1995; Haesaerts et al., 1996, 2010; Damblon, 1997; Damblon and Haesaerts, 1997; Rudner and Sümegi 2001; Musil, 2003). These studies demonstrate that during the MIS 3 a wide spectrum of tree species *e.g.*, *Abies alba*, *Alnus*, *Betula nana*, *B. pubescens*, *B. pendula*, *Carpinus betulus*, *Corylus*, *Fagus sylvatica*, *Fraxinus*, *Juniperus communis*, *Larix*, *Pinus sylvestris*, *P. mugo*, *P. cembra*, *Picea abies*, *P. excelsa*, *Populus*, *Quercus*, *Salix*, *Sorbus aucuparia*, *Ulmus* were present in the lowland and hill zones of E Austria, the Czech Republic

(Moravia, Bohemia), Slovakia, Hungary, Romania and Slovenia. The most diverse woody assemblages were dated to between 35 – 30 ka cal BP (Willis and van Andel, 2004), these also include the oceanic *Taxus baccata* that likely grew in association with *Fagus sylvatica* in Moravia (Mason et al., 1994). Notable is that Moravia in the Czech Republic showed exceptional tree diversity with several temperate deciduous tree taxa. In comparison, the lowlands of the Carpathian Basin were dominated by boreal trees such as *Picea abies*, *Larix*, *Betula* and *Pinus sylvestris* (Rudner and Sümegi, 2001), whereas temperate deciduous tree macrocharcoal fragments (*Carpinus betulus*) are rare in these sequences, suggesting their scarcity in the loess accumulation zone. A greater extent of forest cover (*Pinus*-dominated) during the early part of MIS 3 (55-38 ka) compared to the period after 38 ka was very recently identified in a pollen record from lowlands of Transylvania (Feurdean et al., sub). This difference in the two areas may potentially be explained by the more varied topography of the Czech Republic and its less continental climate. The response of vegetation to climate change during the MIS 3 has been studied in the eastern Hungarian Plain by Nádor et al. (2011), who found *Pinus*, *Picea* and *Ulmus* dominance between 40–30 ka, along with sporadic regional occurrence of *Tilia*, *Carpinus betulus*, *Fagus sylvatica*, *Quercus*, and *Corylus avellana,* but no increases in arboreal pollen between 40 and 30 ka. This pollen record complements the macrocharcoal record in that it suggests the dominance of mixed deciduous-coniferous forests.

Moving to the southeast, a mid to late last glacial (MIS 3) vegetation record from Straldzha Mire in the Thracian Plain, Bulgaria shows the dominance of cold steppe vegetation with herbs until MIS 2 (*Artemisia*, Poaceae, *Polygonum aviculare* type, Chenopodiaceae) (Connor et al., 2013). Notably, the pollen record shows no sign of millennial-scale vegetation fluctuation. On the basis of the pollen data, Connor et al. (2013) inferred the small-scale presence of xeric woodland with *Quercus*, *Juniperus* and Rosaceae trees/shrubs in the *Artemisia*-steppe dominated landscape during the period. Comparable vegetation likely prevailed in the south-easternmost part of the Carpathian region, in Serbia (Marković et al., 2007, 2008; Zech et al., 2013). In Slovenia, the middle last glacial-associated pollen spectra from Ljubljana Moor show fluctuations between mixed coniferous-deciduous woodland comprising *Abies*, *Betula*, *Alnus*, *Corylus*, *Quercus*, *Tilia*, *Ulmus*, *Acer*, *Salix* and *Juglans* and periods of predominantly steppe-dominated landscape with *Pinus* and *Picea* (Šercelj, 1966).

The MIS 3 - 2 transitional sections of the pollen records of the Carpathians and lowlands in E Hungary show: i) a predominance of needle-leaved and cold temperate tree vegetation in the W Carpathians (at Jablunka and Safarka); ii) increased representation of steppe herbs in the more continental E Carpathians (Lake St Anne) and lowlands of W Romania (Lake Stiucii); and iii) recurring fluctuations in AP values in the Carpathians Basin (Fehér Lake, Nagymohos; Rudner and Sümegi 2001; Sümegi et al., 2013; Fig. 3). The last glacial maximum part of these pollen records suggests that some woody cover was maintained in these regions during the maximum northern hemisphere ice extent (between 26.5 and 19 ka cal BP). This picture is similar to the Thracian Plain (42° N) vegetation response in that it shows no large amplitude vegetation change during the last glacial maximum, although cold steppe dominates at this more southerly latitude, pointing to increased continentality towards the south (Connor et al., 2013). Temperate deciduous tree pollen is recorded in the Carpathian area, but macrofossils or charcoal of these taxa have not been reported from the last glacial maximum.

4.2. Spatial vegetation response to the climate conditions at the end of GS-2 (20-14.7 ka cal BP).

A few of the selected high-resolution pollen records in CEE stretch back to the end of GS-2 (20-14.7 ka cal BP). Arranged on a S to N transect, these pollen records reveal three features of the vegetation during this period: i) that the vegetation assemblages were marked by a high proportion of non-arboreal pollen, principally *Artemisia,* Chenopodiaceae and Poaceae; ii) there is an increase in steppe and grasslands along a north (20%) to south (90%) transect, with sites located south of 45 °N (Rila Mountains and the Thracian Plain in Bulgaria) showing the strongest continental conditions; iii) the persistence of open woodlands /parkland forest in CEE (Figs. 4, 5). There is some spatial distinctiveness in the tree species composition and proportion in CEE: i) regions north of 55 °N and east of 20 °E (Latvia, Lithuania, Belarus) contain more abundant pioneer species of the tundra and boreal zone (*Betula nana*, *Betula, Pinus*); ii) in the Carpathian region (55 °N and 15-25 °E Czech Republic, Slovakia, Hungary, Romania), *Pinus* was abundant with a comparatively lower proportion of cold deciduous taxa (*Betula, Alnus, Salix*); iii) in Slovenia (46 °N) *Pinus* dominated the record entirely; iv) in the Balkans there is also a high proportion of needle-leaved taxa (Figs. 4, 5). Pollen of temperate deciduous taxa (*Quercus, Ulmus, Tilia, Carpinus* and *Fagus*) was also recorded in Hungary, Romania and Slovenia (Figs. 4, 5; Fărcaş and Tanțău, 2012). Plant macrofossil remains of trees are virtually absent in all these sequences. However, woody plant macrofossils of conifers dated to the end of GS-2 are known from loess deposits (see Willis and Andel, 2004), and from fluvial sediments in the lowlands of Transylvania (Lascu, 2003). Pollen records covering the end part of GS-2 reinforce the idea that most of the CEE landscapes supported open forest principally needle-leaved and cold deciduous trees, and a small population of temperate deciduous trees during the late GS-2, whereas more compact temperate deciduous populations were confined to latitudes south of 46 °N. Although pollen of long-distance transported or reworked origin could have increased the proportion of arboreal taxa during the glacial period, the prevalence of harsh climatic conditions for growth and reproduction could have reduced pollen production.

4.3 Spatial vegetation response during GI-1e

Fossil pollen and plant macrofossil sequences from the continental records of CEE indicate that there was a large-scale reduction in dry steppe vegetation and a northern latitudinal expansion of boreal forest vegetation around 14.7 ka cal BP, that correlate approximately to the onset of GI-1 e in Greenland. However, the CEE pollen records also show that the magnitude of vegetational response was not uniform; i) regions from Baltic area (north of 55 °N and 25 °E), previously covered or closer to the ice sheets and permafrost (Estonia, Latvia, Lithuania) show abundant pollen of pioneer taxa such as *Betula nana* (Amon et al., 2010; Amon et al., 2012; Veski et al., 2012), while more eastern records from Belarus (south of 54 °N and east of 24 °E) contain a higher proportion of pollen of *Pinus* (up to 90% Zernitskaya, 2005; Makhnach et al., 2009). In addition, plant macrofossil records from the Baltic region suggest that a tundra biome (*Betula nana*) with patchy occurrences of tree birch including *Betula* sect. *Albae* (Stančikaitė et al., 2008) occupied the newly deglaciated areas, while boreal tree taxa (*Betula* and *Pinus*) expanded from 13.4 ka cal BP in Estonia (Amon et al., 2012), at ca. 14.4 ka cal BP in Latvia and Estonia (Heikkila et al., 2009; Veski et al., 2012), and at ~ 14 ka cal BP in south-eastern Lithuania (Stančikaitė et al., 2008) and the northern part of Poland (Gałka et al., 2013).

In the central part of CEE, including the Carpathians region (46-50 °N; 15-22 °E), there was a considerable increase in biomass and an expansion of boreal forests around 14.7 ka cal BP (Figs. 4, 5). Nevertheless, significant elevational distinctiveness in the vegetation existed in this region. For example, pollen records from sites in the lowlands (Kis Mohos in Hungary, Avrig in Romania) indicate the presence of more fragmented or more open forests of needle-leaved (*Larix, Pinus*), and cold deciduous taxa (*Betula, Alnus* and *Salix*); whilst sites in the uplands (Steregoiu, Romania, Lapysky, Slovakia) contained more extensive boreal forests (Figs. 4, 5; Willis et al., 1998; Wohlfarth et al., 2001; Björkman et al., 2002; Pokorný, 2002; Kuneš et al., 2008; Pokorný et al., 2010; Tanțău et al., 2006; 2014; Feurdean et al., 2007; 2012b). Plant macrofossil records from this area support the inference of the local abundance of *Pinus sylvestris, Pinus cembra, P. mugo*, *Betula* and *Salix* in Romania already at 14,500 ka cal BP (Wohlfarth et al., 2001; Feurdean et al., 2012b) and around 13.2 ka cal BP in the Czech Republic (Jankovská, 1984). Further south (south of 46 °N) in Slovenia and Bulgaria, GI-1e is marked by a greater diversity of tree taxa that include needle-leaved taxa such as *Larix decidua* (only dominant in Slovenia), *Pinus diploxylon-type, P. peuce, Juniperus*), xerophytic shrubs

(*Ephedra distachya, E. fragilis-type*), cold deciduous (*Betula, Salix, Alnus*), as well as temperate deciduous taxa (*Quercus, Corylus, Acer)* (Tonkov et al., 2006; Andrič et al., 2009; Connor et al., 2013). The latter group is also locally documented by sub-fossil wood remains of *Quercus, Ulmus* and Rosaceae (Magyari et al., 2008). The lowlands of SE Bulgaria, close to the Black Sea, however, remained predominantly covered by steppe vegetation (Magyari et al., 2008, Connor et al., 2013).

Summarizing our pollen and plant macrofossil data-sets for the onset of the Lateglacial, there is evidence: i) for a northward expansion of boreal forest into CEE; ii) that extensive boreal forests (needle-leaved) as well as small areas of temperate deciduous forests developed in latitudes stretching between 45 and 55 °N; iii) that regions south of 45 °N also included fragmented temperate deciduous forests.

4.4 Spatial vegetation response during GI 1a-c

High-resolution pollen and plant macrofossil records from CEE indicate a further northerly development of boreal forests containing *Betula* sect. *Albae, Betula humilis, Pinus sylvestris, Populus tremula, Picea abies, Juniperus communis* and *Alnus* into the Baltic region between 13.8 and 12.7 ka cal BP, which may correspond to the GI-1a-c warming in Greenland (Stančikaitė et al., 2008, 2009; Heikilla et al., 2009; Amon et al., 2010; 2012; Gaidamavičius et al., 2011; Veski et al., 2012), whereas the expansion of *Picea abies* in Belarus the was dated ca 13.2 ka cal. BP (Zernitskaya et al., 2005; Makhnach et al., 2009). The northern treeline became located in central Estonia at ~58.5°N (Figs. 4, 5). In the Carpathian region (45-50 °N), forest assemblages changed from those dominated by *Pinus* (*Pinus spp., P. sylvestris, P. cembra, P. mugo*) and *Betula* to mixed *Pinus, Picea abies* and *Betula* (*B. pubescens, B. pendula*). Generally, there is an increased proportion and diversity of cold deciduous taxa (*Salix, Sambucus, Alnus, Populus tremula, Prunus padus*) but also of temperate tree species such as *Ulmus, Quercus, Tilia, Fraxinus excelsior* and *Corylus avellana* at most sites in this region (Figs.

4, 5). The plant macro-remains support the inference of more extensive, dense, and diverse forest cover during this time interval (Wohlfarth et al., 2001; Pokorný et al., 2002; Ampel, 2004; Kuneš et al., 2008; Latalowa et al., 2006; Feurdean et al., 2012b; Magyari et al., 2012).

Sites located south of 46 °N (Slovenia) contained almost pure needle-leaved forests (90%), with only minor contributions of cold deciduous (*Alnus, Betula, Salix*) and warm temperate deciduous taxa (*Quercus, Tilia, Fraxinus excelsior, Acer, Corylus avellana*) (Figs. 4, 5). Sites from Bulgaria (Rila Mountains; Tonkov et al., 2008, 2011), on the other hand, witnessed only modest forest expansion, composed of a mixture of needle-leaved, cold deciduous (primarily at higher elevations) and most notably of warm temperate deciduous taxa (mid-low elevations), whereas no forest expansion is visible in the Thracian Plain (Figs. 4, 5).

The response of vegetation to the GI-1a-c warming can be summarized as exhibiting: i) the greatest spatial expansion of forest cover, forest density, and diversity during the Lateglacial; ii) a more consistent spread of warmth-demanding temperate tree taxa; iii) the expansion of more moisture-demanding trees (*Picea abies*) in the Carpathians Mountains; iv) limited forest development in lowlands of SE Balkans (Figs. 4, 5).

4.5 Spatial vegetation response during GS-1

Significant, region-wide changes in terrestrial vegetation composition occurred in CEE around 12,700 cal yr BP, which may correlate with the onset of cold GS-1 event in Greenland. These largely included i) a decrease in plant biomass; ii) fragmentation of the boreal forest and a more southerly displacement of temperate forest; and iii) a re-expansion of steppe and grassland vegetation (Figs. 4, 5). Superimposed on this large-scale pattern of vegetation changes during GS-1 there is considerable north to south distinctiveness in the vegetation composition. In the north-eastern Baltic area (N of 55° N and 25°E) there was a stronger re-expansion of tundra communities (*Betula nana*, *Salix polaris*), whereas trees disappeared (Amon et al., 2012); ii) in the southern Baltic regions (Latvia, Lithuania, N Poland), small populations of boreal tree species (*Pinus*, *Betula, Picea*) survived the cold GS-1 (Stančikaitė et al., 2008, 2009; Gaidamavičius et al., 2011; Veski et al., 2012), iii) in Belarus, a tundra-forest (*Picea*) landscape developed N of 54 °N and E of 24 °E, and boreal forest S of 54 °N (Zernitskaya, 2008; Makhnach et al., 2009). Sites in the Carpathian region (45-50 °N) show fragmentation of the boreal forests and reduced diversity, but also a replacement of large tracts of dry-adapted needle-leaved taxa (*Pinus* and *Larix*) and *Betula* by *Picea abies Alnus, Ulmus, Quercus* (Fărcaş et al., 1999; Tanțău et al., 2006; Feurdean et al., 2007). In Slovenia, a smaller-scale contraction in the forest cover occurred with needle-leaved taxa (*Pinus* and *Larix*) remaining the dominant vegetation type but also preserving temperate deciduous forest composed of *Quercus, Corylus, Tilia, Ulmus* (Andric et al., 2009; Figs. 4, 5). Pollen sequences at sites further south in the Balkans show either a contraction of forest cover (in the Rila Mountains) that consisted of *Pinus*, *Betula* and *Quercus* and a corresponding marked expansion of xeric herb communities, grasses and other cold-resistant heliophilous herbs (Tonkov et al., 2013), or the persistence (in the lowlands) of xeric steppe, semi-desert vegetation, in the area near Black Sea (Connor et al., 2013).

Overall, apart of the general trend of contraction of the forest cover over the CEE during GS-1, there is also an increase in the steppe communities and therefore enhanced continentallity along a N to S latitudinal transect in this region.

4.6. Other short-term fluctuations

High-resolution pollen records from CEE also document smaller vegetation changes occurring around 13.9 ka cal BP (GI1-d), 13.6 ka (GI-c2) and 13.2 ka cal BP (GI-1b) (Fig. 5). This indicates that short-lived climate fluctuations have also produced some response in the vegetation composition in continental areas (Tanțău et al., 2006; 2014; Feurdean et al., 2007, 2012; Stančikaitė et al., 2008; Ammon et al., 2012; Magyari et al., 2012; Veski et al., 2012).

4.7. Onset of the Holocene and early Holocene (11.7-8 ka cal BP)

Pollen and plant macrofossil records indicate that, from about 11.7 ka, there was a significant increase in biomass production, a retraction of cold- and dry-adapted taxa and a general northward advance of many tree species into areas that were covered by permafrost during the GS-1 (Figs. 4, 5). The species range shift was not uniform over the whole CEE. In the Baltic region (northern Poland, Lithuania, Belarus, Latvia and Estonia), both pollen and plant macrofossil data suggest the establishment of *Pinus–Betula* forest, enriched by *Picea* at ca. 11.7 ka cal BP (Zernitskaya et al., 2005; Heikkilä et al., 2009; Veski et al., 2012), but temperate deciduous forests (*Ulmus, Quercus, Fraxinus*) were largely absent from this region until about 10.5-10 ka cal BP (Stančikaitė et al., 2008, 2009; Gaidamavičius et al., 2011; Gryguc et al., 2014; Figs. 4, 5). At low and middle elevations in the Carpathian region (including Hungary, Czech Republic, Slovakia), there was an initial increase in open woodlands of cold deciduous temperate taxa (*Alnus, Betula, Salix*) at around 11.7 ka cal BP. This was then followed rapidly (11.3 ka cal BP) by a large-scale increase in temperate forests dominated by *Ulmus, Quercus, Tilia, Acer, Fraxinus excelsior, Corylus avellana,* though the forests preserved a more open character in lowlands (Willis et al., 1998; Tanțău et al., 2006, 2009; Magyari et al., 2010; Feurdean et al., 2012; 2013). This forest composition was preserved at least until 8 ka and represented a larger extension of temperate forest than today. Plant macrofossil analysis at these sites also indicates that *Larix* was a significant component of the very early Holocene forests likely as a response to continental conditions (Feurdean et al., 2007; Magyari et al., 2012b). A rapid expansion of *Pinus* and temperate deciduous taxa was documented in Slovenia (Andrič et al. 2008, 2009). In the Balkans (Rila Mts., Bulgaria) the rapid climate warming initiated a widespread of pioneer *Betula* forests with *P. sylvestris/mugo*, *P. peuce* for the time interval 11.6-9.8 ka at mid-higher elevations altitudes, which shaped the tree-line for nearly 4000 years after the onset of the Holocene. The fossil pollen record also revealed the beginning of a wide distribution of mixed *Quercus* forests with *Tilia*, *Ulmus*, *Fraxinus excelsior*, *Acer* below the birch zone. These forests reached their maximal distribution *ca.* 10000-9800 cal. BP (Tonkov et al., 2013). Lowlands in SE Bulgaria recorded a delayed forest expansion due to the prevalence of drier climatic conditions (Connor et al., 2013).

5. Key findings

i) Analysis of loess deposits suggests more pronounced phases of coarse-grain deposition, associated with drier and probably colder climate, during the MIS 3 than during the last glacial maximum. This is likely to be a consequence of changes in general atmospheric circulation due to initial ice sheet growth, as well as changes in depositional regime of the Danube fluvial system. During the MIS 2, enlarged northern European ice masses may have partially blocked penetration of the Atlantic air to the east, with strong anticyclonal circulation over the Fennoscandian Ice Sheet during the peak of the last glacial phase. The inference of warmer condition during MIS 3 is also supported by a more continuous growth of Romanian speleothems through this period.

ii) Loess-covered lowland areas in Serbia, SE Hungary, Romania and Bulgaria that are characterised by warm/dry macroclimate today were dominated during the MIS 3 by warm steppe vegetation, often with *Artemisia*. By contrast, similar loess covered areas but with more humid climatic conditions supported predominant parkland boreal forests accompanied by some temperate deciduous trees (*Picea abies*, *Pinus sylvestris*, *P. cembra*, *Larix decidua*, *Ulmus*, *Salix* and *Alnus*). Despite the high-resolution studies of dry loess steppe areas south of 45 °N, millennial-scale vegetation fluctuations have not been recognized. This suggests that temperature and precipitation fluctuations during the MIS-3 were of relatively low magnitude, failing to trigger major shifts in biomes or that the changes were of significant magnitude but did not cross critical thresholds for biome shift. On the other hand, a few available records from lowlands and moutaines areas between 45 and 48 °N suggest recurring fluctuations between boreal forest-steppe and steppe vegetation. This suggests that millennial-scale climatic oscillations drove a stronger vegetation response in these more humid macroclimate areas, interstadials were characterised by boreal and temperate tree advances lasting for 200-300 years.

iii) Most records from the continental CEE cover the period 14.7 and 8 ka cal BP and show that this region experienced climate changes more or less synchronous (within centennial-scale age errors) with those around the North Atlantic region. However, the magnitude of these climatic shifts appears to be less dramatic in the continental part of Europe than in more oceanic Western Europe. Thus, whereas the onset of GI-1e in Greenland was marked by a 10°C increase in annual temperature, the corresponding warming in CEE is only of about 2.8 – 3°C. Similarly, the cooling associated with the onset of GS-1 in Greenland was of about 1-2 °C for MAT. The climate records from CEE show that temperature changes were more pronounced in winter than in summer during both cold and warm periods of the Lateglacial indicating enhanced seasonality. Precipitation dropped markedly at the onset of cold periods, suggesting increased continentality. In contrast, early Holocene seasonality was driven by high summer insolation and therefore increased summer temperature.

iv) The consequence of lower amplitude cooling in CEE compared to Western Europe implies that vegetation was less drastically impacted and allowed for the persistence of open boreal forests at latitudes below 55 °N even during the coldest intervals of the last glacial. However, higher resolution pollen records covering the Lateglacial clearly indicate that vegetation responded sensitively to these climate shifts, with the most pronounced changes visible at 14.7 (GI-1e), 13.8 (GI-1c-a), 12.7 (GS-1), and at 11.7 ka cal BP (GS-1/Holocene transition). This further underscores the impact of climate change on vegetation across a broad region (Giesecke et al., 2011).

v) Differences exist in the temporal response of vegetation to the climate shifts compared to the actual climate shifts in the Greenland ice core record. Thus, while vegetation responded to GI-1e warming, the magnitude of this vegetation response was smaller compared to the magnitude of temperature increase suggested by the Greenland oxygen isotope record at 14.7 ka cal BP. Conversely, a strong vegetation shift is visible in most pollen records during G1c-a, at a time when the NGRIP record indicates a more modest temperature increase.

vi) On a spatial scale, the records from CEE show that the magnitude of the vegetational response follows a S-N latitudinal and elevation trend. Vegetation at more northern locations appears more strongly impacted by climate changes between 8 and 60 ka, whereas the more southern locations appear more stable. There is also a marked N to S increase in steppe communities, suggesting an increase in continentality following a N-S latitudinal transect. From the these pollen records it is apparent that besides the influences of the North Atlantic, other centers of climatic variability (the Mediterranean Sea, NW Russia and the Black Sea) have created a complex climatic region and vegetation pattern.

6. Suggestions for the future

The key points above not only highlight the main findings, but also the major gaps and problems in palaeoclimatic data from CEE for the period covering 60-8 ka, as well as a selection of future directions for improvement. Numerous records have poor chronological control, mainly because of too few dates and use of bulk sediment. There is also a subjective tendency towards wiggle-matching and tuning of time scales, often falsely synchronising the forcing (climate) and response (vegetation). Searching for (crypto) tephra layers such as the Campanian Ignimbrite (39,280 ±110 cal yr BP), Vedde Ash (12,007-12,235 b2K cal yr BP), and Laacher See tephra (12,880±40 varves yr BP), would better constrain chronologies and allow for correct identification of lags in the response of regional climate systems and vegetation to both external and internal forcings. In this respect, an important step has been achieved by the identification of the Laacher See Tephra in the Trzechowskie palaeolake (Wulf et al., 2013) and Węgliny (Housley et al., 2013). These advances have allowed a precise correlation between pollen and lithological records in Western and Eastern Europe, showing that the abrupt environmental changes and associated impacts on vegetation were synchronous in these regions at the B-A/YD transition. In addition, the use of statistically-secure age-models could improve chronologies.

Quantitative climate reconstructions in the CEE are extremely rare. Therefore, a major future research direction is the construction of local calibration sets and transfer functions to improve the existing, insufficiently quantified biotically-derived paleoclimate reconstructions. The different present-day climate to that of Western and Northern Europe, where most of the calibration sets used for CEE originate, adds a strong bias to the quantitative reconstructions. Except for pollen, there is no single proxy that is investigated in a similar manner in the whole area making proxy inter-comparison difficult. This calls for a coordinated effort to identify sites from various climatic settings that need to be investigated in order to obtain a coherent picture of patterns in past climate changes.

While the application of new proxies or methods could provide a much clearer image of the region's past climate, we believe that a systematic use of the well established, classical proxies (i.e., accurately dated and quantified) could also result in an improved understanding of the past climate and environmental changes in the area.

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Figures caption

Figure 1. Location of sites discussed in the text. Numbers refer to sites listed in Table 1: 1 – Lake Bled (SI), 2 – Żabieniec Bog (PL), 3 – Brazi Lake (RO), 4 – V11 Cave (RO), 5 – Lake Sergeyeyskoe (BY), 6 – Lake Ginkunai (LT), 7 – Jezioro Linówek (PL), 8 – Kobylnica Wołoska (PL), 9 – Lake Kurjanovas (LV), 10 - Lake Nakri (EE), 11 - Labský důl (CZ), 12 – Švarcenberk (CZ), 13 – Kis Mohos (HU), 14 – Steregoiu and Preluca Ţiganului (RO), 15 - Avrig (RO), 16 –

Straldzha (BG), 17 – Trilistnika (BG), whereas small letters refer to loess sites: a - Dolni Vestonice (Antoine et al., 2013); b – Katymar (Bokhorst et al., 2011); c – Tokaj (Schatz et al., 2011); d – Zmajevac (Banak et al., 2013); e – Petrovaradin (Marković et al., 2005); f – Irig (Marković et al., 2007); g – Mońorin (Bokhorst et al., 2011); h – Titel (Bokhorst et al., 2009); i – Surduk (Antoine et al., 2009); j – Crvenka (Stevens et al., 2011); k – Tyszowice (Jary and Ciszek, 2011); l – Dubavka (Bokhorst et al., 2011); m – Radymo (Bokhorst et al., 2011); n – Likkvin (Rutter et al., 2003); o – Korostylievo (Rutter et al., 2003); p - S. Bezradychy (Bokhorst et al., 2011); q – Sazhijka (Bokhorst et al., 2011); r – Pyroove (Bokhorst et al., 2011); s – Stayky (Kadereit and Wagner, 2014); t – Korshov (Jary and Ciszek, 2011). Golobovo (loess site in Russia, not shown).

Figure 2. Selected palaeoclimate reconstructions from CEE between 15 and 8 ka cal BP plotted against the NGRIP δ18O curve (Rasmussen et al., 2006) and INTIMATE event stratigraphy of Blockley et al. (2012b).

Figure 3. Vegetation changes during mid to late last glacial (MIS 3, 2) in selected terrestrial pollen records from CEE. The taxa are grouped into a summary percentage diagram where each pollen type was assigned to a major vegetation type following a simple biome scheme.

Figure 4. Vegetation changes between 14.7 and 8 ka cal BP in selected high-resolution terrestrial pollen records from CEE. The taxa are grouped into a summary percentage diagram where each pollen type was assigned to a major vegetation type following a simple biome scheme. All records are plotted using the best available chronology for each individual site.

Figures 5. Vegetation changes at selected time slices between 17 and 8 ka cal BP. The time slices were selected to match significant climatic shifts during the investigated time period. The taxa are grouped following the same scheme as in Figure 4 and 5.

Tables

Table 1. List of compiled records from CEE in the INTIMATE chronological framework, specifying the dating method used, the climate variable that was reconstructed and the used proxy.

Table 2. Summary of inferred climate changes between 14.7 and 8 ka cal BP at individual high-resolution sites from CEE.

Table 3. Major vegetation types (megabiomes) in CEE Europe. Each pollen type was assigned to one of these megabiomes.

Table 4. Temporal and spatial environmental dynamics over the Eastern European loess belt. Abbreviations: CP-continuous permafrost; DP-discontinuous permafrost; T-tundra; TA-taiga; DF-forest; FS-forest steppe; PL-mosaic parkland; MS-modern steppe; CLS-cold loess steppe; WLS-warm loess steppe; DWLS-dry warm loess steppe.

Table 1

Nº	Archive	Country	Site	Chronology			Reconstructed variable	Quantified proxy	References
				Type of dating	Number of dated points	Mean temporal resolution			
1	Lake sediments	Slovenia	**Lake Bled**	^{14}C, tephra	2 3	69 (isotopes) 180 (pollen)	Temperature	Bulk carbonates δ^{18}O Pollen Plant macroremains	Andrič et al., 2009, Lane et al., 2011
2		Poland	**Żabieniec bog**	^{14}C	5	252	Temperature	Chironomids	Plociennik et al., 2011
3		Romania	**Lake Brazi**	^{14}C	7	124	Temperature	Chironomids	Toth et al., 2012
4	Speleothemes	Romania	**V11 Cave**	U/Th	10	63	Temperature	Calcite δ^{18}O	Tămaş et al., 2005
5	Pollen in lake sediments /Peat	Belarus	**Lake Sergeyeyskoe**	^{14}C	5	121	Vegetation	Pollen	Makhnach et al., 2009
6		Lithuania	**Lake Ginkunai**	^{14}C	8	56	Vegetation	Pollen	Stancikaite et al., 2008, 2009
7		Poland	**Jezioro Linówek**	^{14}C	2	200 (pollen) 40 (lant macroremains	Vegetation Lake level	Pollen Plant macroremains	Gałka et al., 2014
8			**Kobylnica Wołoska**	^{14}C	6	66 (pollen) 18 (plant macroremains	Vegetation	Pollen Plant macroremains	Kołaczek et al., in press.
9		Latvia	**Lake Kurjanovas**	^{14}C	6	66	Vegetation	Pollen Plant macroremains LOI	Heikkilä et al., 2009
10		Estonia	**Lake Nakri**	^{14}C	9	80 (pollen) 30 (macro)	Vegetation	Pollen Plant macroremains LOI	Amon et al., 2012; Veski et al., 2012
11		Czech Republic	**Labský důl**	^{14}C	5	165	Vegetation	Pollen	Engel et al., 2010
12			**Švarcenberk**	^{14}C	3	60	Vegetation	Pollen	Pokorný, 2002, Pokorný et al., 2010
13		Hungary	**Kiss Mohos**	^{14}C	8	163	Vegetation	Pollen	Willis et al., 1998
14		Romania	**Preluca Ţiganului** **Steregoiu**	^{14}C	12 12	65 35	Vegetation Temperature Precipitation Lake level	Pollen Plant macroremains Zoological remains LOI Micro-macrocharcoal Mineral magnetic measurements	Björkman et al., 2002; Feurdean et al., 2007, 2012b; Ampel, 2004
15			**Avrig**	^{14}C	10	104	Vegetation	Pollen	Tanţău et al., 2006
16		Bulgaria	**Atolov Straldzha**	^{14}C	7	790	Vegetation Biomes	Pollen Micro-charcoal Mineral magnetic susceptibility	Connor et al., 2013
17			**Trilistnika**	^{14}C	6	293	Vegetation	Pollen	Tonkov et al., 2008; 2012

Table 2

Chronology		NW Slovenia	S Romania	W Romania	NW Romania	Central Poland	Baltic region
Event	**Age (b2k)**	**Lake carbonates $\delta^{18}O$**	**Chironomids**	**Speleothem $\delta^{18}O$**	**Pollen-based**	**Chironomids**	**Pollen and macrofossil -based**
8.2 ka BP	8300 – 8140	Cold			Cold		Cold
9.3 ka BP	9350 – 9240	Cold		Cold	Cold		Cold
Holocene	11703	Warm	Warm	Warm	Warm		Moderate
GS-1	12896 - 11703	Cold and dry	Moderate	Cold and dry	Moderate, with very cold winters, dry	Mild	Cold
GI-1a	13099 – 12896	Moderate, drying tendency	Moderate	Warm	Slightly warm, wet	Warm	Moderate
GI-1b	13311 – 13099	Moderate	Moderate	Cold and wet	Moderate, cold winter	Warm	Cold
GI-1c	13954 – 13311	Moderate	Moderate	Warm	Warmest during the LG, warm winter, wet	Warm, colder than GI-1e	Moderate
GI-1d	14075 – 13954	Moderate, wetter	Cold	Cold	Cool winters, slightly warm summer	Warm	Cold
GI-1e	14692 – 14075	Warm and dry	Moderate	Very warm	Warm and dry	Warm	Cold
GS-2a		Very cold	Very cold			Very cold	Very cold

Table 3

Megabiomes	**Characteristic pollen taxa**
Coniferous trees	*Picea, Pinus, Abies, Larix, Juniperus*
Cold deciduous trees	*Alnus, Betula, Salix, Populus*
Temperate deciduous trees	*Ulmus, Quercus* (deciduous-type), *Tilia, Corylus, Acer, Fraxinus, Acer, Carpinus, Hedera, Ilex, Fagus, Viscum*, *Sambucus, Viburnum, Cornus, Frangula, Myrica, Prunus, Sorbus*
Warm temperate taxa	*Quercus* (evergreen-type), *Olea, Carpinus orientalis/Ostrya, Loranthus, Fraxinus ornus-type, Rhamnus/Paliurus, Euonymus, Jasminum, Colutea, Cotinu*s
Grass and shrubs	Ericaceae, *Calluna, Hippophae,* Poaceae, Cyperaceae, other NAP
Xerophythic herbs	*Artemisia* and Chenopodiaceae/Amaranthaceae

Table 4

Period/Loess subprovinces	Early last glacial	Middle last glacial	Late last glacial	Early Holocene
Between the Alps and the Carpathians	CLS	FS-PL-WLS	CLS-T	DF-FS-TA
N of the Carpathian Mts.	DP	FS-T-TA	CD-T-CLS-TA	DF-FS-TA
Middle Danube	PL-CLS-DWLS	PL-WLS-DWLS	CLS-PL	FS-PL-MS
Lower Danube and Northern coast of the Black Sea	DWLS-CLS	PL-WLS-DWLS	DWLS-CLS	FS-PL-MS
Ukrainian and Russian lowlands	DP-CLS	FS-WLS-T	DP-T-CLS	DF-FS-TA-MS

Figure 1

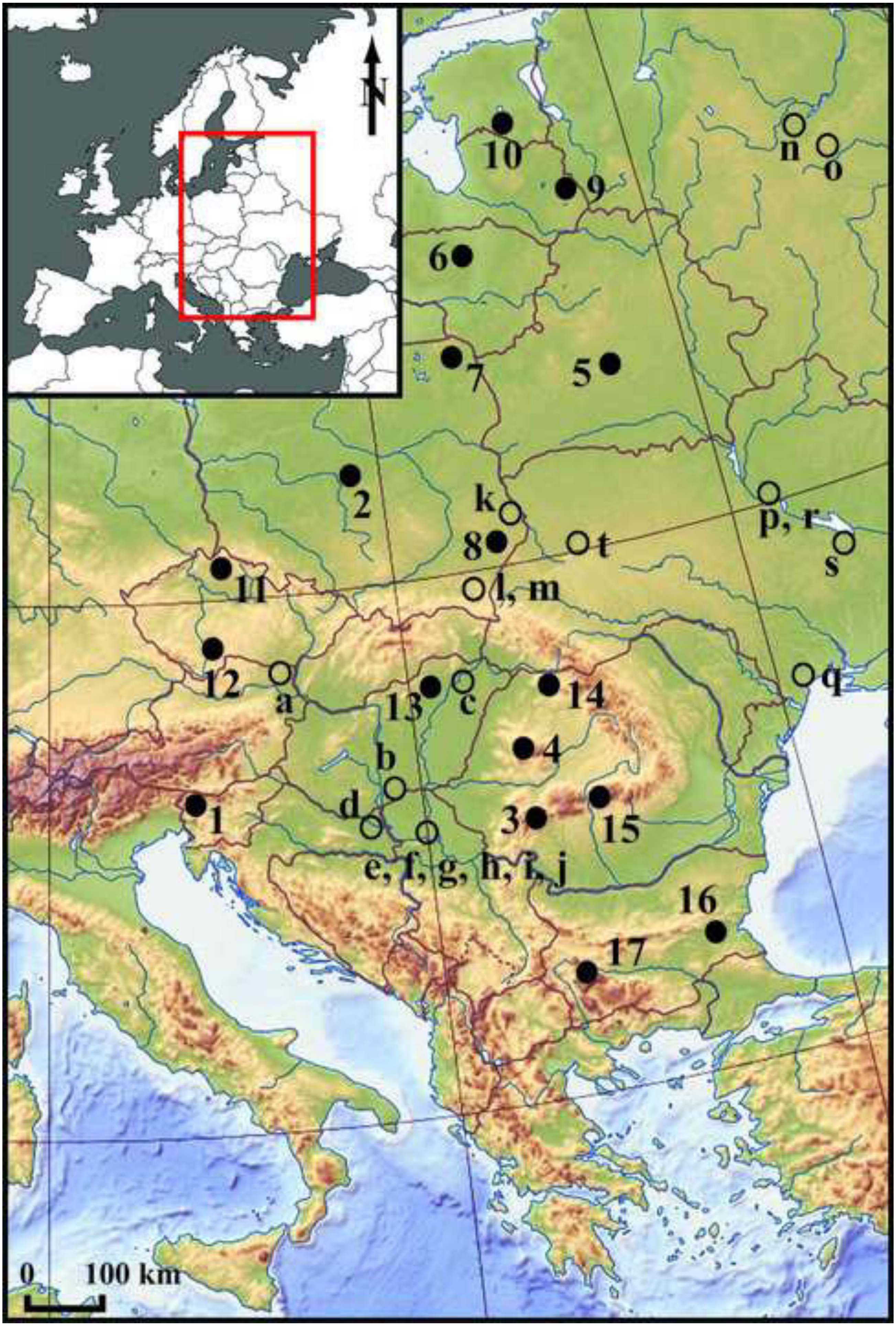
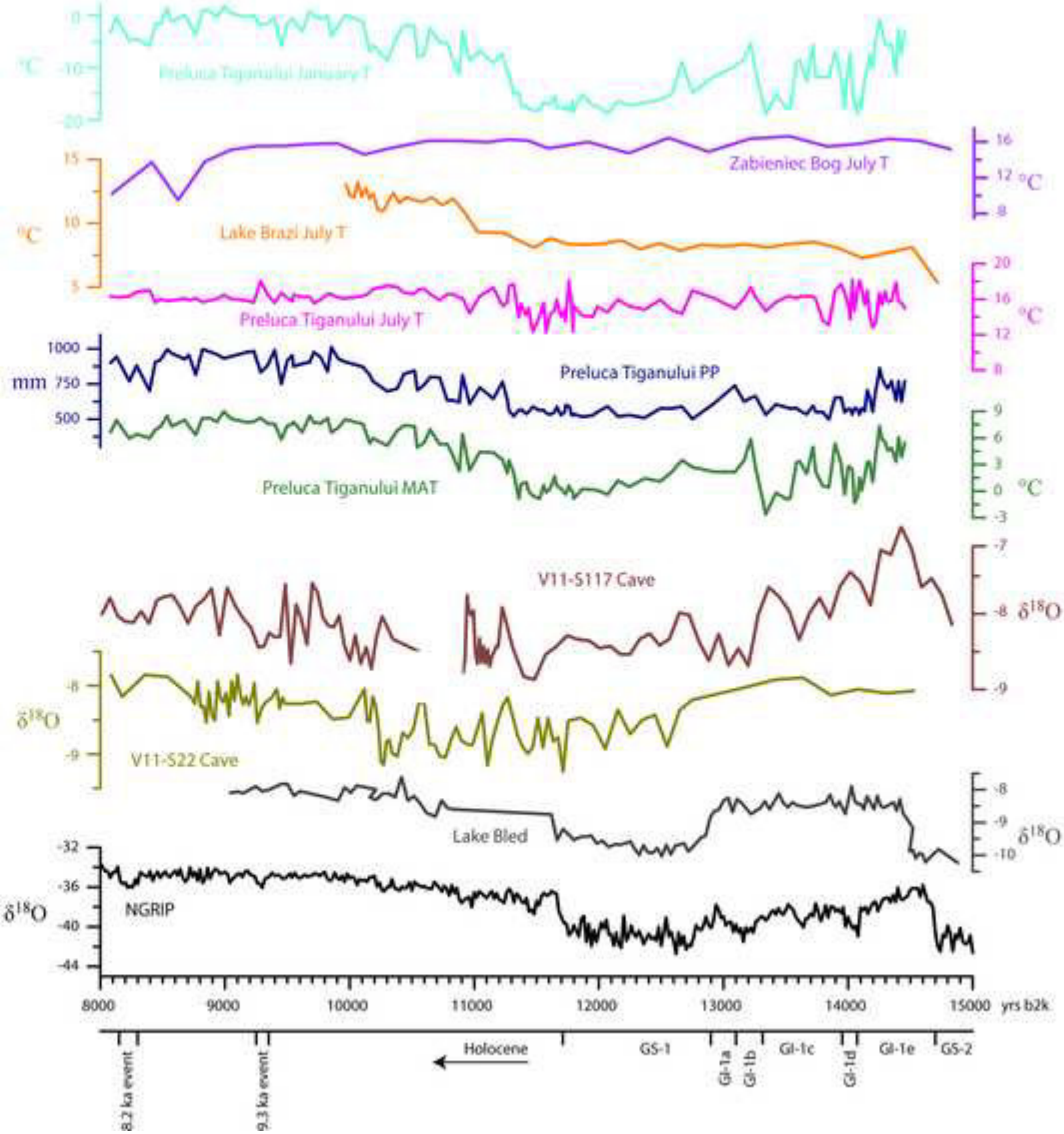

N
10
9
n
o
6
7
5
2
k
p, r
8
t
s
11
l, m
12
a
13
c
14
q
4
b
d
1
3
15
e, f, g, h, i, j
16
17
0
100 km

Figure 2



°C
0
-10
-20
Preluca Tiganului January T
Zabieniec Bog July T
16
12
8
°C
15
10
5
°C
Lake Brazi July T
Preluca Tiganului July T
20
16
12
8
°C
1000
750
500
mm
Preluca Tiganului PP
9
6
3
0
-3
°C
Preluca Tiganului MAT
V11-S117 Cave
-7
-8
-9
δ18O
-8
-9
δ18O
V11-S22 Cave
Lake Bled
-8
-9
-10
δ18O
-32
-36
-40
-44
δ18O
NGRIP
8000
9000
10000
11000
12000
13000
14000
15000
yrs b2k
8.2 ka event
9.3 ka event
Holocene
GS-1
GI-1a
GI-1b
GI-1c
GI-1d
GI-1e
GS-2

Figure 3

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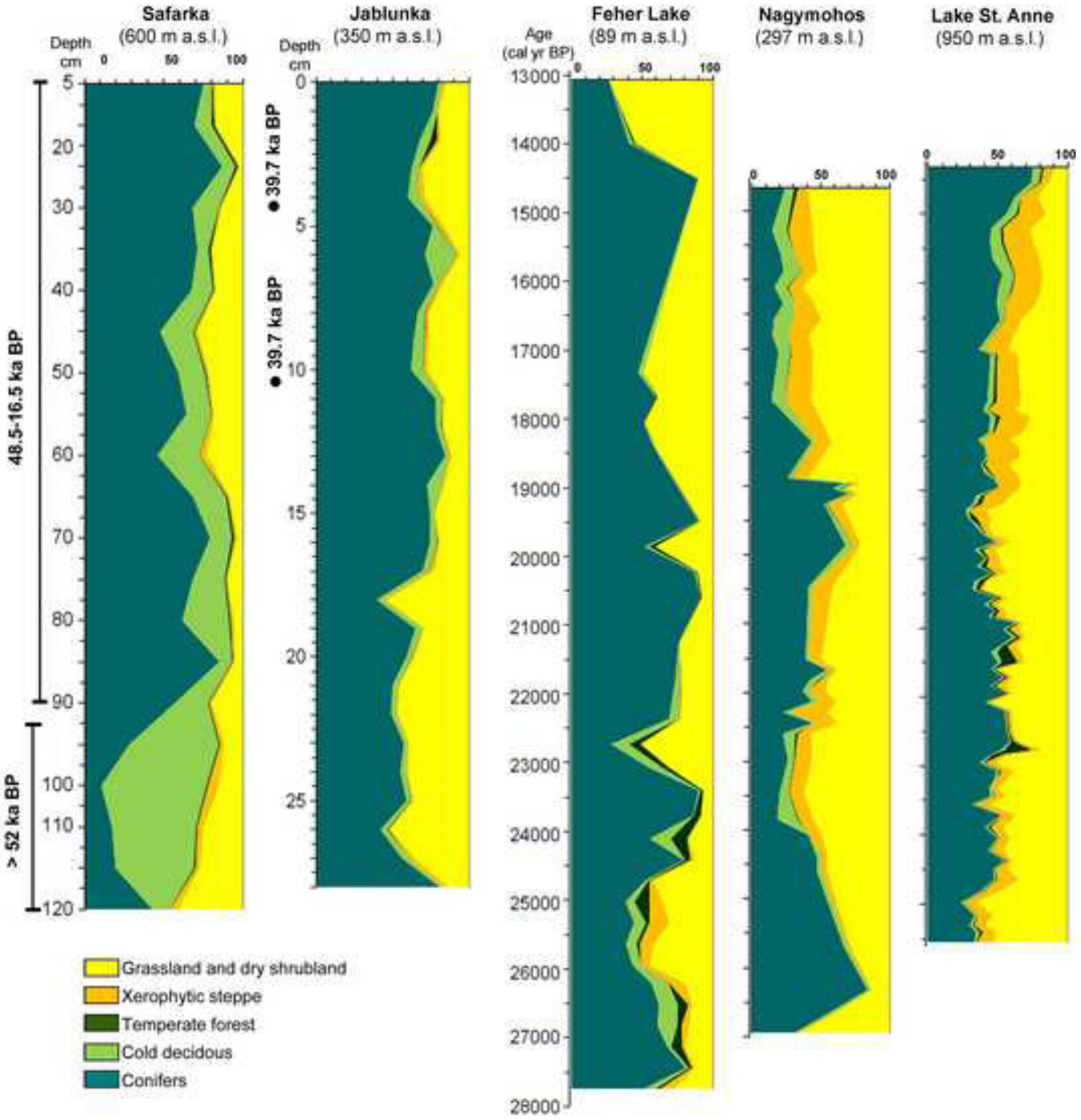

Figure 4

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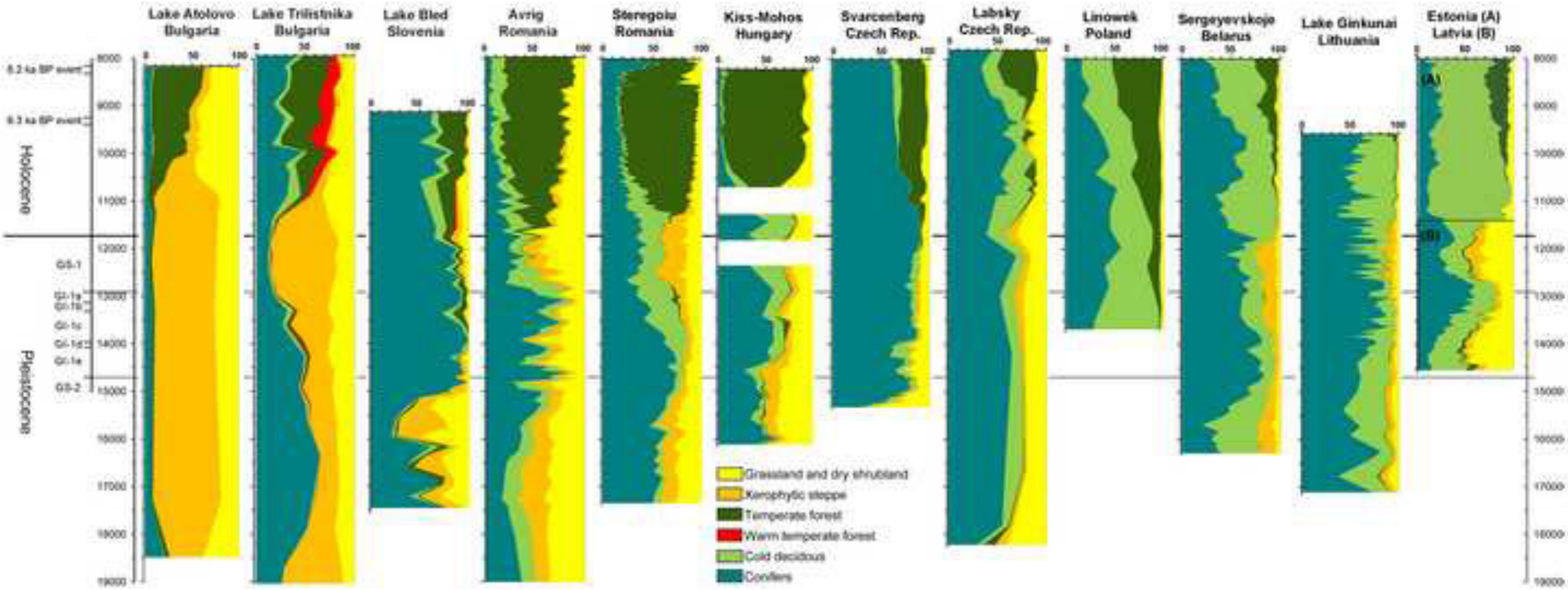

Figure 5a

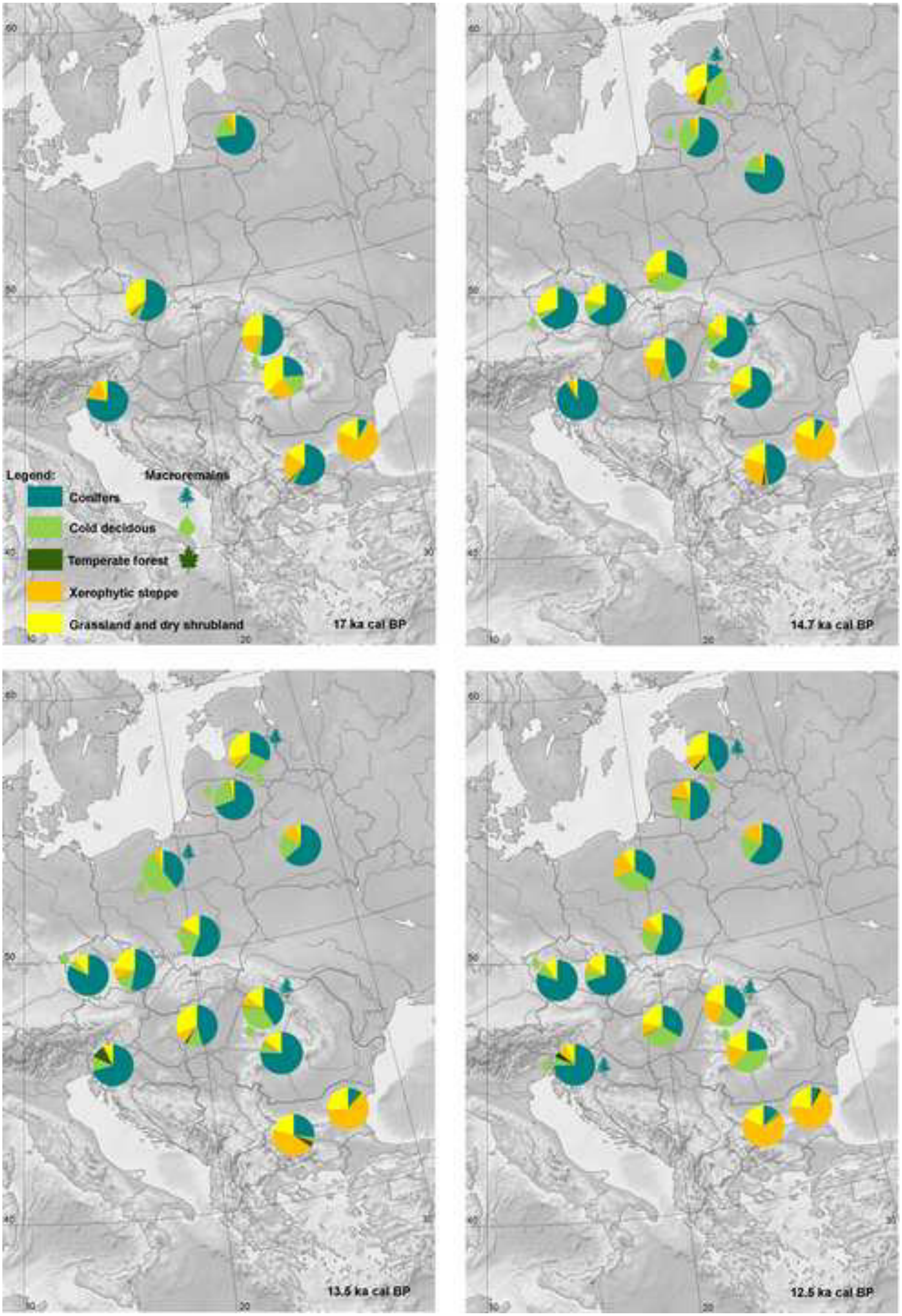
Legend:
Macroremains
Conifers
Cold deciduous
Temperate forest
Xerophytic steppe
Grassland and dry shrubland
17 ka cal BP
14.7 ka cal BP
13.5 ka cal BP
12.5 ka cal BP
60
50
40
10
20
30

Figure 5b

Click here to download high resolution image