

Mammal Extinction Facilitated Biome Shift and Human Population Change During the Last Glacial Termination in East-Central Europe Enikő

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Abstract

Studying local extinction times, associated environmental and human population changes during the last glacial termination provides insights into the causes of mega- and microfauna extinctions. In East-Central (EC) Europe, Palaeolithic human groups were present throughout the last glacial maximum (LGM), but disappeared suddenly around 15 200 cal yr BP. In this study we use radiocarbon dated cave sediment profiles and a large set of direct AMS ^{14}C dates on mammal bones to determine local extinction times that are compared with the Epigravettian population decline, quantitative climate models, pollen and plant macrofossil inferred climate and biome reconstructions and coprophilous fungi derived total megafauna change for EC Europe. Our results suggest that the population size of large herbivores decreased in the area after 17 700 cal yr BP, when temperate tree abundance and warm continental steppe cover both increased in the lowlands Boreal forest expansion took place around 16 200 cal yr BP. Cave sediments show the decline of tundra associated narrow-headed vole and arctic lemming populations at the same time and the expansion of steppic common vole. We found the last dated appearance of arctic lemming at $\sim 16\,640$, narrow-headed vole at $\sim 13\,340$, and estimated the last appearance of woolly mammoth at 12 690 – 16 150 (median: 15 210) and reindeer at 8300 – 14 480 cal yr BP (median: 12 550) using the PHASE model in OxCal. The population decline of the large herbivore fauna slightly preceded the terrestrial vegetation change and likely facilitated it via restricted grazing and the accumulation of plant biomass. Furthermore, we conclude that the Late Epigravettian population had high prey-fidelity; they left the basin when these mammals vanished.

Introduction

Despite the richness of vertebrate records from cave deposits and open air sites from the Late Pleistocene¹, 20th century paleontological research has not taken the opportunity to date rigorously the latest appearance of large mammals and rodents during the last glacial termination in EC Europe (the eastern part of Central Europe), and also failed to date systematically cave mammal bone stratigraphies for the last 40 000 years, the time period for which AMS ^{14}C dating would have been a perfect choice^{2,3}. Only in recent years we see a resurgence of Upper Weichselian megafauna research with re-visiting and dating key localities often associated with human occupation^{4–6}. The more our understanding of Late Epigravettian human lifestyle, economy and hunting strategy increases, the clearer is that the abrupt disappearance of mobile Epigravettian groups from the Carpathian Basin (CB) around 15 200 cal yr BP is related to changing environmental conditions, such as the rapid disappearance of their dominant prey, the reindeer (*Rangifer tarandus*), the decimation of secondary preys such as wild horse (*Equus ferus*), and the worsening visibility of the landscape at hunts due to forest cover increase^{7,8}.

Here, we focus on one megafauna element, the woolly mammoth (*Mammuthus primigenius*) and several ungulate and rodent species that co-inhabited the CB with a full glacial ecological setting that is relatively well-understood^{9–14}.

Using a large dataset of dated mammoth bones, two cave profiles with known human occupation and five multi-proxy paleoecological records from lake and mire sediments covering the last glacial maximum (LGM) and last glacial termination (Fig. 1), we test a specific paleoecological hypothesis relating rapid climate change to population dynamics; namely that transitions from cold to warm intervals were briefly optimal for grazing megafauna that was then followed by rapid regional extinctions¹⁵. We also examine the order of faunistic and vegetation biome changes and its casual linkage. As it has been demonstrated in a few cases^{16–18}, megafauna collapse usually acts as secondary main driver in vegetation change by leaving behind accumulated plant biomass that is prone to auto-ignition, and resultant wildfires then lead into abrupt plant ecosystem shifts with the establishment of completely different biomes.

Studied cave sites and the mammoth bone collections

The studied caves are in Northern Hungary, in the Pre-Carpathian hill region (Fig. 1). Jankovich Cave is a well-known archaeological site in the Gerecse Hills that includes layers from the Middle Paleolithic to the Late Upper Palaeolithic. In our study the Late Upper Palaeolithic layer is in focus that yielded a small lithic tool collection^{19,20} most likely belonging to the Late Epigravettian. Situated at 330 m a.s.l. on a steep east facing slope, 20 m below the peak, its 88 m long chamber has been excavated repeatedly since 1913, and block II excavated by László Vértes in 1956 was selected for study (Suppl. Fig. 1) where a cold adapted microfauna was replaced by temperate species²⁰ and assigned to the Pleistocene/Holocene boundary. We selected 21 bone samples from 13 layers for AMS ¹⁴C dating (Suppl. Tables 1 & 2).

Rejtek I Rock Shelter is situated in the Bükk Mts at 534 m a.s.l. on an east facing slope, about 10 m above the valley bottom (Fig. 1, Suppl. Fig. 2). Our AMS ¹⁴C measurements were done on profiles II (upper 4 layers) and III (layers 5-8)²¹. These two profiles were earlier combined on the basis of depth²² and faunistic and floristic changes were published accordingly (Suppl. Figs. 2 & 3; Suppl. Tables 1 & 3). Late Upper Palaeolithic stone tools were detected²³, detailed charcoal and mollusc analyses were done^{4,24,25}, and bone assemblages were studied quantitatively^{22,26}. 24 bone samples from 8 layers were selected for dating (Suppl. Tables 1 & 3). During the selection procedure priority was given to mammal species with missing or uncertain data on last occurrence: e.g. steppe pika (*Ochotona pusilla*), arctic lemming (*Dicrostonyx torquatus*), narrow-headed vole (*L. (S.) gregalis*), reindeer (*R. tarandus*), and willow grouse (*Lagopus lagopus*).

Woolly mammoth was common in the CB during the Weischelian glaciation, ca. 400 specimens and 6 skeletons were found in Hungary, but ¹⁴C dates were only available for 8 specimens²⁷. In scope of this study we selected 21 localities (Suppl. Table 4, Fig. 1) for AMS ¹⁴C dating.

Cave localities, lake and mire sites used for the pollen-based climate and biome reconstructions in this study are described in detail in the Supplementary Material.

Results

Last glacial termination faunal changes and last detection times

Stratigraphically consistent, down-profile aging dates were obtained in both caves below 1 m sediment depth (layers 8–12 in Rejtek, layers 5–10 in Jankovich), while in the top meter mixed Holocene and Pleistocene ages pointed to significant disturbance, likely relocation of bones from previous excavations (Jankovich), or burnt bones had weak insufficient collagen preservation unsuitable for dating (Rejtek, Suppl. Tables 1–3). The age range of the bone assemblages in the two caves is different: Jankovich layers 5–10 date between 17 550 and 15 300 cal yr BP, while Rejtek layers 8–12 span 13 450–9 950 cal yr BP. Faunal changes at the Pleistocene-Holocene transition were only traced at Rejtek. The age-depth models (Suppl. Figure 4) suggest that sediment accumulation rates were relatively even in both caves, *ca.* 0.5 mm yr⁻¹. Major faunal changes in the older Jankovich profile suggest that common vole (*Microtus arvalis*), narrow-headed vole (*L. (S.) gregalis*) and arctic lemming (*D. torquatus*) were dominant in the vole fauna after the last glacial maximum (LGM: 26 – 21 ka cal BP) up until 16 360 cal yr BP; this assemblage was replaced by common vole (*M. arvalis*) and bank vole (*Clethrionomys glareolus*) dominance by 15 540 cal yr BP suggesting significant warming and the disappearance of steppe-tundra habitats. Radiocarbon dating confirms that this change started after Heinrich event 1 (HE-1) and ended by the onset of the Bølling/Allerød Interstadial (GI-1e: ~14 700 cal yr BP) (Fig. 2; Suppl. Figure 5). The Holocene onset is characterised by further increase in the forest dweller bank vole (*C. glareolus*) suggesting further increase in forest cover. In terms of the vole assemblage inferred vegetation summarized in Fig. 2, a transition from wooded steppe tundra to continental forest steppe is inferred at ~ 15 540 cal yr BP. The stratigraphic vole relative frequency diagram from Jankovich Cave in Suppl. Figure 5 also includes the NGRIP $\delta^{18}\text{O}$ record and implies that the arctic lemming and tundra vole (*D. torquatus* & *M. oeconomus*) dominance between 17 000–16 300 cal yr BP is likely connectable to the HE-1 cooling. Steppe pika (*O. pusilla*) retreated after this interval (Suppl. Table 1). Associated large mammalian fauna of Jankovich Cave also indicates this climatic change. Cave bear (*Ursus spelaeus*), reindeer (*R. tarandus*), cave lion (*Panthera (Leo) spealea*), arctic fox (*Vulpes lagopus*) and horse (*Equus sp.*) characterize the lower layers that gradually disappear upwards in the sequence of the cave. Note however that large mammalian bones were not directly ¹⁴C dated.

Vole and rodent relative frequency diagrams from the Rejtek I Rock shelter along with macrofauna element compositional change (Fig. 2; Suppl. Figure 6) demonstrate that accumulation started during the Allerød interstadial (~ GI-1b) and the major change in this record is the common vole → bank vole (*M. arvalis* → *C. glareolus*) dominance change at around 12 200–11 700 cal yr BP that shows good agreement with the Holocene transition and the faunal change suggests forest expansion. European pine vole (*M. subterraneus*) and wood mouse (*Apodemus sylvaticus*) relative frequencies also increase at the Holocene transition supporting the inferred warming and forest cover increase. In the Allerød warm period willow grouse (*L. lagopus*; dated to 14 610–15 190 cal yr BP; Suppl. Table 1), rock ptarmigan (*L. mutus*), steppe pika (*O. pusilla*), reindeer (*R. tarandus*) and steppe bison (*Bison priscus*; bone with low collagen) were still present, but they disappeared in the Holocene layers (Fig. 2; Suppl. Figure 6). This suggests a

Late Glacial (LG) persistence of some cold adapted taiga, forest tundra and steppe elements. This cave sequence is exceptional by the available detailed charcoal record from the same sediment layers in which the mammal bones were found. As shown in Suppl. Figure 3 the dominant trees in the LG landscape of Rejtek were needle leaved: Norway spruce (*Picea abies*) and Arolla pine (*Pinus cembra*) charred wood remains were found together with Scots pine (*P. sylvestris*), and from ca. 13 000 cal yr BP mixed deciduous, maple (*Acer platanoides*), field elm (*Ulmus campestris*), hornbeam (*Carpinus betulus*) and beech (*Fagus sylvatica*) dominated charcoal assemblages suggested a LG expansion of several early and late successional deciduous trees^{4,24}. Particularly striking was the appearance of beech and hornbeam that spread later at 300 m a.s.l. in the Bükk Mts, around 6500 cal yr BP^{28,29}. Its LG presence supports isoenzyme and chloroplast (cp) microsatellite DNA studies inferring possible cryptic populations in the N Hungarian Hills³⁰. The mollusc fauna of Rejtek also pointed to over 65 % forest dwellers (Clausiliidae, *Cochlodina cerata*) in the LG and Early Holocene layers pointing to a forested landscape^{4,25}.

Finite ¹⁴C dates suggest that arctic lemming (*D. torquatus*) likely disappeared or its population significantly decreased in the Gerecse Hills around 16 640 cal yr BP, narrow-skulled vole (*L. (S.) gregalis*) around 13 340 cal yr BP, while steppe pika (*O. pusilla*) survived into the Early Holocene; the youngest detection time is around 11 015 cal yr BP at Rejtek (Suppl. Table 1; Fig. 3). We also dated several reindeer (*R. tarandus*) bones; the youngest date from a stratigraphically consistent, undisturbed layer was ~ 15 195 cal yr BP (Suppl. Table 5; Suppl. Figure 7). Taking into account other published reindeer localities in the CB (15 sites) we used the Phase model in OxCal³¹ to estimate the last appearance of reindeer. The end boundary in the model provides an estimate at 8300–14 480 with a median at 12 550 cal yr BP.

Radiocarbon ages from the woolly mammoth (*M. primigenius*) bone assemblages from the CB (Suppl. Table 4; Suppl. Figure 8) suggest that out of the 40 bones dated, 12 had low collagen content unsuited for dating, 16 samples dated beyond 40 000 ¹⁴C BP and 12 provided dates suitable for calibration.

Combined with earlier published dates from the CB, Suppl. Figure 8 summarizes the distribution of the 2σ calibrated age ranges using Intcal20³². The youngest known woolly mammoth is dated to 16 180 (15 830–16 010) cal yr BP from Csajág³³; there are eight bones dated younger than 20 ka, nine between 20–30 ka and twenty dated beyond 30 ka cal BP. Although the number of dated bones is certainly still just a small fraction of the bones available in museum collections, they show an apparent absence between 22–24.5 ka and 27.4–32.5 ka cal BP. These data furthermore suggest that woolly mammoth was common in the CB after the LGM until 18 ka cal BP, population decline was strong by 16.2 ka cal BP, and the species likely persisted locally during the coldest LGM period. The Phase model (n = 26) suggests last appearance between 12 690–16 150 with a median at 15 210 cal yr BP. If we leave out the problematic Zók site and burnt bones from the Phase modelling (n = 22), the estimated last appearance interval is still very similar (12 050–16 110; median: 15 270 cal yr BP).

Last glacial termination vegetation changes from pollen and plant macrofossil records

Pollen based biome reconstruction of five EC European localities (Fig. 2) suggests that the vegetation was quite diverse during and directly after the LGM depending on elevation, water availability and soil type. Alluvial plains near water courses and mid elevation mountain sites were covered by cool coniferous forest steppes (e.g. around Fehér Lake and Lake St Anne), locally tundra vegetation was dominant in cold wet basins (Nagymohos Peat Bog, Kokad Mire), while the dominance of Scots pine (*Pinus sylvestris*) and juniper (*Juniperus communis*) pollen in nearly all pollen records translated into the xerophytic woodland and scrub biome type generally together with cold steppe (Fig. 2). As we have demonstrated earlier, the non-analogue climate of the Late Pleniglacial (LPG) resulted in non-analogue vegetation types that best compare with the modern vegetation of South Siberia³⁴. Quantitative comparison of modern and fossil pollen spectra pointed to the dominance of wet and mesic grasslands and dry steppes in the Carpathian Basin. Wooded vegetation types (continental and suboceanic hemiboreal forest, continental taiga) appeared as significant analogues only in a few cases during the LGM and more frequently after 16 ka cal BP. These results together with the plant macrofossil records from the same sites (Suppl. Material) suggest that the LPG landscape of the CB was dominated by cold steppe or steppe tundra outside the river floodplains, while wet and mesic grasslands occurred in the floodplains. Woody vegetation was confined to river valleys and wet north-facing hill slopes, and scattered trees were likely also present on the loess plateaus. The dominant woody species were larch (*Larix*), Scots pine (*P. sylvestris*), dwarf pine (*P. mugo*), arolla pine (*P. cembra*), Norway spruce (*Picea abies*), common birch (*Betula pendula*), downy birch (*B. pubescens*), dwarf birch (*B. nana*), juniper (*Juniperus sp.*), sea-buckthorn (*Hippophaë rhamnoides*), poplar (*Populus*), willow (*Salix*) and alders (*Alnus glutinosa* and *A. viridis*). Biome shifts are prevalent earliest between 17 000 and 16 000 cal yr BP at two localities: Lake St Anne in the Eastern Carpathians and Kokad Mire in Eastern Hungary (Figs. 2 & 3). In the mountains cold deciduous forest, cool coniferous forest and forest steppe replaces the steppe and taiga biome dominance of the preceding HE-1 cooling. A much more abrupt biome shift took place at Kokad around 16 200 cal yr BP from tundra to cool coniferous forest (Fig. 2)³⁵ that was followed by a second biome shift to cool mixed forest at 14 740 cal yr BP. This biome persisted into the Early Holocene here. A similar biome shift towards mixed leaved (boreo-nemoral) forest was also detected in the Eastern Carpathian site at 14 500 cal yr BP suggesting the expansion of temperate deciduous trees during the LG interstadial (GI-1). At Kokad, grazing indicator fungi (*Sporomiella*, Sordariales and Type HdV55a) were studied together with pollen, and they show the disappearance of these fungi at 16 780 cal yr BP (Fig. 3)³⁵. Around the same time microcharcoal accumulation rate increased in the sediment and stayed high until ca. 15 000 cal yr BP suggesting frequent wildfires in the region between 17 700–15 000 cal yr BP (Fig. 3.). Furthermore, if we compare the rodent relative frequency diagram of Jankovich Cave with the pollen record of Kokad, a clear coincidence is seen between the steppe tundra – cool coniferous forest steppe transition and arctic lemming disappearance (Fig. 3). If we look at Fig. 3 that compares selected pollen types, palynological richness (representing floristic diversity here) and microcharcoal accumulation rates (indicative of regional fire intensity), several differences are apparent between the lowland Kokad and the mid mountain St Anna localities. First, warming at ~ 16 200 cal yr BP and even at 14 700 cal yr BP did not lead into massive afforestation in the lowland; instead, a modest forest increase was accompanied by the expansion of grass-steppes. Sedges (Cyperaceae) representing the tundra

vegetation, declined at both sites at ~ 16 200 cal yr BP, but only sagebrush (*Artemisia*) increased at the mid mountain site, in addition to the rapid increase of pines (*P. diploxylon* type) suggesting the expansion of continental steppes together with conifer dominated forests here. A second striking difference is in the regional fire history. The lowland site was characterised by increased fire activity from 17 800 cal yr BP until the LG onset (14 700 cal yr BP) when broad-leaved trees became dominant in this region. The onset of the fire increase pre-dates the estimated disappearance of the megafauna, but certainly appears at the time of the drastic population decrease of these megaherbivores. It also seems that floristic diversity correlates well with vegetation openness and vegetation type; in case of the lowland site, the tundra \diamond cool steppe \diamond cool coniferous forest steppe change resulted in an increase in palynological diversity; while at the mid mountain site palynological diversity drastically decreased when closed mixed leaved and taiga forests started to dominate from the LG onset (~ 14 700 cal yr BP). This has got implication for the grazing megafauna as well: first of all, the least diverse floristically was the tundra ($E(T) < 20$), much more diverse were the forest steppe biomes around Lake St Anne in the Carpathian mid-mountain ($E(T) \sim 30$), and the least diverse were the cool mixed closed forests of the LG – EH in the mid mountain. Based on the radiocarbon dates from woolly mammoth and reindeer (Suppl. Figures 7 & 8), populations of these animals declined when locally tundra (steppe tundra) disappeared, but the lowland semi-forested landscape with its sustained herb diversity was nutritionally more favourable to them than the forested mid mountain region.

Figure 2 shows pollen inferred July mean temperatures at Kokad using two different transfer functions: weighted averaging least square partitioning (WA-PLS, based on 209 taxa) and modern analogue technique (MAT, based 43 taxa)³⁵. While the WA-PLS reconstruction shows that between 19 440 and 16 700 cal yr BP pollen-inferred summer mean temperatures were stable and fluctuated between 14.5 and 15.7°C, the MAT based reconstruction shows lower values and high amplitude fluctuation; a distinct cooling is present between 17 900 and 16 280 cal yr BP with inferred summer mean temperatures between 7.5 and 12.7°C. This interval coincides with HE-1 (17 850–16 200 cal yr BP), and the reconstructed temperature values remarkably mimic the vole thermometer based summer mean temperature values obtained at Jankovich Cave²⁰ (Fig. 2) corroborating that the MAT based reconstruction is likely realistic. Following this event, July mean temperatures increased rapidly to 16–18°C. As we discussed³⁵, these pollen based reconstructions suffer from non-analogue situations and overfitting in case of the MAT method, and when compared with the climate model based simulation (green line on Fig. 2), the reconstructed values are considerably lower in the Early Holocene. Both the vole thermometer and pollen based summer temperature reconstruction demonstrate that the highest amplitude warming took place before the LG onset, around 16.2 ka cal BP in the CB and summer mean temperatures decreased only modestly during the Younger Dryas climatic reversal (Fig. 2) corroborating earlier proxy based reconstructions from the CB lowlands and SE Carpathian mountain sites^{36–39}.

Discussion

The order of events: ecosystem changes in the Carpathian Basin and Europe during the last glacial termination

Our multi-proxy data (Fig. 3) suggest that the collapse of the large herbivore fauna slightly preceded or coincided with the terrestrial vegetation change in the CB. In addition to the radiocarbon dated bones of woolly mammoth (Suppl. Figure 8), fungal spores (*Sporomiella*, HdV55a) living in the dung of large grazing mammals were studied at the lowland Kokad locality, and both dataset confirms a population decrease from 17.2 ka cal BP that likely culminated around 16.2 ka cal BP, when the last dated bones of mammoth appear in the studied assemblages. When we compare the order of events, we see that the population size decrease of large grazing mammals, in this case indicated by both fungal spores and radiocarbon dates, preceded the vegetation change, thus we may infer that the decreasing population size of large grazers likely facilitated the vegetation change via restricted grazing and the accumulation of plant biomass. As demonstrated by the Kokad microcharcoal record, regional fires were more frequent from 17.8 ka cal BP in the eastern lowland of the CB up until 14.3 ka cal BP when the spread of temperate woody species started. We also see correlation between the last mammoth ^{14}C date and the transformation of the herbaceous vegetation at the Kokad locality (sedge (Cyperaceae) decrease, chenopod (Chenopodiaceae) peak, sagebrush (*Artemisia*) and grass (Poaceae) increase), therefore the picture is less definite here than in North America, where fungal spore, charcoal and pollen studies demonstrated that the population size decrease of megaherbivores preceded the vegetation change¹⁶. In the CB grazing indicator fungal spores are less frequent in the LP and LG deposits, therefore less conclusive; in addition, radiocarbon dates suggest coincidence of the vegetation change and megaherbivore finite radiocarbon dates. Overall, our data suggest that large herbivore population size likely decreased earlier than the biome shifts took place, and thus the limiting factor for large grazing mammals was not the decreasing availability of food resources, but their intolerance of increased warmth. Furthermore, regional wildfire histories were divergent in the mountain and lowland localities and largely depended on tree cover (Fig. 3). From regional summaries we know that wildfires were generally more frequent during the Early Holocene in EC Europe, and in conifer forest dominated regions during the LG^{9,40}. These increased fire frequencies were explained by orbital forcing (enhanced continentality: warmer than present summers, cold winters, seasonal drought stress); however, the same studies also concluded that once temperate broadleaved forest established, biomass burning was high at ~ 45% tree cover and decreased to a minimum at between 60% and 70% tree cover, i.e. wildfire frequency was strongly correlated with changing tree cover in this region. In the high mountain regions where conifer-dominated forests expanded during the last glacial termination and persisted in the Holocene, biomass burning was highest at ~ 60–65% tree cover and steeply declined at > 65% tree cover. In Fig. 3 two paleo records demonstrate this pattern: the mountain site (Lake St Anne) shows increased microcharcoal influx when needle leaved forest cover increase around the site¹³, while wildfires are less frequent when steppe biomes are present. Furthermore, when deciduous trees expand in the lowland to form boreo-nemoral woodland, wildfire indicator micorcharcoal influx values decrease (Kokad). These data corroborate that biomass burning was controlled by tree cover and was the highest at medium tree cover in the region.

The microfaunal changes and the vole community inferred vegetation changes from Jankovich Cave and Rejtek I Rock Shelter are the first rigorously dated cave sequences that inform us about ecosystem changes during the last glacial termination in Northern Hungary. Their merit is to demonstrate that the time of the faunal turnover was not the LG onset but the post HE-1 warming (see Jankovich Cave record on Fig. 2 and Suppl Figs. 5–6) that occurred at ~ 16.2 ka cal BP.

Such high-resolution microfaunal records are rare in Europe. In Hungary two cave faunal assemblages were revisited recently^{4,41} including Rejtek I Rock Shelter and Petényi Cave (also called Peskő II Rock Shelter situated at 735 m a.s.l. in the Bükk Plateau), where mollusc shells were used for dating the earlier studied sequences that also contained undiagnostic Late Upper Palaeolithic artefacts such as retouched bladelets. As demonstrated in Suppl. Table 3, the mollusc shell based dates are close to our oldest estimates in the LG interstadial layers (11–12) of Rejtek I Rock Shelter, or mollusc ¹⁴C ages are older, while in the Early Holocene layers there is a good agreement between the bone collagen and mollusc carbonate based ¹⁴C dates. Overall, this discrepancy, plus the demonstrated deposition hiatus during the LG interstadial (between ~ 14 530 and 9270 cal yr BP) in Petényi Cave, and the older dates for some large grazer or predator bones in Rejtek I Rock Shelter and Jankovich Cave (e.g. cave bear, reindeer and bison bones) warn us that the interpretation of cave sediment faunas has to be treated with caution, and the best dating results and faunal based inferences can be obtained from micromammal assemblages. Furthermore, the bone and charcoal assemblages in the bottom layer of Petényi Cave (dated between 15 180–14 530 cal yr BP) pointed to the development of a transitional flora and fauna (boreo-nemoral forest dominated by spruce) in the Bükk Plateau^{4,22,42} supporting the pollen records from the CB that afforestation and warming started directly after HE-1.

In Europe systematically analysed and radiocarbon dated Late Pleistocene – Early Holocene cave sediment sequences with rich bone assemblages are rare. The few that cover a similar time period are in Western France^{43,44}, Spain⁴⁵ and Ukraine⁴⁶. In addition, a recent summary work⁴⁷ compares ecosystem changes at a regional scale for the last 50 000 years. The faunal turnover at 16.2 ka cal BP that we identified in Jankovich Cave was also detected in two French cave sequences (Peyrazet Cave and Coulet des Roches). In both cases changes in the small mammal communities between the Pleistocene and Holocene were the result of a succession of climatic events that started at the end of HE-1. Several rodents that occur in temperate and forested habitats today (e.g. garden dormouse (*Eliomys quercinus*), wood mouse (*A. sylvaticus*), bank vole (*C. glareolus*), Mediterranean pine vole (*Microtus (Terricola) duodecimcostatus*)) appeared in the middle or at the end of the LG, while the cold-adapted species (e.g. arctic lemming, narrow-headed vole) gradually disappeared^{43,44}. The three radiocarbon dated reindeer bones from the Peyrazet Cave gave an age range 13 835–15 410 cal yr BP⁴³ that is slightly younger than our results from Jankovich Cave, and mainly fall in the Bølling interstadial. Similar faunal turnover and climatic changes were observed in the El Mirón Cave sequence⁴⁵, where increased forest species diversity was detected between 18 and 11 ka cal yr BP, while *Pliomys lenki* (an extinct Pleistocene vole) and some other species disappeared mainly at the end of the YD.

According to Puzachenko and Markova⁴⁷ the CB belongs to the Central European South region, where after the significant species richness decrease of the LGM, the number of species was gradually restored between ~17.5–13 ka BP to the value characteristic for late MIS-3. At the same time, some members of the mammoth fauna disappeared. If we compare our local last detection times (youngest ¹⁴C dated individuals) from Rejtek I Rock Shelter and Jankovich Cave with the regional disappearance times reported by Puzachenko and Markova, we can conclude that all Late Pleistocene species disappeared earlier from the CB than from the rest of the region. Even though the number of systematically dated cave sequences is still low in the CB, and thus later local extinction times are plausible, these relatively early local extinction times are likely connectable to the southern geographical position of the basin and also to the biome mosaic that characterised this region during the LPG and LG.

In comparison with the aforementioned areas, the Grot Skeliastyi Rock Shelter in south-western Crimea shows a completely different Pleistocene-Holocene faunal transition⁴⁶. Only the large herbivore species became extinct from this assemblage (wild horse, steppe bison), most other taxa persisted from the Pleistocene into the Holocene without losses likely due to Crimea's geographic position and milder climate. Its relevance for the CB lies in the vegetation and fauna of our south-eastern lowland areas that via the Iron Gate are directly connected to the Pontic Crimean territories and hold several common taxa⁴⁸. Many of the Pontic species originated from this climatically relatively stable area, and as the differences of the faunal records demonstrate, Pontic species likely migrated into the CB during the last glacial termination period⁴⁹.

Plaid ecosystems reverting to equilibrium ecosystem mosaics: key for steppe fauna survival

Sommer and Nadachowski⁵⁰ showed that faunal communities during the LGM contained a combination of typical cold-adapted faunal elements alongside with temperate faunal elements in the Balkans (except Greece), in SW France and in the Carpathian Region. Consequently, in these regions delayed expansion of new faunal communities in response to climate change were not, or much less influenced by delayed immigration. When we examine the order of changes in different ecosystem components, this has to be taken in account, and as demonstrated for higher plants^{12,34,49}, a similar situation applies to certain woody and herbaceous elements of the temperate forest and forest steppe flora.

According to the Plaids and Stripes Hypothesis⁵¹, the main cause of the Late Pleistocene megafauna extinction was the cessation of short-term climate fluctuation during the last ice age that added a dimension of temporal complexity, which is now missing from many modern ecosystems. Millennial- and centennial-scale high amplitude climate fluctuations kept ecosystems out of balance as plant and animal species struggled to keep up with repeated shifts in their environments. Advantageous eco-physiological attributes, such as greater mobility, lower cost of locomotion, greater dietary breadth and higher metabolic efficiency allowed the Late Pleistocene fauna to flourish in these disequilibrium 'plaid' settings. It

is also suggested that due to frequent climatic disturbance, early successional plant communities dominated by forbs and graminoids were the key elements in supporting dense populations of megafaunal herbivores^{52,53} on immature and thus more productive soils. The transformation of the plaid ecosystems towards a striped structure during the LG and Early Holocene can be followed well on European and Eurasian biome simulation maps⁵⁴ in support of this hypothesis. Our pollen based biome reconstruction, microfaunal change in the CB cave deposits and climate model simulations all suggest that in the CB the rapid transformation of the plaid landscape took place from 16.2 ka cal BP, and the major element was the expansion of temperate and boreal woodland species and the overall gradual increase in woodland cover that disfavoured mammoth and reindeer as demonstrated by our data. On the other hand, if we look at current and simulated plant biomes in the CB, we see that the striped boreal and cold temperate biomes break up in the lowlands of the basin, where the so called equilibrium mosaic ecosystem (with edaphic steppes and temperate forest steppe) persisted throughout the Holocene due to edaphic and hydrological reasons⁴⁸. This deviation from the regional trend likely had an overarching consequence during the Holocene climate stability allowing for the longer subsistence of mega-herbivore mammal species in the lowlands, as demonstrated by several studies^{3,55,56}. Although climate change led to the replacement of the ungulate species spectrum due to partial afforestation (to e.g. Aurochs, bison, elk and moose expanded), early warming around 16.2 ka cal BP was detrimental to large bodied cold-steppe, tundra-steppe adapted mammoth (woolly rhino and giant deer likely disappeared even earlier). As a very distant and indirect parallel, the lowlands of the CB are somewhat similar to the African savannah, where dryland ecosystems are particularly susceptible to millennial-scale boom-and-bust cycles in primary productivity⁵⁷ and therefore plaid ecosystems are pertinent.

Local herbivore extinctions in context of the European extinction history

Reindeer We know from range modelling that the global potential range of reindeer declined by 84% between 21 and 6 kyr BP⁵⁸. It was explained by rapid climate change particularly after HE-1. Starting from its modern July mean temperature tolerance of < 12–13 °C and a metabolic adaptation to < 15 °C⁵⁹, its distribution dynamics in the CB suggest that reindeer was common in the CB during the LGM (from ca. 23 ka cal yr BP) and its population strongly declined by ca. 15.2 ka cal BP (Suppl. Table 5) with a modelled last appearance at ~ 12 550 cal yr BP. Range dynamics of reindeer in Europe were summarized by Sommer et al.⁶⁰ who presented only four context dated reindeer findings from the CB, all of which were dated between 18–25 ka cal BP and none later. Recently, Zöld Cave from the central CB⁸ yielded a reindeer bone dated to 15.4–16 ka cal BP and further reindeer remains were associated with a charcoal date 14.9–15.3 ka cal BP. In this context our dating results of several reindeer bones from Jankovich Cave with a calibrated (2σ) age range of 15 085–20 540 cal BP (Suppl. Table 5) suggest that reindeer persisted in the basin after the LGM, and its local extinction likely occurred later than assumed by Sommer et al.⁶⁰. Our data suggest that reindeer population declined considerably around 15.2 ka cal BP.

Comparing this timing with the pollen and chironomid inferred climate reconstruction and biome records (Figs. 2 & 3)³⁸ we conclude that reindeer persisted in the cool conifer forest steppe environment of the basin for about 1000 years, and its population decline predated the emergence of cool mixed (coniferous-deciduous) forests around 14.7 ka cal BP. The species was abundant during the LGM and persisted during the subsequent Late Epigravettian (LE) period as demonstrable by the relatively large number of LE sites in the lowlands and hills of Hungary where reindeer bones were present. In Southern Sweden, reindeer extirpation took place at the transition from open pine-birch forest to pine-deciduous dominated forest transition. In the CB this coincidence of deciduous tree expansion and reindeer decline cannot be demonstrated, although both elm (*Ulmus*) and hazel (*Corylus*) were already expanding regionally in the GHP at 15.2 ka cal BP without a biome shift at that time (Fig. 2). It is likely that in the continental interior of the continent the rapidly increasing summer temperatures had a direct effect on the local reindeer population that likely left the basin due to metabolic adaptation to < 15 °C. As our climate reconstructions demonstrate, the lowlands were certainly too warm for reindeer by 15.2 ka cal BP, but also the mid mountain regions (Fig. 2). Another striking feature of the GHP is that during the abrupt biome shift from tundra to cool coniferous forest biome, the lowlands and low hills of the CB remained partially steppe covered, which character of the landscape must have helped the survival of grazers if metabolic/physiological adaptation made it possible. The timing of its withdrawal from the CB agrees well with the dates of the youngest/latest Epigravettian campsites^{8,61}. Even though the Epigravettian population also hunted horse by this time⁸, the coincidence of these two events suggests prey fidelity and environmental determinism.

Woolly mammoth

Available summaries on European ungulate extinction times suggest that woolly mammoth (*Mammuthus primigenius*) occurred in the ice-free parts of Europe during the Weichselian

Glacial until 14 ka cal BP ago when its populations collapsed due to warming⁶². Moreover, the endemic European mammoth population became extinct after 24 ka cal BP and was replaced by mammoths of a Siberian genetic clade, which had been colonizing Europe since 34 ka cal BP⁶³. If we look at the history of woolly mammoth in the East-Central European Region, we see that inside the Austrian Alps, an area occupied by an extensive ice-stream network during the LGM, these animals migrated several tens of kilometres into alpine valleys during the first half of MIS 3⁶⁴ when ice-free conditions were in the major valleys. Over 230 bones were examined in Austria, and their distribution suggests that mammoth was present in river valleys and adjacent loess covered forelands of the Alps. Considering the two periods of apparent absence of woolly mammoth in the CB (32.5–27.4 and 24.5–22 cal BP; Suppl. Figure 8.), the onset of the latter period coincides with a massive dust accumulation period above Greenland (see Ca²⁺ on Fig. 3) followed by two short interstadials (GI-2.1 & GI-2.2). Regarding the older time interval, four Greenland interstadials fell in this (GI-3-4-5.1-5.2; Suppl. Figure 8)⁶⁵, and we know mainly from loess mollusc studies that the lowlands of the CB were covered by boreal parkland forests at these milder time

intervals⁶⁶. Furthermore, variations in glacial dust deposition on centennial–millennial timescales in the CB and Greenland were synchronous⁶⁷. Even though the number of ¹⁴C dated mammoth bones is still low, if the detected low mammoth population number or absence is valid, then it is likely that the warmer and more forested periods were disadvantageous for its populations in the CB. Moreover, the European mammoth population extinction after 24 ka cal BP likely also affected the CB, where the Siberian clade's expansion is probable after 22 ka cal BP based on our ¹⁴C measurements.

Epigravettian hunters and megafauna extinction in the CB: the relationship between human population and faunal change

Even though human activity as a result of hunting and habitat modification are often cited as the principal driving force in megafauna extinction⁶⁸, the diversity of extinction patterns observed on different continents has led to increasing recognition of the potential synergistic role of climate change⁵⁸. As demonstrated by Cooper et al.⁶⁹, extinction of genetic clades coincided in many cases with rapid warming events in absence of human presence in North America. These events involved the rapid replacement of one species or population by a conspecific or congeneric across a broad area. It appears that cold conditions were not an important driver for extinctions even in the presence of anatomically modern humans in Europe. In the CB Early Epigravettian groups were present during the LGM (GS-2.1b-c) and Late Epigravettian in the GS-2.1a and early GI-1 period⁷. According to Lengyel et al. (*in press*) Early Epigravettian (26 – 20 ka cal BP) hunter-gatherers subsisted on reindeer and wild horse, with reindeer being the dominant. A marked change was detected in the dominant prey at the Late Epigravettian sites (20-15.2 ka cal BP), when reindeer fell drastically, while wild horse became dominant and mammoth was present again until ca. 15 ka cal BP. These changes suggest that the LGM reindeer population grew thinner in the CB during the last glacial termination. It was also demonstrated that a decrease in human population of the CB took place at the end of the Late Epigravettian⁸. So far only a single site, Lovas (14 – 13 ka cal BP)⁷⁰, and stray finds from Mezőlak, Nádasladány and Csór–Merítő-puszta (13.7–13.46 ka cal BP)^{71,72} are known from Transdanubia that are contemporaneous with the Epi-Magdalenian Culture of Czechia⁷³ and the Arched Backed Point techno complex of Poland⁷⁴.

These findings attest that human groups with new persistence strategies appeared in the western CB about 1000 years after the mammoth, reindeer and wild horse hunters left (note the apparent absence of ¹⁴C dated sites between 15 – 14 ka cal BP). The Lovas site provided evidence for Eurasian elk (*A. alces*) and Red deer (*C. elaphus*) hunting and using of their bones for ochre mining^{75,76}. From these yet fragmentary data we may conclude that the Late Epigravettian population that likely left the CB around 15.6–15.2 ka cal BP had strong prey fidelity and hunting habits resulted in the tracking of megafauna elements. Supporting this argument are the recently dated Late Palaeolithic camp sites (13-11.7 ka cal

BP) further north in Slovakia, and only a few in Southern Poland⁷⁷ where the fauna is too poorly preserved to determine hunted species.

Conclusions

In this paper we tested the hypothesis that transitions from cold to warm intervals were briefly optimal for grazing megafauna that was then followed by rapid extinctions¹⁵. Our results support this hypothesis in that the dated bone assemblages of both woolly mammoth and reindeer attest to relatively large and increasing population sizes after the LGM until c. 16.2 ka cal BP. Our paleoclimate and biome reconstructions suggested that major warming at 16.2 ka cal BP was however detrimental to these populations likely due to the intolerance of increased warmth in case of reindeer. We also demonstrated that in the CB pollen inferred biome changes slightly postdated the local population decline of woolly mammoth and reindeer; megafauna population estimates based on fungal spores were less conclusive, furthermore wildfires played a significant role in the vegetation transformation at the last glacial termination, when the array of biome change was divergent. Afforestation by cold deciduous and cool coniferous trees was rapid in the mid mountains from 16.2 kyr cal BP, while steppe tundra biomes transformed into boreo-nemoral forest steppe in the lowland localities.

When we compare the increasing number of well dated Late Epigravettian sites and their associated fauna in the CB with our pollen inferred biome and climate reconstruction, we infer that the reason for the relatively abrupt disappearance of the Epigravettian hunters was the diminishing population size of their dominant preys (both reindeer and wild horse), while vegetation change was more gradual. Placing this in a European context, the CB behaved similarly to some south and south-west European areas, and underwent earlier (post HE-1) and drastic faunal and human population changes in response to early warming after the LGM than more north-westerly and northerly locations in Europe.

We found that cave faunas in general can be used to estimate local extinction times. Direct AMS ¹⁴C measurements on the investigated species are requisite; large mammal bones from the same sediment layer often give deviating (older) ages from the associated micro-mammal fauna. Since Late Pleistocene cave faunas have extensively been studied and preserved in museum collections in the CB, there is still ample opportunity to resolve the many open questions of rapid faunal changes at the last glacial termination in this region of Europe.

Methods

Bone sampling from the museum collections

The primary consideration in selecting remains was to choose large or medium sized mammal species or larger sized micromammals that were members of the vertebrate fauna in the Carpathian Basin during the Late Pleistocene but went extinct in the latest Pleistocene or in the Holocene. Since our aim was to

determine the probable age of disappearance, we preferably sampled the bones of the same species from all layers in the sequence if it was possible.

Radiocarbon dating, age-depth modelling

The selected bones were first subjected to physical preparation including surface removal by a Dremel device, grinding and sieving. Then 600 mg of the 0.5-1 mm fraction was placed into a test tube to perform the acid-base-acid treatment (ABA), using 0.5M HCl and 0.1M NaOH reagent, rinsing the sample with ultrapure water in between. The pH of the samples was then adjusted to 3 and the test tubes were put in a block heater at 75 °C for 24 h to gelatinize the collagen. The liquid gelatine samples were then filtered using a 2 µm glass fibre filter and freeze dried for two days. For combustion, ~4 mg gelatine sample together with MnO₂ reagent was placed to a glass combustion tube, which was, after sealing, heated to 550 °C^{78,79}. The obtained CO₂ gas was then purified and reduced to solid graphite, applying a customized sealed tube graphitization method⁸⁰. The ¹⁴C measurements were performed using the EnvironMICADAS AMS instrument at the ICER laboratory⁸¹.

¹⁴C ages were calibrated into calendar years using the Calib Rev. v. 8.2.html software and the Intcal20 calibration curve³². Age-depth modelling for the cave sediment sequences was done with the Bacon package in R using Bayesian probability statistics⁸². The woolly mammoth and reindeer radiocarbon dates presented in Supplementary Tables 4 and 5 were calibrated against the IntCal20 dataset using OxCal version 4.3 and incorporated within a single Phase model in OxCal version 4.3 in order to provide an estimate of the last appearance dates^{31,83}. The 'Phase' command is a grouping model. It assumes no geographic relationship between samples, and that the ages represent a uniform distribution between a start and end boundary. The posterior distributions allowed us to determine probability distribution functions (PDFs) for the beginning and end of the phase. Modelled ages are reported here at the 95% probability range in thousands of calendar years BP (years; relative to AD 1950).

Re-analysis and re-plotting of the mammal bone assemblages

Bone assemblages were re-analysed for taxonomic inconsistencies by Piroška Pazonyi. Stratigraphic diagrams of the vole and other small mammal faunas were plotted in Psimpoll 2.27 and edited in Corel Draw 16.

Quantitative climate reconstruction (pollen & vole thermometers)

The method of the pollen-based summer mean temperature (T_{JJA}) reconstruction from Kokad Mire was described in detail in Magyari et al.³⁵ In brief, the European Modern Pollen Database (EMPD) was used as training set⁸⁴. 209 terrestrial pollen types were used for the summer mean temperature reconstruction that was further reduced to the dominant 43 taxa for the modern analogue technique reconstructions. The training set has 2687 modern pollen samples, of which 1240 are located below 600 m above sea level. Modern T_{JJA} (mean air temperature for June, July and August) for each site was included in the EMPD climate data file. We developed quantitative pollen-based transfer functions for T_{JJA} using weighted averaging-partial least squares (WA-PLS) regression⁸⁵ with five components. We used leave-one-out cross-validation⁸⁶ to evaluate the model performance and estimated performance statistics such as coefficient of determination (r^2) between measured and predicted values, root mean square error of prediction (RMSEP) and maximum bias for each WA-PLS transfer function. We transformed the surface pollen data to square-roots to reduce the noise of the data⁸⁷, applied randomization t-test⁸⁸ for selecting the most appropriate WA-PLS component for TJJJA reconstructions, and calculated sample-specific standard errors for the reconstructions with a bootstrapping procedure with 1000 cycles⁸⁹. We performed the WA-PLS transfer functions and associated T_{JJA} reconstructions with the RIOJA package in R⁹⁰. We assessed statistical significance of the WA-PLS based T_{JJA} reconstructions with the approach involving 999 randomizations developed by⁹¹ and conducted these significance tests with the R package PALAEOSIG⁹¹. An alternative transfer function, the modern analogue technique (MAT) was also used to derive T_{JJA} . This method does not require real calibration and is based on a comparison of past assemblages to modern pollen assemblages. The similarity between each fossil and modern pollen assemblage is evaluated by the chord distance metric^{92,93}. In this study 6 modern pollen spectra that had the smallest distance were considered as the best modern analogues of the given pollen spectrum and were subsequently used for the reconstruction. If the chord distance was above a threshold defined by a Monte-Carlo method⁹², the modern sample was considered as bad analogue, and was not taken into account in the reconstruction. Estimates of climatic parameters were obtained by taking a weighted average of the values for all selected best modern analogues, where the weights used were the inverse of the chord distance. MAT based T_{JJA} reconstruction and statistical tests were run in R using the RIOJA package. In this study we focus on the reconstruction of a single climatic parameter, T_{JJA} . The aim of the reconstruction is to compare the pollen-based T_{JJA} record with the extinction times of both mega and microfauna elements and we also compare the pollen based TJJJA reconstruction with the vole-thermometer based T_{July} reconstruction from Jankovich Cave and Rejtek Rock Shelter^{20,22}. The method is a paleozoogeographical calculation based on the principle of actualism; it is used to determine the July (summer) temperature of the accumulation period of different samples^{20,94}. Present-day optimum temperature of the distribution of certain vole-species was given in Jánossy and Kordos²². These are 15 °C for *Myodes*, 17.5°C for *Arvicola*, 21°C for *Microtus arvalis*, 19°C for *Microtus agrestis*, 10°C for *Lasiopodomys gregalis*, 12.5°C for *Microtus oeconomus* and 7.5°C for *Dicrostonyx*. After the multiplication of the values of mean July temperature with the percentage of the species in question

compared to other vole-species, these values were summed up and divided by 100. *Microtus nivalis* was not taken into account because it is a mountain species, therefore its distribution is not zonal^{20,22}.

Biome reconstruction

For the pollen assemblage based biome reconstructions we used the technique of Prentice et al.⁹⁵ improved further by Tarasov et al.⁹⁶. The first step was the assignment of the pollen taxa to plant functional types (PFT). We used the biome-PFT-taxon matrix published in Allen et al.⁹⁷. Plant functional types occupy specific bioclimatic spaces that can be assigned to one or several biomes. The biome-PFT matrix is a list of biomes, indicating which PFTs are characteristic for each biome. The next step is the calculation of biome affinity scores⁹⁵. This equation sums up the square roots of pollen percentages within a PFT and sums up the affinity scores within a biome characterised by a set of PFTs. Eventually, the pollen sample is assigned to the biome with which it has the maximum affinity. The threshold value above which a taxon is considered is 0.5%. If the arboreal pollen sum is <70%, the temperate forest biome is replaced by wooded steppe⁹⁷. In this paper we present the stratigraphic plot of the main biome affinity scores and the assigned biomes.

Declarations

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Author contributions

EKM wrote the manuscript, was responsible for the pollen analyses, for the conceptualization, methodology, supervision, project administration, funding acquisition, review & editing; ZSZ and JK took part in the visualisation and statistical analyses of the data; PP and MG analysed the bone assemblages, wrote part of the manuscript, took part in the conceptualization; IM was responsible for the stable and radioactive isotope analyses, wrote part of the original draft, reviewed & edited the manuscript; IP analysed pollen samples and took part in data visualisation; GYL was responsible for archaeological data acquisition, reviewed & edited the manuscript; AV took part in the sample collection, reviewed & edited the manuscript.

Competing Interests Statement

None declared under financial, general, and institutional competing interests.

Data Availability Statement

The data that support the findings of this study are openly available in Mendeley Data at <http://dx.doi.org/10.17632/9kwbj5y54j.1>.

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Figures

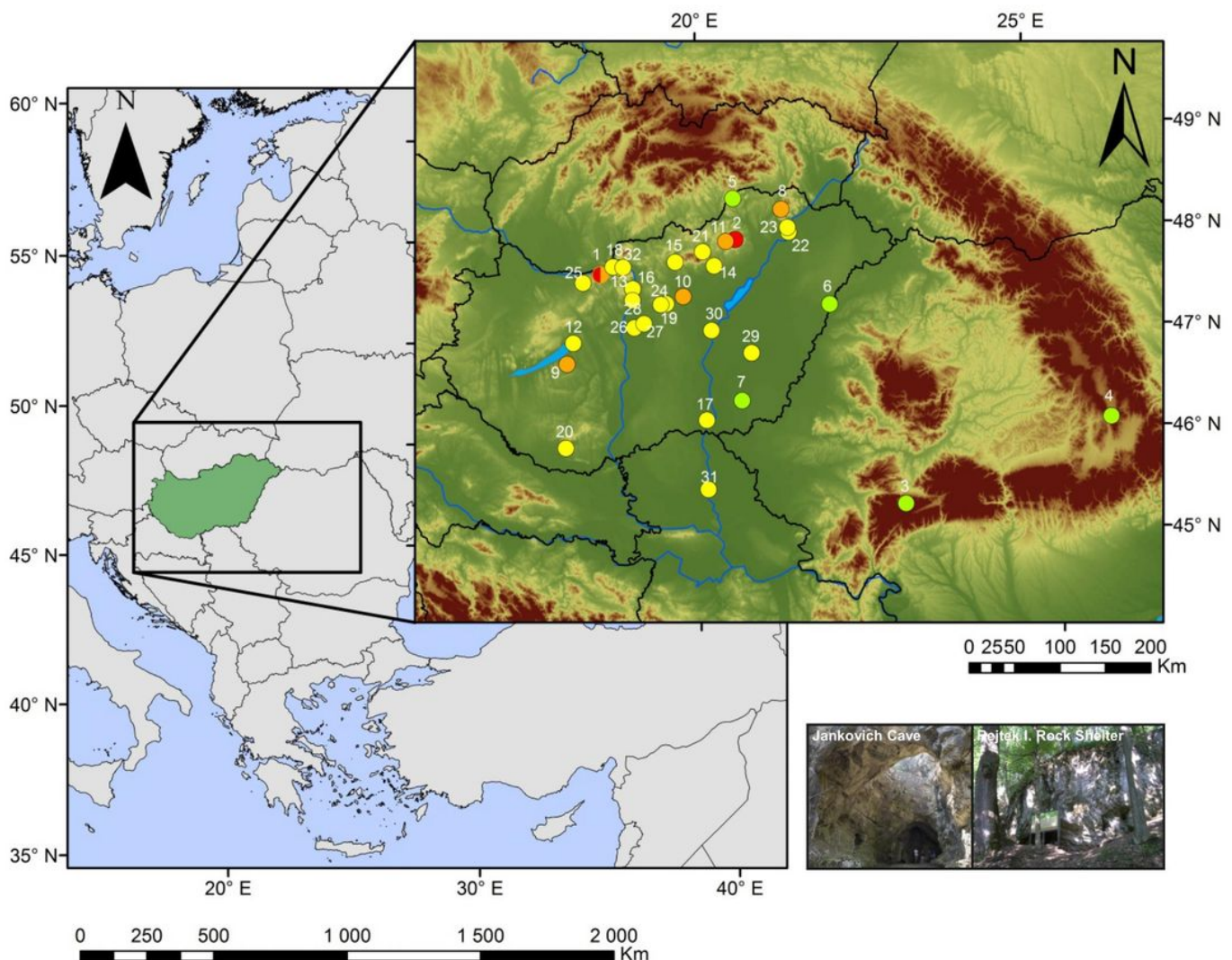


Figure 1

Location of the studied cave sites (1-2), pollen records (3-7), dated reindeer (*Rangifer tarandus*) (1, 8-11) and dated woolly mammoth (*Mammuthus primigenius*) bones in the Carpathian Basin (a) and in East-Central Europe (b). 1: Jankovich Cave; 2: Rejtek I Rock Shelter.; 3: Taul dintre Brazi36; 4: Lake St Anne13; 5: Kelemér Nagymohos34; 6: Kokad Mire35; 7: Kardoskút Fehér Lake98; 8: Arka; 9: Ságvár; 10: Jászfelsőszentgyörgy ; 11: Peskő Cave; 12: Csajág; 13: Pilismarót; 14: Feldebrő; 15: Szurdokpüspöki; 16: Budapest-Csillaghegy; 17: Szeged-Öthalom; 18: Esztergom-Gyurgyalag; 19: Tápiósüly; 20: Zók; 21: Mátraderecske; 22: Tarcal; 23: Bodrogkeresztúr; 24: Mende; 25: Tata-Porhanyó quarry; 26: Kiskunlacháza; 27: Ócsa-Felsőbabád; 28: Lágymányos; 29: Gyoma, River Tisza; 30: River Tisza; 31: Törökbecse; 32: Zebegény

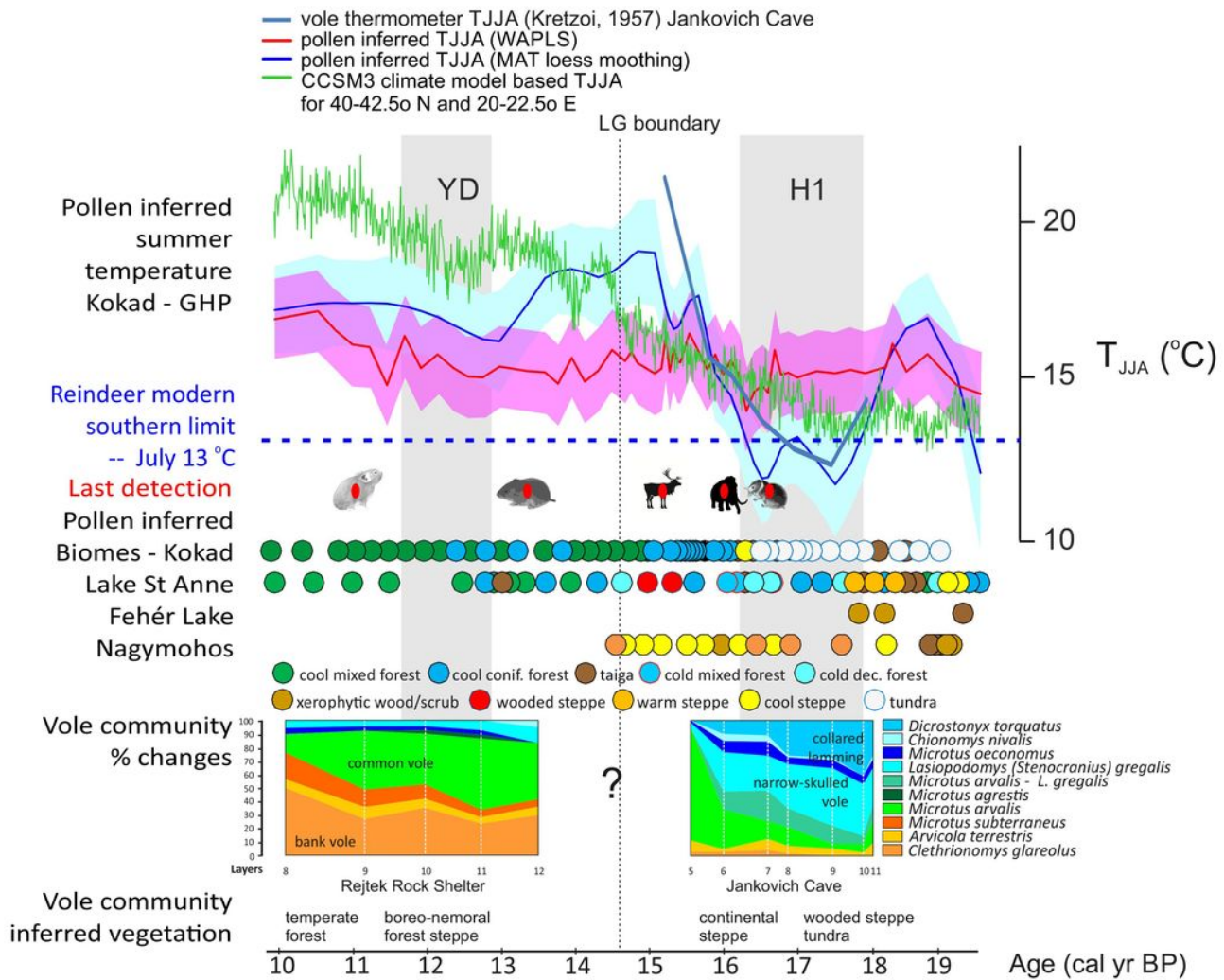


Figure 2

Vole community changes through time in two Carpathian Basin cave sediment profile AMS 14C dated in scope of this study (Jankovich Cave, Rejtek Rock Shelter); vole community inferred vegetation; pollen inferred biome reconstruction on the basis of five pollen records from the Carpathian Region (for locations see Fig. 1); last detection times of micro- and macrofauna elements in this study, pollen inferred summer mean temperature reconstructions (WAPLS, MAT) on the basis of the Kokad Mire pollen records (redrawn and modified from Magyari et al.35) and CCSM3 climate model based summer mean temperature simulation for the Kokad grid cell from PaleoView

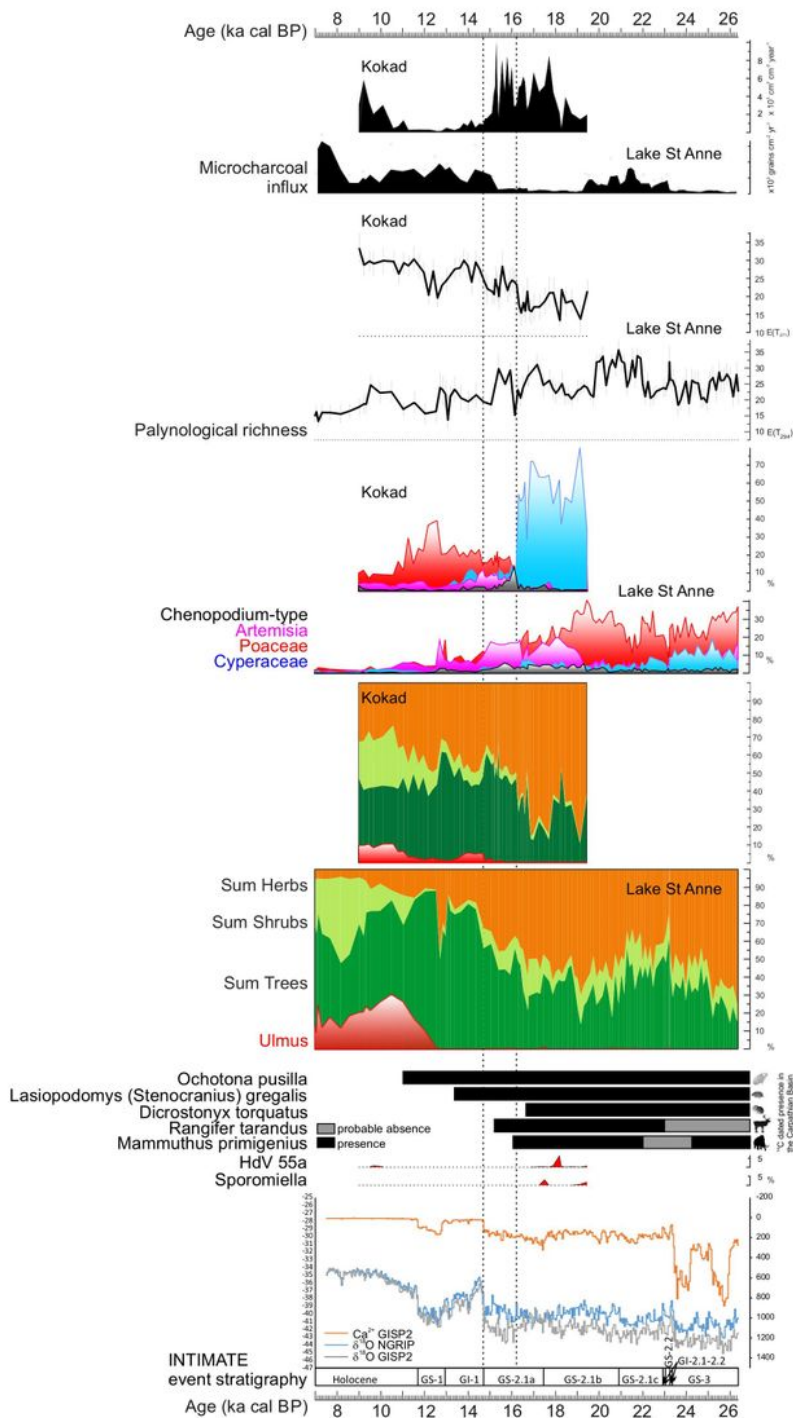


Figure 3

INTIMATE event stratigraphy plotted along the NGRIP and GISP2 $\delta^{18}O$ and Ca^{2+} ice core records from Greenland⁶⁵; selected dung fungal spores (*Sporormiella*, HdV55a) indicating the presence of large bodied grazers in the Kokad pollen profile³⁵; calibrated BP intervals of presence for selected mega- and microfauna elements in the Carpathian Basin dated in scope of this study; summary pollen diagrams from two sites (Lake St Anne - 950 m a.s.l.¹³ and Kokad Mire - 112 m a.s.l.³⁵) showing the cumulative percentage of total tree, shrub and herb pollen types and elm (*Ulmus*) pollen, and separate non-cumulative relative frequency curves for major herb pollen types (*Chenopodium*-type, *Artemisia*, *Poaceae*, *Cyperaceae*), palynological richness and microcharcoal influx curves from the same pollen sites

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