Eifel Megafauna succumbed to forest increase

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This file contains four documents

(1) Increasing forest cover in the Eifel region 11,000 years ago resulted in the local loss of megafauna December 14, 2022

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(2) Thresholds for the presence of glacial megafauna in central Europe during the last 60,000 years 21 November 2022

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(3) Supplementary material to (2).

(4) Mammal extinction facilitated biome shift and human population change during the last glacial termination in East-Central Europe

Enikő Katalin Magyari, Mihály Gasparik, István Major, György Lengyel, Ilona Pál, Attila Virág, János Korponai, Aritina Haliuc, Zoltán Szabó & Piroska Pazonyi Mammal extinction facilitated biome shift and human population change during the last glacial termination in East-Central Europe. *Sci Rep* **12**, 6796 (2022). https://doi.org/10.1038/s41598-022-10714-x

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Increasing forest cover in the Eifel region 11,000 years ago resulted in the local loss of megafauna

Sediment cores obtained from Eifel maar sites provide insight into the presence of large Ice Age mammals in Central Europe over the past 60,000 years.

Herds of megafauna, such as mammoth and bison, have roamed the prehistoric plains in what is today's Central Europe for several tens of thousands of years. As woodland expanded at the end of the last Ice Age, the numbers of these animals declined and by roughly 11,000 years ago, they had completely vanished from this region. Thus, the growth of forests was the main factor that determined the extinction of such megafauna in Central Europe.

This is the conclusion reached in a study conducted by Professor Frank Sirocko of Johannes Gutenberg University Mainz (JGU), together with researchers from the Max Planck Institute for Chemistry, the University of Wollongong in Australia, and the University of Göttingen. The project involved the analysis of sediment layers taken from two Eifel maars, i.e., former volcanic craters that had subsequently become lakes. The researchers used these to reconstruct landscape changes and megafauna abundance in the area over the last 60,000 years. The results showed that human hunters and large mammals had actually co-existed here over several thousand years. "The sediments from the Eifel maars have provided us with no evidence that it was humans who were responsible for the eradication of these animals," stated Sirocko. The so-called overkill hypothesis discussed in North America could thus not be confirmed for Central Europe.

Previous vegetation and animal populations can be identified from pollen and fungal spores in sediments

For the purpose of their study, the research partners used sediment cores from the Eifel maars that Sirocko and his team had systematically drilled and archived over the past 20 years.

The recent article published in *Scientific Reports* details the investigation of pollen and spores present in the cores obtained from Holzmaar lake and the infilled maar of Auel located in the Volcanic Eifel. While pollen documents the vegetation of the past, fungal spores provide evidence of the presence of large mammals because certain mold fungi only colonize the dung of bigger herbivores.

On the basis of the grains of pollen, the researchers established that some 60,000 to 48,000 years ago the Eifel region was covered by spruce woods that succumbed to several cold phases, which transformed the landscape into more open forest steppe. This kind of terrain remained predominant from 43,000 to 30,000 years before the present. Subsequently, the forest tundra of the Eifel became an Ice Age polar desert where only grass grew.

The megafauna fecal fungal spores show that it was these environments which were continuously inhabited by large mammals from 48,000 to some 11,000 years ago. Datable bones found in caves in Belgium and gravel deposits in the Rhine valley document that mammoth, woolly rhinoceros, bison, horses, reindeer, and giant deer found the cold phases more accommodating. The sparse forests of the warmer phases were the preferred habitat of red deer, elk, and the European bison.

Development of woodlands deprived megafauna of their food source

The primary cause of the decline and eventual extinction of large mammals in Central Europe was the growth of forests. "As the trees began to take over, the large herbivores lost access to their main staple food, namely grass," explained Sirocko. Neither the extreme climatic fluctuations of the last 60,000 years nor local volcanic activity and associated fire events appear to have played a role in their extinction. At the same time, the arrival of modern humans in Central Europe 43,000 years ago also had little effect on the presence of local megafauna. Instead, times at which extensive numbers of large mammals were living here coincided with periods in which there was a denser population of humans. "This is most apparent some 15,000 years ago. At that time, we find the largest herds of megafauna along with the archaeologically confirmed presence of human hunters in the Rhine valley," Sirocko pointed out. The Magdalenian culture site at Gönnersdorf in northern Rhineland-Palatinate has been extensively excavated by the Römisch-Germanisches Zentralmuseum Mainz -- Leibniz Research Institute for Archaeology (RGZM) in Mainz.

The researchers claim that even in this period, towards the end of the last Ice Age, grassed landscapes were still spreading. This was the era in which the solar irradiation of the Northern Hemisphere began to increase and global sea levels started to rise, eventually flooding the formerly land regions in the English Channel and the North Sea and thus presumably progressively forcing the herds of megafauna away to seek refuge in Central Europe. "The many late glacial maar lakes and silted-up swamps in dried-out maars in the Eifel region must have proved particularly attractive to megafauna," concluded Sirocko. "And it was the resultant large herds that must have enticed the late Ice Age hunters."

Sediments of the Eifel maars do not substantiate the overkill hypothesis

According to the research team, the fact that hunters and megafauna occupied the same region concurrently demonstrates that human beings did not cause the disappearance of large mammals from Central Europe -- in other words, the maar sediments of the Eifel region do not furnish proof that the overkill hypothesis put forward for North America can be corroborated here. The large mammals migrated away only when birch forests began to predominate in the terrain 13,300 years ago. From 11,000 years ago there is no longer evidence of the presence of large herds of megafauna as thick woods had taken over the Eifel, a setting in which large mammals could not survive.

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Thresholds for the presence of glacial megafauna in central Europe during the last 60,000 years

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Lake sediment records from Holzmaar and the infilled maar of Auel (Eifel, Germany) are used to reconstruct landscape changes and megafauna abundances. Our data document a forested landscape from 60,000 to 48,000 yr b2k and a stepwise vegetation change towards a glacial desert after 26,000 yr b2k. The Eifel landscape was continuously inhabited from 48,000 to 9000 yr b2k by large mammals, documented by the presence of spores of coprophilous fungi from *Sordaria* and *Sporormiella* fungi that grow on fecal remains of the megafauna. Megafauna reached higher numbers during cold stadial climates but was present also during the warmer interstadials. Highest abundance was at 56,500/48,500/38,500/33,000/27,000/21,000/16,200/14,000 yr b2k, i.e. under different climate regimes. Some of these dates were associated with clear human presence, which indicates that megafauna was not overkilled by humans. In contrast, human presence could quite likely have been stimulated by the abundant food supply. Megafauna presence decreased significantly when tree abundance increased during interstadials. The Megafauna disappeared finally at 11,400 yr b2k with the development of the early Holocene forest cover, which appears to be the most important threshold for megafauna presence.

The Eifel is a volcanic field located in the western part of central Europe (Fig. 1a, b). It has a total of more than 250 volcanic structures including 68 maar lakes (60 of which are infilled lakes), which makes it an ideal research field to study the relationships between climate, volcanism, vegetation, landscape and ecology. The sediment cores studied here were drilled by the ELSA-Project, which has systematically cored all accessible Eifel maar sites, lakes and infilled maar structures over the recent years[1–4], see more information on all ELSA cores on the webseite www.ELSA-Project.de. We use cores from the Holocene maar lake of Holzmaar and the infilled Pleistocene maar lake of Auel, both of which have a similar landscape structure with riverine inflow from catchments of about 5 km length (Fig. 1c, d). These large catchments are important for our study on the megafauna, because it provides a large area, where large animal herds must have grazed.

Sirocko et al.[1] recently have presented the stratigraphy for those records – the ELSA-20 time series of C_{org}(chlorins)[1], reproduced in Figs. 4, 5, 6, 7. The samples used for this study are from the same cores, have a thickness of 10 cm, were freeze dried, gently homogenized and subsampled for pollen/spores, alkanes, and lithium isotope analysis. This collection of 1000 samples is presented with this paper as the ELSA-20-Stack. Supplementary Table S1 documents the details about the samples; their exact positions in the cores are also documented in Supplementary Figs. S1–S5.

The ELSA-20-Stack also includes the Holocene, which was analyzed in core HM4 from Holzmaar, 30 km distant to Auel. Holzmaar is smaller than Auel, with a diameter of 325 m, but has also a catchment of 6 km length (Fig. 1d). The samples used for this study are from the same cores, and were subsampled for the analysis of pollen/spores, leaf waxes (*n*-alkanes), and lithium isotopes. Supplementary Table S1 documents sample details, with their position in the cores documented in Supplementary Figs. S1–S5.

In this article, we combine the reconstruction of the Marine Isotope Stage (MIS) 3 vegetation in the Eifel (based on pollen, leaf waxes and lithium isotopes), with a study of spores of coprophilous fungi (SCF) from large

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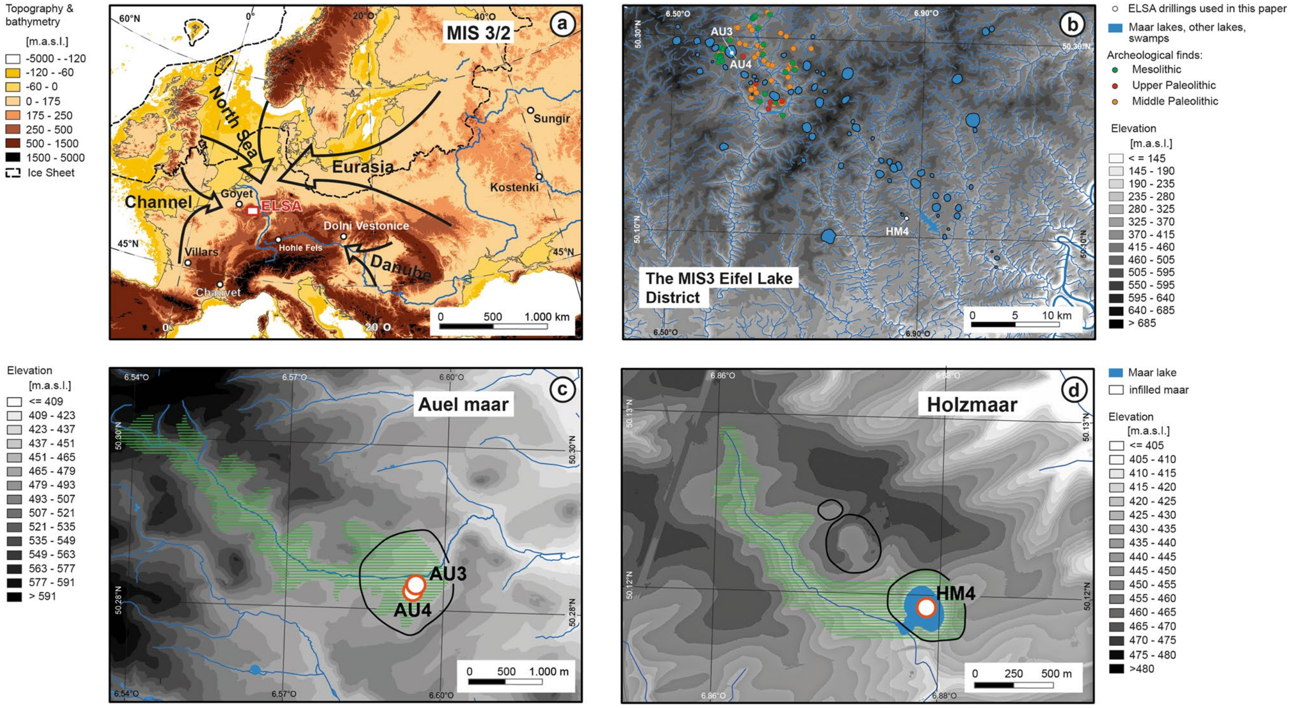

Figure 1. Maps, (**a**) Digital Elevation of Europe with potential corridors for MF migration, (**b**) Maar lakes during the MIS3, (**c**) catchment of the infilled maar lake at Auel, (**d**) catchment of the Holzmaar lake. The maps were made with QGIS 3.16 (https://qgis.org) from ETOPO1 1 Arc-Minute Global Relief Model (NOAA National Geophysical Data Center, 2009), a model of Earth's surface that integrates land topography and ocean bathymetry.

mammals, which must have grazed in the catchment of the small rivers with inflow into the maar lakes (Fig. 1c, d). We identify the presence of megafauna in the catchment of the lake by analysis of SCF[5–7], which were counted together with pollen analysis. *Sporormiella* and *Sordaria,* the two most abundant SCF[8], are regularly found in the sediment from several Eifel maar lakes, but highest spore concentrations were found in the sediments of the infilled maar lakes of Auel and Holzmaar. Using a composite record of SCF (Fig. 2) from both sites, we have studied the presence of megafauna in the Eifel region and compared it to global climate parameters (Fig. 3) and local vegetation (Fig. 4). We present the spore data as counts instead of proportionally as done for pollen data (Figs. 4, 5, 6, 7). This is mainly because spores are present in Last Glacial Maximum (LGM) samples, while pollen is often absent from those samples. However, at least there must have grown grasses, because we see the dropping of grass eating mammals. We attribute this absence to the differential dissolution of pollen in comparison to the thick-walled spores, which apparently survived in the oxygenated deep water of the glacial maar lake. Detailed information on the pollen/spore sample preparation and statistical treatment of the pollen and spore record are given in the Method Section. Spectra of all 32 taxa analyzed are presented in Supplementary Figs. S6–S9. Figures 4, 5, 6, 7 of this main text present only selected pollen. Megafauna includes by definition animals from 45 kg up to 1000 kg[9]. The finding of bones in the caves of Goyet and Spy (Belgium) document the MIS3 mammals in the larger Eifel region in the most detail[10]. Further animal remains are available from the Gravettian open air site of Mainz-Linsenberg in the Rhineland to the west and more distant by Aurignacian and Gravettian layers of cave site in the Swabian Jura to the south[11–13]. Based on such skeletal analyses we know that western central European humans of the MIS3 mostly hunted on (young) mammoth, wooly rhinoceros, bison, and herd animals of lower weight like horse and reindeer. However, these studies lack a fine-chronological resolution. High resolution, well dated European terrestrial records for MIS3/2 times are still scarce and it is thus not possible to evaluate the landscape for all of Europe during MIS3. We thus use a digital elevation model to outline four potential corridors, which could have facilitated long distance migration into the Eifel area (Fig. 1a). One route is along the Danube and Rhine rivers, the second from Eurasia, the other two via the dry North Sea or the Channel regions. All of these regions were subject to intense landscape change during MIS3/2.

The climate along the Danube and the Eurasian corridor has been investigated in detail recently[14,15]. The processes causing landscape change in the two other corridors from the Northwest and West cannot be evaluated precisely, because they were dominated by changes in global sea level[16]. Sea level had dropped in steps from a highstand in the early MIS3 to the LGM low level, which must have had a significant impact on megafauna migrations from the North Sea and Channel corridors into central Europe (Fig. 1a).

Data from 56 natural archives have been compiled recently[17]. They generally outline the stadial/interstadial pattern that is well known from the Greenland Ice Cores[18]. Regional climate signals, however, are difficult to compare between records, especially since ^{14}C dating for the early MIS3 is problematic. The annually continuous ELSA-20 C_{org}(chlorins) record from Auel and Holzmaar is at the moment the only record in central Europe to

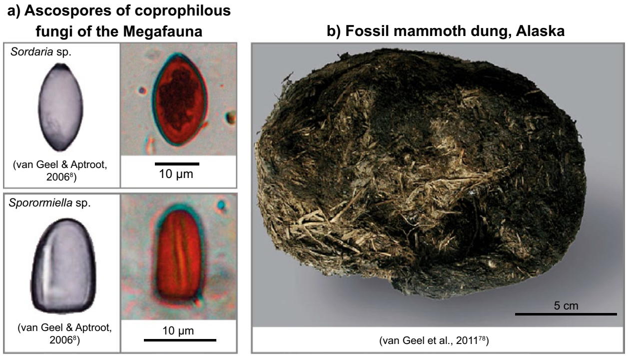

Figure 2. Ascospores of coprophilous fungi, (**a**) photos of spores in textbook[8] and in the ELSA-Stack samples, (**b**) fossil mammoth dung[78].

cover both MIS3 and MIS2 and is in addition fully correlated with the Greenland GICC05 chronology[1]. Here, we use these continuous and undisturbed maar lake sediments to document the presence/absence of megafauna and its relation to climatic, environmental change, human hunting pressure and volcanism. The effect from volcanic eruptions can be tested because the sediments contain layers of ash from 6 large eruptions, which are well visible in the core photos and which can be used to correlate the Auel cores to other ELSA cores[19,20].

Results

Reconstruction of the Eifel climate during the last 60,000 years.

Variations in summer insolation during MIS3 on the northern hemisphere was high in the early and late MIS3, with slightly lowered insolation during the middle MIS3 (Fig. 3). On millennial timescales, North Atlantic sea surface temperatures were characterized by five abrupt episodes of cooling known as Heinrich Events H5–H1, which were linked to the collapse of the Laurentide ice sheet[21] (Fig. 3). Temperatures derived from Greenland ice reveal that the cold conditions of the last ice age were interrupted by 17 warm episodes, called interstadials (Fig. 3). The ELSA-20 C_{org}(chlorins) record shows the North Atlantic stadials/interstadials in perfect match with European temperature variations (Fig. 3). Accordingly, the megafauna (and early humans) in the Eifel lived in a climate regime strongly under North Atlantic control.

The NGRIP-tuned ELSA-20 stratigraphy was used to calculate sedimentation rates in the Auel maar lake, which document soil erosion, thus precipitation and vegetation cover in the catchment of the Eifel maar lakes[16] (Fig. 3). The maximum sedimentation rate of 7 mm/yr was reached at Auel during some MIS3 stadials, in particular H6 and H5 (Fig. 3). The sediments of these sections are all fine-grained silts and clays, uniform with only few faint laminations about 5 mm thick, thus matching the values of the tuned sedimentation rate. Accordingly, Eifel landscapes received intense precipitation during stadials. The fine-grained uniform lithology of the stadial sections suggests that precipitation was dominated by summer rains. Winter meltwater events (flood layers) were prominent only during times free of vegetation during several of the Heinrich events[23]. The early MIS3 stadials were thus not perennially arid, but MIS3 rain, which we locate mainly in the frost-free summer and fall months, transported eroded clay particles into the lakes.

Stadial spring, however, could have been quite arid, indicated by the deposition of loess at many sites in Europe, but also by the presence of eolian material in the lake sediments. The ELSA cores have been studied for eolian dust proportions, which were high during stadials, in particular during Heinrich events[24–27]. We present in Fig. 5 a new approximation to characterize excess silicon (Si) in the Auel cores on an annual basis, directly comparable to the climate time series of the ELSA-20 C_{org}(chlorins) and Si/Al records. To approximate the eolian Si proportion of the bulk Si record, we normalize the two diatom proxies (C_{org} and Si/Al) to a C_{org}/(Si/Al) ratio, which separates the diatom silicon from those silicon proportions from clastic mineral grains like quartz. The C_{org}/(Si/Al) ratio (excess Si) time series indicates the proportion of quartz-bound Si, which is from eolian dust during glacial times[28]. This dust proxy varies with the stadial to interstadial rhythm and increases continuously from the early MIS3 to the LGM, when it reached highest values after 26,000 yr b2k and documents the maximum dust content in the Auel sediments during the LGM (Fig. 7).

Another important aspect of palaeo-environmental reconstruction is soil development and how it relates to changes in climate and vegetation cover. Past changes in soil development can be derived from the lithium isotope composition of sediments (noted δ^7Li), which documents clay formation[29,30]. Lower δ^7Li values indicate extensive clay formation, and by proxy suggest landscape stability (i.e. decreased soil erosion) and soil development. The forested millennia of the early MIS3, which coincides with wet climatic conditions, is associated with active soil formation, as illustrated by negative δ^7Li values in the Auel sediments (Fig. 3)[29]. This can be explained as a vegetation cover dominated by trees would promote landscape stability[31] allowing for active soil development. After about 50,000 yr b2k, δ^7Li values increase, possibly reflecting active erosion and resulting in the sediments deposited being derived mostly from remnant, poorly-developed soils. For the remainder of the Pleistocene, δ^7Li values remain relatively high (close to values expected in poorly-developed soils) except for a negative excursion coinciding with Greenland Interstadial 9 (GI9). This observation indicates that prevailing dry conditions between 45,000 and 15,000 yr b2k resulted in poorly developed soils. Negative δ^7Li values are only observed again between 6000 and 2000 yr b2k, coinciding with warmer and wetter conditions, and a vegetation cover dominated by trees.

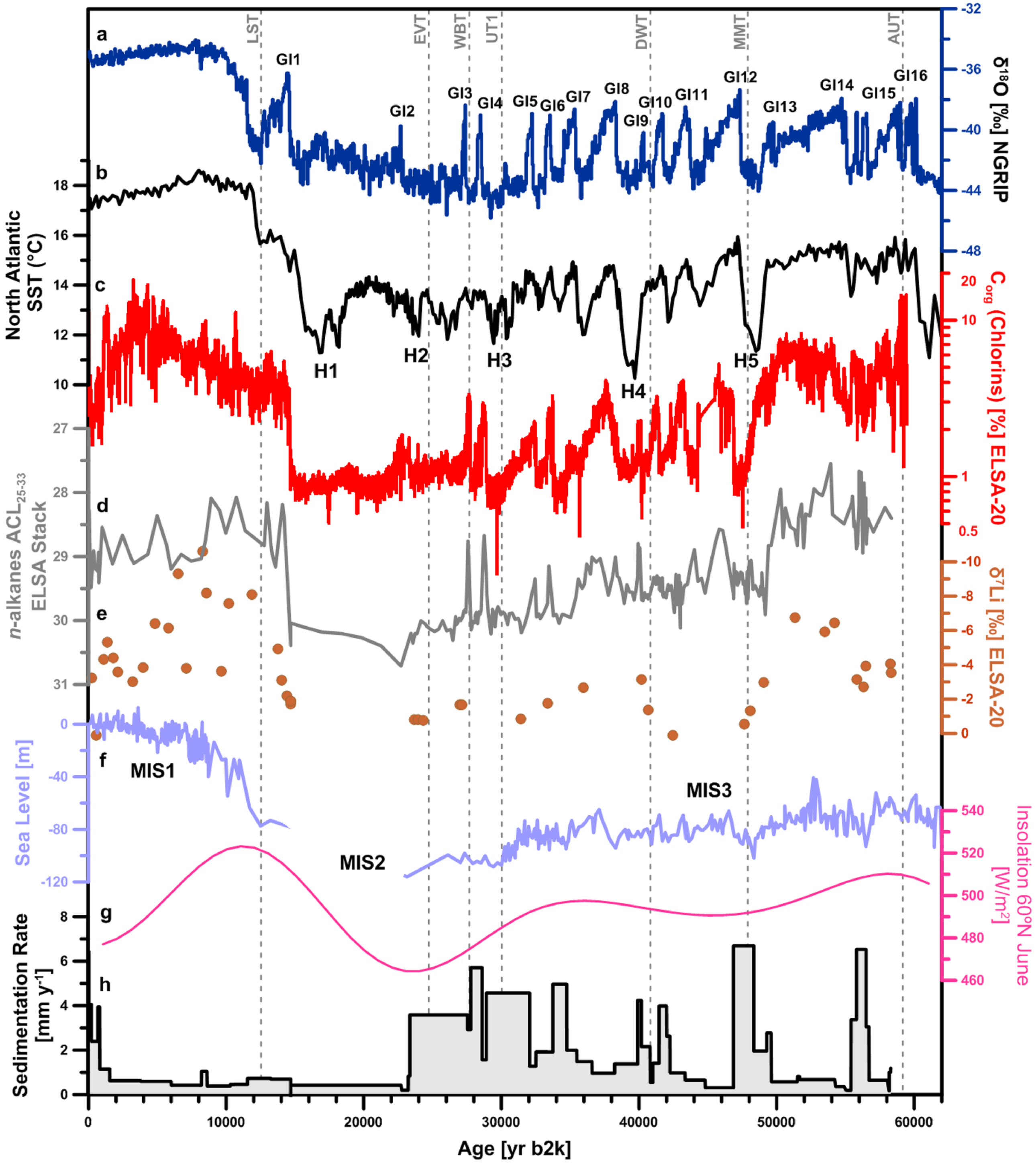

Figure 3. Selected global climate records in comparison to sedimentological and tephra records of the ELSA-20-Stack. Insolation[81], sea level[16], North Atlantic Sea surface temperatures[21], NGRIP $\delta^{18}O$[18], Eifel Tephra[45].

Reconstruction of the Eifel vegetation by analysis of pollen, botanical macroremains and leaf waxes.

The analysis of pollen, botanical macroremains and leaf wax compounds (long-chain *n*-alkanes) in the ELSA-20 record indicate that the abrupt temperature changes recorded by lake productivity tracers were coupled to major changes in structure of terrestrial ecosystems. The distribution and isotopic composition of long-chain *n*-alkanes can be used to reconstruct past changes in vegetation. Although there is considerable interspecific variation, C4 grasses tend to synthetize *n*-alkane with a maximum around C_{31} and a relatively high proportion of C_{33}, while C3 trees and shrubs tend to show a maximum around C_{29} and a relatively higher proportion of C_{27}[32,33]. The average chain length (ACL) index can be used to express changes in the carbon number of the most abundant *n*-alkane homologue[34]. In general, in the ELSA-20 record, the ACL of leaf waxes approaches values typical of C3 trees, shrubs and grasses during warm periods of the Holocene and interstadials of MIS3,

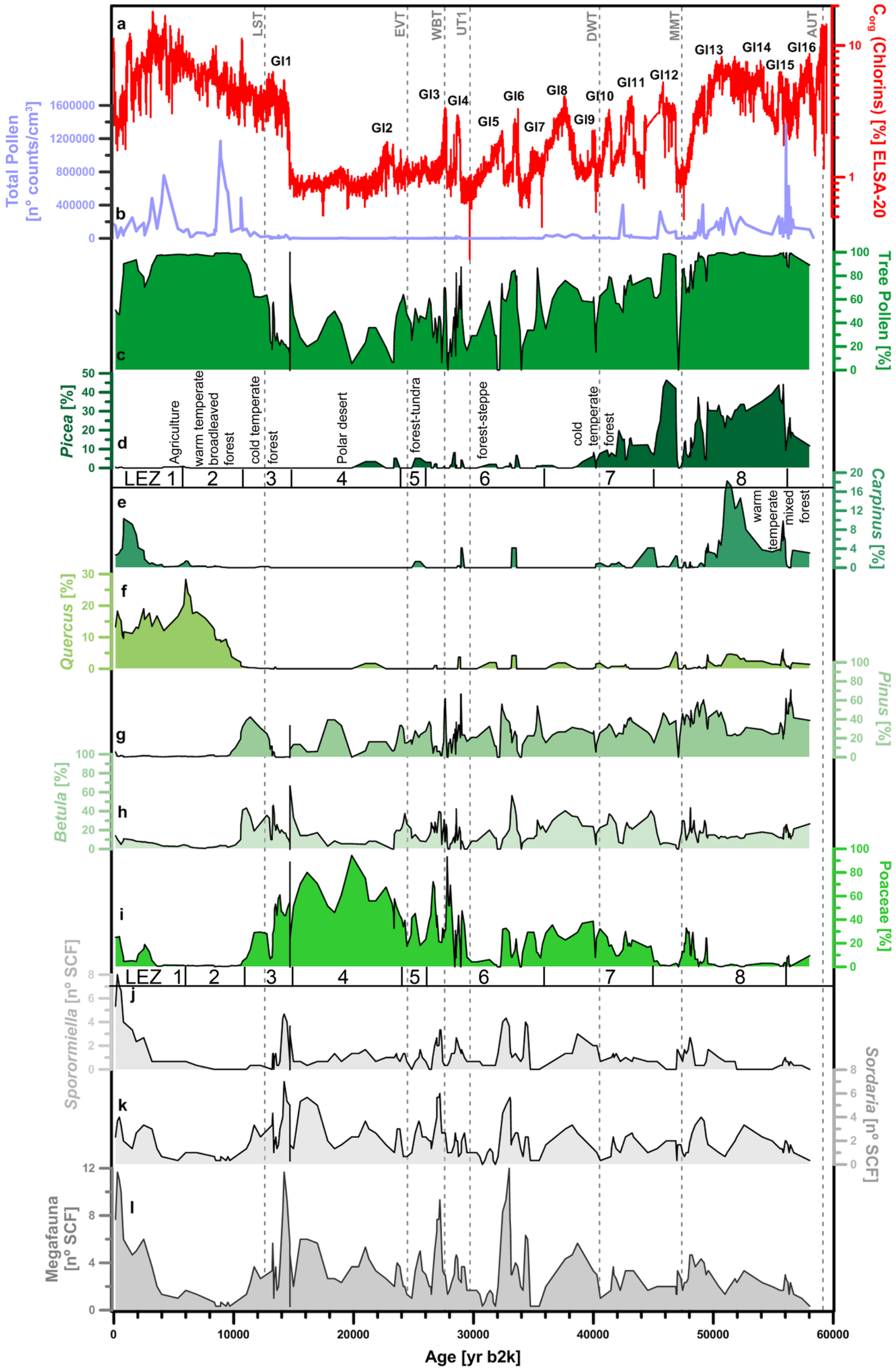

Figure 4. Selected pollen and spores during the last 60,000 years. The plots are based on all samples with countable pollen grains. The curves are smoothed with a three-point running mean. Values for all taxa counted see Supplementary Figs. S8, S9. Landscape Evolution Zones (LEZ)[2].

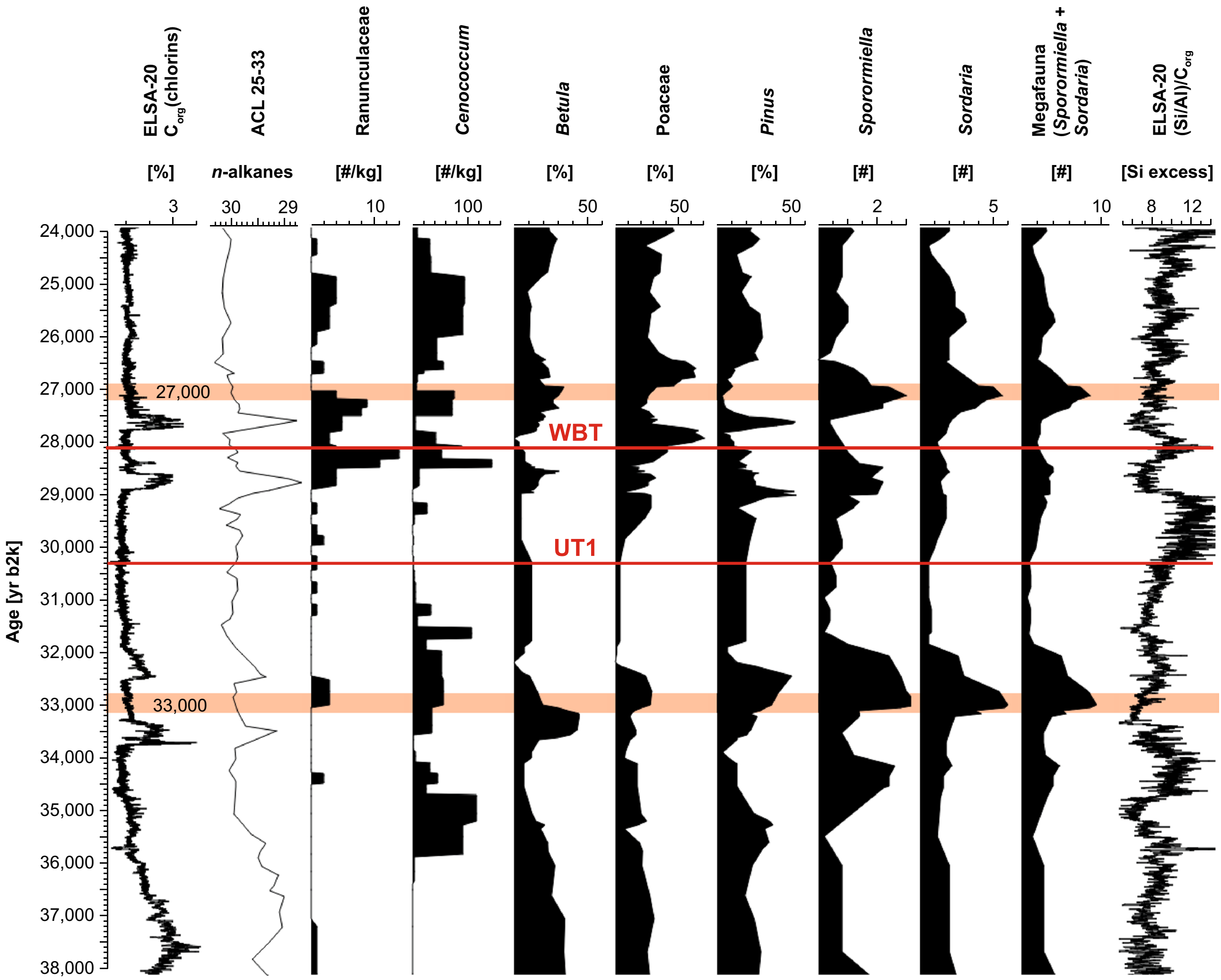

Figure 5. Selected pollen, botanical macroremains, and spores from 38,000 to 24,000 yr b2k. The plots are based on those samples with more than 20 countable pollen grains. The curves are smoothed with a five-point running mean. Values for all taxa counted see Supplementary Figs. S8, S9. Brownish bars indicate the times of high Megafauna presence.

but show values characteristic of C4 grasses during cold periods (i.e. LGM and most MIS3 stadials) (Fig. 3). Althought, the species of C4 grasses could not be identified, the *n*-alkane pattern is in good agreement with the long-term changes in vegetation types recorded in pollen assemblages, which show a clear dominance of grass pollen from the family Poaceae (which includes C4 grasses) during cold periods.

The time series of pollen reveals a forested landscape dominated by spruce (*Picea*), oak (*Quercus*), hornbeam (*Carpinus*) from 60,000 to 48,000 yr b2k (Fig. 4, Supplementary Fig. S9). This phase terminated abruptly with the North Atlantic cold event Heinrich 5 (H5) at 48,000 yr b2k, when hornbeam disappeared, which indicates a sharp drop of Mean Annual Air Temperature below 5°C[35]. The pollen evidence is matched by an increase in the ACL of *n*-alkanes, which suggests an abrupt drop in C3 vegetation, and an increase in C4 grasses at 48,000 yr b2k. These changes may be linked to seasonal changes in precipitation, as well as changes in summer temperatures during cold periods (Fig. 3). Many samples of the subsequent millennia, i.e., during H5, are pollen sterile, while the sedimentation rate was at a maximum. Accordingly, H5 was a cold and wet stadial (see above), with vegetation almost absent. The Li isotope record (Fig. 3) shows increasing δ^7Li values between ca. 50,000 and 47,000 yr b2k, indicative of a possible stripping of the well-developed soils of the early MIS3, followed by little soil development consistent with an absence of vegetation. The pollen assemblages of the interstadials after H5 (GI12, 11, 10 and 9) are characteristic of an open woodland, termed Landscape Evolution Zone (LEZ) 8 in Sirocko et al.[2].

We observe another extreme cold phase at 43,000 yr b2k, when the sediments of five different maar lakes show indications of frozen sediment relocation, well visible in the Auel record[1]. This extreme cooling event will be presented in an upcoming publication. While this cold phase could have been significant for the migration of the early Aurignacian humans into central Europe, it did not affect megafauna presence. Megafauna survived also the time of the Campanian Ignimbrite at 39,800 yr b2k and the subsequent H4 cold event, which was also characterized by high sedimentation rates at Auel, and was thus again cold and wet, but with at least some

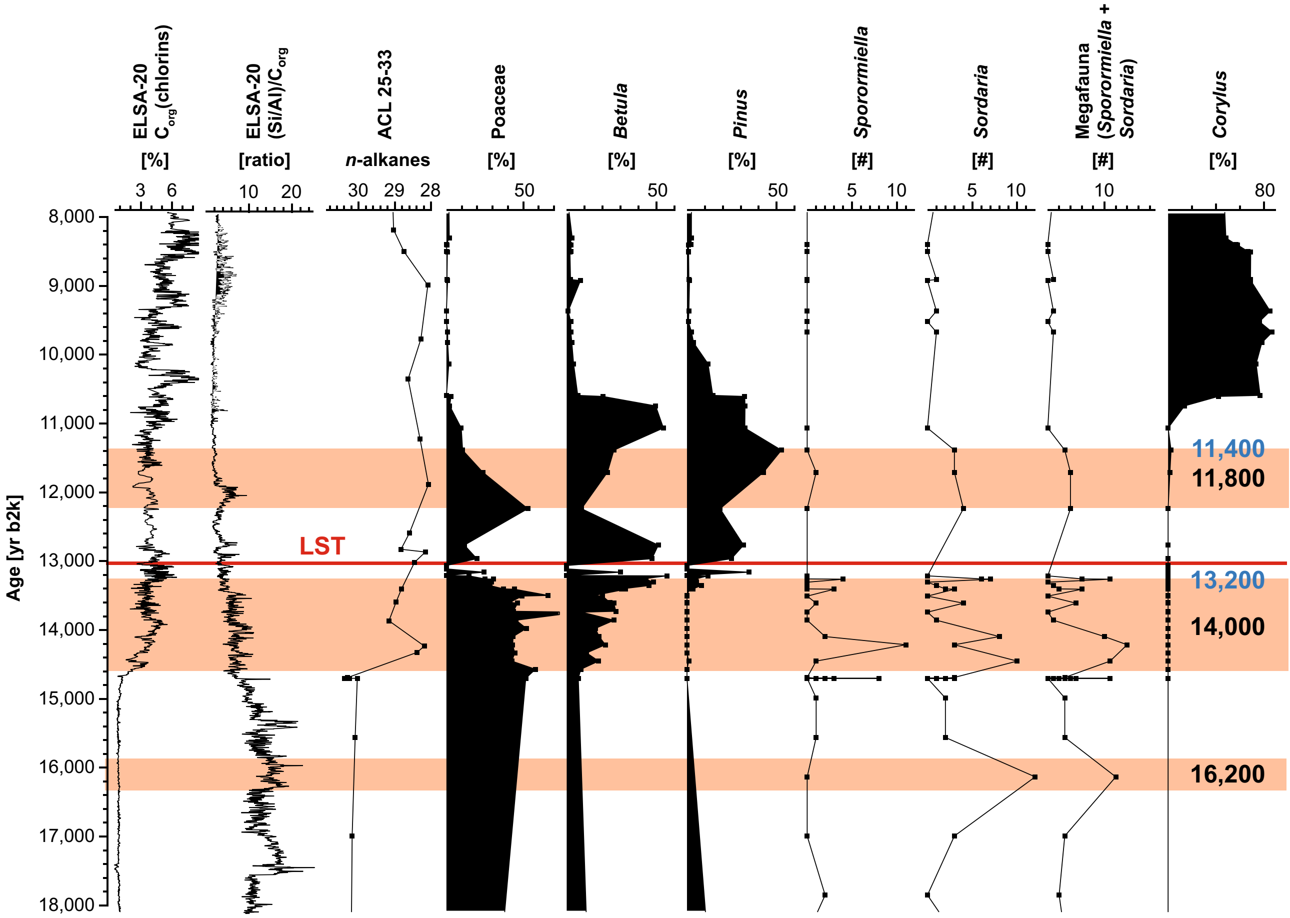

Figure 6. Selected pollen and spores from 18,000 to 8000 yr b2k. The plots are based on those samples with more than 20 countable pollen grains. Values for all taxa counted see Supplementary Figs. S8, S9. Brownish bars indicate the times of high Megafauna presence.

vegetation and thus megafauna presence. The vegetation of the subsequent GI8 is similar to that of preceding GI12–9, however, tree pollen was low and spruce disappeared, while grass pollen further increased. This time period falls into the interval of the lowest summer insolation of the middle MIS3 (Fig. 3).

Insolation on the northern hemisphere increased again after 35,000 yr b2k (Fig. 3) and we observe an increase of all trees during GI7–3 (Fig. 4, Supplementary Fig. S9). In particular GI4 and GI3 reveal a clear spike in the *n*-alkane ACL record, indicating that these interstadials had again high tree abundance. Lithium isotope compositions show poor soil development during this period (Fig. 3). It is possible that despite tree cover increasing, it did not reach the threshold value allowing for landscape stability and soil development as observed during the early MIS3 and the mid Holocene. This threshold value in tree cover needs to be exceeded in order to achieve landscape stability and thus significant soil development to take place[31]. These interstadials appear to have had warmer summers than the preceding GI14–GI8; an observation, which cannot be explained by orbital controlled insolation. Instead changes in the North Atlantic Meridional Overturning Circulation (AMOC) must be invoked to explain the temperature anomalies of these warm interstadials[1].

The landscape after GI4 was a tundra, well documented by seeds of terrestrial Ranunculaceae (Fig. 4). The tundra (LEZ 5) terminated at about 25,000 yr b2k (Fig. 4) and the landscape turned into a cold desert with frequent dust, a situation that intensified after 23,500 yr b2k[26]. The subsequent LGM was dominated by grass pollen and some moss macroremains; ostracods were apparently very abundant in the cold and well oxygenated water of the LGM maar lakes. Many samples of the LGM are pollen sterile, either because of a temporary absence of vegetation or a complete dissolution of pollen in the well-oxygenated water of the LGM maar lake. Pollen of subarctic taxa is observed in very low count numbers and show only grass, pine and birch pollen. These observations are consistent with the high ACL values of *n*-alkanes, which indicate that under coldest conditions the vegetation was dominated by C4 grasses.

The abundance of grass decreased after 16,000 yr b2k but continued to be the main vegetation during and even after the first North Atlantic warming starting at 14,700 yr b2k (Fig. 4). Birch, pine and willow increased slowly in the catchment of Auel and Holzmaar, which fits the vegetation development documented in other Holocene pollen records from the Eifel maar lakes[36,37]. It was around 13,300 yr b2k that pine and in particular birch developed for the first time into a more dense forest[38]. Between 25,000 and 15,000 yr b2k, high δ^7Li values suggest that sediments delivered to the lakes derived from poorly-developed soils, a consequence of sparse

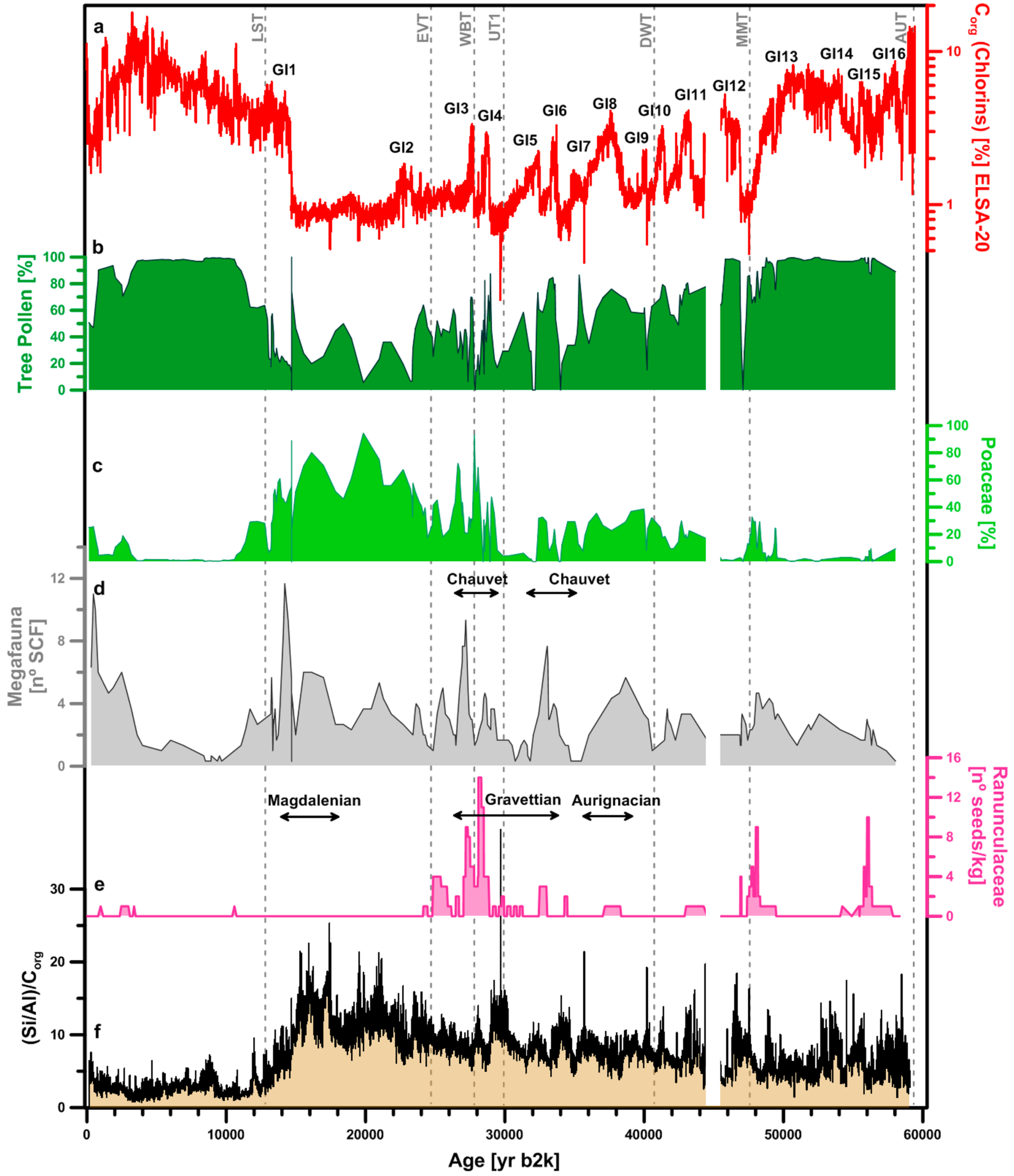

Figure 7. Synthesis of environmental change to explain the presence/absence of Megafauna during the last 60,000 years. The plots are based on all samples with countable pollen grains. All curves are smoothed, C_{org} and Si excess with a 100 year resolution, the pollen and spores to a resolution of 200–500 years.

vegetation and dry conditions. It is not until dense forest developed that δ^7Li values decrease, possibly indicative of landscape stability and soil development.

Grass, with some pine, birch, juniper, and willow characterize the subsequent Younger Dryas (YD). The second abrupt deglacial warming at 11,600 yr b2k was followed by several centuries of decrease in all late pollen of subarctic taxa, but an increase in hazel, which became visible in the pollen record from 11,200 yr b2k onwards (Fig. 6). First presence of hazel was followed by increasing numbers of oak and other thermophilous broadleaf trees, which formed an early Holocene forest cover (see Supplementary Fig. S9). This extensive tree cover would have contributed to landscape stabilization, allowing for soil development, as illustrated by low δ^7Li values from 6000 to 2000 yr b2k (Fig. 3).

Reconstruction of the presence of megafauna by analysis of spores from coprophilous fungi. The presence of megafauna is documented by the occurrence of spores from *Sporormiella* and *Sordaria*, which occur in the Auel record for the first time during the stadial climate conditions from 59,000 to 56,000 yr b2k, when the spruce forest turned into a tundra for several centuries (Fig. 4). Which of the four migration corridors the animals used to migrate into central Europe is not known, in any case they moved into a landscape with abundant terrestrial Ranunculaceae, thus most likely a tundra-like environment. The spruce trees characterizing all the rest of GI17–14 disappeared during this tundra phase, and it is only during the tundra phase that megafauna appears in the sedimentary record of Auel (Fig. 4). The signal is best visible in the *Sporormiella* record as a small solitary maximum (Fig. 4); the respective megafauna disappeared promptly with the spruce reforestation after about 1000 years, highlighting the prime role grassland (absence of trees) played for megafauna presence.

The next appearance of the megafauna in the sediment record was with the cooling event at 48,000 yr b2k, after which high numbers of SCF (a proxy for megafauna) appear in the Auel record during the wet and cold millennia of H5. Megafauna presence during the subsequent GI12–11 time period is difficult to quantify, because sedimentation was disturbed in the Auel lake, and all other lakes of this time period, shortly after GI12. Megafauna was however clearly present during the subsequent geomagnetic Laschamp excursion at 42,500 yr b2k. Its abundance was not strongly affected by the Campanian Ignimbrite at 39,500 yr b2k, and it was also present during the H4 event at 39,000 yr b2k, which was again cold and humid.

The 3000 year-long GI8 record reveals taxa as before (Fig. 4), but other trees like *Ulmus* increased also in abundance (see Supplementary Fig. S9). Megafauna was present during GI8, but not in high abundance. It was only after 35,000 yr b2k that *Sordaria* and *Sporormiella* increased. The only parallel vegetation change is an increase of *Cenococcum*. The sclerotia of this ectomychorrhizal fungus form on the roots of a variety of plants on both hemispheres and all climates from the arctic to the tropics[39]. The coincidence of *Cenococcum* and high megafauna abundance is best explained by the decrease of vegetation cover—mainly trees—which caused higher erosion rates into the lake. The most pronounced megafauna maximum develops during the stadial after GI7, and synchronous with the well-dated terminal first phase of art painting in the French Chauvet cave[40].

The next maximum of SCF abundance is with three spikes between 29,000 and 27,000 yr b2k. The landscape was a tundra during these millennia, but it is again a time of active cave art creation at Chauvet. One explanation for this coincidence could come from environmental changes in the potential migration corridors leading into central Europe; probably the most likely mechanism to synchronize megafauna and human migrations. These millennia witnessed the global fall of sea level at the MIS3 / MIS2 transition. The connection between England and the European mainland developed during this time. Simultaneously, the landscape of Scandinavia and Russia must have changed in front of the expanding continental ice sheets, which were recently dated to the stage of the "Brandenburger ice advance", after 30,000 yr b2k[41]. A well-known archeological site for the millennia after GI4 is the Czech Site of Dolní Věstonice, which is at the southern Russian corridor, where mammoths were hunted extensively from 31,000 to 29,000 yr b2k[42,43].

The last Ranunculaceae seeds that documented a tundra landscape disappear at 25,000 yr b2k, but this did not terminate megafauna presence. In contrast, both *Sordaria* and *Sporormiella* reached maximum values after the LGM, when only grass was present and dust activity increased with a change in the main wind direction, reconstructed from the Dehner Maar sediments[26–28] (see also the new C_{org}/(Si/Al) dust proxy; Figs. 5, 6). The LGM section of the Auel maar has many samples with no pollen at all. Either grass had disappeared or the water was so well-oxygenated that pollen dissolved. If pollen was indeed dissolved in oxygenated water, grass and megafauna could have been present continuously from 24,000–13,300 yr b2k. Megafauna was thus possibly present during all of MIS2, but the relative proportion of *Sordaria* and *Sporormiella* changed at 16,000 yr b2k, possibly related to an increase of horse presence, which was the most abundant hunting prey at Gönnersdorf (80 km distant to Auel) at that time[44].

Surprisingly, the first strong warming episode of the North Atlantic at around 14,700 yr b2k had no strong effect on the Eifel landscape and megafauna presence. Organic matter in the lake sediments increased with warming, probably due to the development of a summer stratification and the development of a seasonal suboxic deep water; but the environment around the lake did not change immediately. Grass persisted throughout the first centuries of the deglacial, and only scattered juniper characterized the immediate changes in the landscape at 14,700 yr b2k[37]. Apparently, the late glacial herbivore herds expanded as long as grass was present. The higher temperature could have even encouraged the growth of herds, because it would have increased the length of the summer season.

The megafauna presence decreased with the development of the deglacial birch and pine forest, in particular after 13,400 yr b2k (Fig. 6), i.e., during the development of the first birch forests, which mainly affected the *Sporormiella* record. The megafauna responsible for this spore did not return to its glacial presence during the subsequent YD. *Sordaria*, possibly representing reindeer, reached a final maximum during the YD, when trees decreased, but did not disappear, whereas grasses spread. Both spore types further decreased with the spread of pine and birch during the early Preboreal (11,600–11,000 yr b2k). It was however not until 10,740 yr b2k that *Sordaria* was reduced to a background level (Fig. 6). Both types of SCF were absent during the Mesolithic times of the early Holocene Mixed Oak forest, but returned with the deforestation (spread of grass) during the onset of Neolithic landscape use (Figs. 4, 7), probably representing cattle in the opening woods and later on meadows.

Discussion of processes controlling the occurrence of megafauna

An analysis of the impact of climate and environment on the mammals and early human cultures in central Europe must take into account that fire and ash from volcanoes can have a strong impact on a landscape. If a tephra is rich in potassium, the ash affects soil formation and the vegetation positively; whereas primitive ash compositions, like in the Eifel, are non-fertile. In addition, human presence can be interrupted by explosive volcanic eruptions. The tephra record of the ELSA-Tephra Stack[45] (Fig. 3) shows that volcanic activity had no lasting effect on the vegetation and animals that lived in the Eifel over the past 60,000 years.

Generally, it is assumed that periods of warming may have had a strong effect on the occurrence of megafauna. This hypothesis is not supported by the observation that grass persisted throughout the warming event at 14,700 yr b2k and also that the spore record was not affected by the North Atlantic warming. An increase in temperature alone apparently did not strongly change landscape structure. However, warming is clearly documented in the lake sediments by the increase of C_{org}(chlorins) content at that time, which must have been caused by the development of thermal lake stratification during summer, causing deep anoxia and thus an increase in organic carbon preservation.

Cold temperatures were no more a problem for the megafauna than warming periods, as they survived even the coldest conditions of stadials, Heinrich Events and the LGM. Precipitation may not have been a serious challenge for the megafauna either, as shown by the maximum spore concentrations during phases of the earlier MIS3, which are associated with higher sedimentation rates. These high sedimentation rates at Auel are caused by high clay content and were thus apparently a function of the riverine contributions and precipitation. Visible flood layers in the Auel sediments were associated with snowmelt events[23], which however show no relation to megafauna presence. The general increase of sedimentation rate is most likely due to perennial precipitation, which was apparently high in all stadials. Accordingly, temperature and precipitation alone cannot be regarded as prime factors for megafauna habitats.

Neanderthal Humans are recorded in Europe for the entire period from around 300,000 to 40,000 yr b2k[46] and must have inhabited the spruce forest of GI17–12. The first appearance of Anatomically Modern Humans (AMH) in Europe might have been as early as 57,000 yr b2k in southeastern France[47], but in central Europe at that time only Neanderthals were to be reckoned with. The first appearance of megafauna overlaps with late Neanderthals. This is reflected by the presence of spores of both *Sporormiella* and *Sordaria* during the few centuries after GI16, when Ranunculaceae seeds and absence of spruce pollen indicate the development of tundra with herds of megafauna, but only for a few centuries.

The geographically closest evidence for late Neanderthals in the larger Eifel area comes from the Goyet Cave in Belgium from around 40,000 yr b2k[48]. The cave is about 120 km from Auel. There is clear evidence that Neanderthals at that time hunted horses, reindeer, young mammoths and woolly rhinoceroses[48–50], which we believe to be the mammals that produced the feces on which *Sporormiella* and *Sordaria* grew.

It is still strongly debated when the first Aurignacian people exactly arrived in central Europe. Dates from 43,000 to 37,000 yr b2k have been proposed[51–53], but without doubt before the long and warm interstadial GI8. Aurignacian people were present in the caves of the Swabian Jura and produced some of the first fully sculptural works of art in human history around 40,000 yr b2k[52]. The AMH living in the Goyet cave are genetically most similar to the AMH living in Kostenki (Russia) and have been described as part of the ancestral European Founder Population[54]. Following the indications as outlined in this paper, they should have come along the Russian corridor and followed the megafauna herds into a landscape where grass started to spread after the millennia of the extreme North Atlantic H4 cold event.

It is however only after GI8 that first Aurignacian cave paintings were dated by both ^{14}C and U/Th to 37,000–33,500 yr b2k in the French Chauvet cave[40]. Spore concentrations in the Auel record show low megafauna presence during this time, but the most pronounced spike in the megafauna record is exactly at the end of the Chauvet painting phase. It would be speculative to construct a common mechanism behind this, but a high resolution comparison of the Auel megafauna presence and the terminal painting phase at Chauvet might shed a light on this.

The next episode of cave art at Chauvet is from 31,000 to 28,000 yr b2k, which falls into the Gravettian, starting in central Europe around GI6 at about 34,000 yr b2k and lasted until GI3, at about 27,000 yr b2k[55]. The Auel record shows that these millennia had witnessed spikes of trees, however only during the warm centuries of GI5, 4, 3. These late MIS3 interstadials might have been warmer than the preceeding interstadials GI8–6. All interstadials were related to the intensity of the AMOC[1], but in addition, GI5–3 fall into a period of increased summer insolation (Fig. 3). It is possible that the North Atlantic AMOC intensification and the general increase of summer insolation were superimposed during the forested interstadials. In between the interstadials, Ranunculaceae were abundant and indicated local or temporary tundra landscape during the stadials, as soon as the AMOC collapsed.

GI4 at 28,000 yr b2k was the warmest of the Gravettian interstadials; spores show high megafauna presence during the interstadial and after the interstadial. It is in line with the observation that human population size in central Europe increased between 43,000 and 29,000 yr b2k and started decreasing only after 28,000 yr b2k[56,57].

Climate changed drastically at 26,000 yr b2k, well visible in the paleobotanical record at Auel, but also in the subsequent almost complete absence of humans in central Europe. This is a time when humans either migrated south to glacial refugia or, more likely, became extinct in many parts of central Europe. There are archeological arguments against a southward migration[57], but also genetic ones: demographic modelling of ancient genomes shows that human populations underwent a significant reduction in size around 27,000 yr b2k accompanied by a split into southeastern and southwestern subpopulations[58]. The Auel record shows that some megafauna however remained in the seasonal grassland of central Europe which can be taken as an indication that they were clearly better adapted to the cold than humans (Fig. 7). Little is known about the presence of humans during the LGM in the Eifel region itself. At the site Wiesbaden-Igstadt, in the central Rhineland, and in the Swiss Jura there is sporadic evidence for human presence, which can probably be assigned to GI2[59,60].

The pollen spectrum and the increased presence of SCF indicate that the Eifel landscape was covered by grass from 16,000 to about 13,300 yr b2k, with trees in increasing numbers after the first Late Glacial warming at 14,700 yr b2k. Both *Sordaria* and *Sporormiella* were abundant until 13,300 yr b2k (Fig. 6) and indicate a constant late glacial megafauna assemblage. *Sporormiella*, however, decreased sharply at 13,300 yr b2k, synchronous with the increase of birch and pine pollen, which formed the first deglacial central European forests. We suspect that mammals like the giant deer *Megaloceros* could not live in a forest and moved into open landscapes like Ireland, where *Megaloceros* reached its maximum population density during the Allerød[61] when the Eifel, and other parts of central Europe, were apparently covered by a dense birch and pine forest. Following Zimov's[62] suggestions, Megafauna may not be affected by vegetational change, but may itself suppress the development of woodland by grasing. Thus, migration of herbivores may result in the decrease of herbs and grasses in favor of tree species. From our data, we can not conclude the exact interplay between Megafauna and vegetation, however, we see a returning pattern of forest closure and disappearance of Megafauna. Strong presence of humans in the Rhineland hundreds of years before the 14,700 yr b2k warming is attested by the Magdalenian sites such as Gönnersdorf and Andernach. The Magdalenians hunted mainly horse and reindeer, while a few mammoth and rhinoceros remains seem to be of sub-fossil origin[63]. During the subsequent period of the Allerød elk, red deer and aurochs was the main prey[64,65]. Sporadic presence of reindeer hunters can be mentioned for the Younger Dryas[66]. The impact of humans on the megafauna in this region during these dramatic climatic and environmental changes cannot be reconstructed at the moment. Ongoing DNA analysis in the Auel sediments might provide some clue into the interrelations between late glacial humans and the megafauna.

Conclusions

Megafauna abundance shows no relation to periods of active volcanism in the Eifel, suggesting that volcanic activity and associated fire events did not play a role in megafauna extinction. The presence of megafauna does not seem to have been affected by humans either. In fact, megafauna was most abundant in the period from 33,000/27,000 yr b2k, probably fostering human presence of (late) Aurignacian and Gravettian hunters in central Europe. For example, the close connection between the presence of megafauna and humans is documented in the Rhineland for the horse hunter site of Gönnersdorf at ca. 15,500 yr b2k, where it is likely that large herds attracted human hunters. In addition, megafauna inhabited open woodland, steppe, tundra, and even the polar desert of the LGM when only seasonal grass and moss were accessible. Thus, megafauna apparently tolerated all climates, including abrupt warming and cooling events as long as grass grew in abundance.

The main causal mechanism for the decrease and eventual disappearance of megafauna was the development of woodlands. Most likely, as forests grew, the large herbivores lost their main food — grass — and were no longer able to migrate long distances between seasonal grassland regions. The extent to which forests were also an obstacle to a rapid escape from hunters and predators cannot be inferred from the available time series of SCF. Wolves and humans may have had a much greater chance of killing young calves in a dense forest than in an open landscape. In summary, the evaluation of the ELSA-20 stack analysis strongly suggests that forestation was the main factor affecting the presence or absence of megafauna in central Europe during the late Quaternary.

Materials and methods

The Eifel maar lakes. The Eifel is located west of the Rhine in Germany; it experienced 200–300 m of uplift during the Cenozoic, leading to the formation of more than 60 Pleistocene maar eruptions. Eight of these maar lakes are today still filled with water, of which six have more than 20-m-deep waters with anoxic conditions at the bottom. All other maar structures are infilled Pleistocene lakes. The largest of these maar lakes were dated by the ELSA Project[2–4] and erupted during the last 130,000 years[19,20] (Supplementary Table S1). Mapping of the ejecta from large and small structures indicated that the smaller ones erupted simultaneously with nearby larger structures. According to the ELSA datings of the large Pleistocene maar structures, we expect up to 60 maar structures to have been lakes or swamps during MIS3. Accordingly, we present in Fig. 1b map of the "MIS3 Eifel Lake District" with up to 60 lakes/swamps and numerous creeks (partly dammed by lava flows) that drained towards the Mosel river.

Palynology. We have analyzed pollen for 250 samples along the entire stack (Figs. 4, 5, 6, 7 of main text, Supplementary Figs. S6–S9). At least two of these pollen samples for each interstadial and stadial have been further analyzed for spores. Each pollen/spore sample spans a depth range of 1 cm and represents a volume of about 1 cm^3. The sediment was treated with potassium hydroxide solution (KOH), hydrochloric acid (HCl) and hydrofluoric acid (HF). For acetolysis, acetic acid ($C_2H_4O_2$) and a mixture (9:1) of acetic anhydride ($C_4H_6O_3$) and sulfuric acid (H_2SO_4) was used. Centrifugation was done at 3000–3500 rpm for 5 min. The samples were sieved at 200 µm and later filtered at 10 µm. *Lycopodium*-spore tablets were added for calibration of absolute pollen volumetric concentration. The samples were mounted with liquid, anhydrous glycerol ($C_3H_8O_3$). Pollen counting was done under an optical microscope at a maximum of 600-fold magnification. Total pollen content (#/ccm) has been calculated using the known number of *Lycopodium* spores in added tablets[67].

In most samples we were able to count up to 300 pollen grains, however, some stadial samples just show 20 countable pollen grains. 20 counts are statistically problematic, but these samples include often only three taxa (*Pinus, Betula,* and Poaceae). Samples with less than 20 pollen grains have been regarded as being pollen sterile, either because pollen was not produced or dissolved in the oxygen rich stadial and glacial deep water. We document the number of counted pollen grains and also the absence of pollen in Supplementary Figs. S6–S9 and Supplementary Tables S2, S3, S4. In particular the absence of pollen outline a clear pattern; with minimum vegetation during the H5 and H4 events.

In this study, we focused on Holzmaar and Auel sediments, but typical vegetational compositions like during the early MIS3, that is dominated by spruce, are also visible in pollen spectra from other Eifel maar lakes (see Supplementary Fig. S10, Supplementary Tables S5, S6, S7).

Paleobotanic macroremains. The botanical macroremains for core AU2 had been already published[2]. Time series are not reproduced here, but we include in Figs. 5, 7 the data of Ranunculaceae and *Cenococcum*, which are important to outline phases of tundra vegetation, soil erosion, and the LGM.

Ranunculaceae (crowfoot family) have a worldwide distribution, predominantly in areas with temperate to boreal climates. In the Auel drill core, seeds from Ranunculaceae were abundant during the forest-tundra phase, 29,000–24,000 yr b2k (LEZ 5). Many of the non-aquatic *Ranunculus* species are tolerant to moist soils typical for tundra environments. We therefore use terrestrial Ranunculaceae as the most reliable indicator for tundra vegetation.

Spores of coprophilous fungi — Indicators of the presence of herbivores. The spore records of *Sordaria* and *Sporormiella* are presented in this study (Figs. 4, 5, 6, 7). Representatives of both genera are coprophilous, which means that they need feces as a substrate. Both taxa are established indicators for the presence of megafauna[5,68–70].

Sordaria ascospores are ellipsoidal with one pore at the top of the spore (Fig. 2)[8]. The spores have been detected on dung of various herbivore species, among them mammoth, moose, and cattle[71–73]. The spores serve as an indicators for Pleistocene megafauna[5,69] as well as domesticated animals[7,74].

Sporormiella ascospores show three or more septa; the spores fall apart in separate cells, each one with a germ slit (Fig. 2)[8]. *Sporormiella* species are obligate coprophilous and were recorded on feces of, among others, mammoths, cows, rhinoceros, horses, moose, reindeers, and hare[68,72,75–78]. Spore records of *Sporormiella* were used to estimate herbivore biomass flucutations during the Pleistocene[5,68] and the Holocene[6].

Alkanes. Long-chain odd-carbon number *n*-alkanes are important components of the protective waxes that coat the leaf surfaces of almost all land plants. Their insolubility in water, negligible volatility, chemical inertness, and resistance to biodegradation make them excellent biomarker compounds. The distribution and isotopic composition of long-chain *n*-alkanes can be used to reconstruct past changes in vegetation. Although there is considerable interspecific variation, C4 grasses tend to synthetize *n*-alkane with a maximum around C_{31} and a relatively high proportion of C_{33}, while C3 trees and shrubs tend to show a maximum around C_{29} and a relatively higher proportion of C_{27}[32]. The average chain length (ACL) index can be used to express changes in the carbon number of the most abundant *n*-alkane homologue[34]. C4 grasses have average ACL values of 30.66 ± 0.83, while C3 trees and shrubs show average ACL values of 29.00 ± 0.83[33]. In most environments, estimates of change in vegetation type using ACL agree well with those indicated by its carbon isotopic signature, and correlate with those obtained by independent proxies such as pollen abundances[79].

Samples were freeze-dried and homogenized and the *n*-alkanes were extracted and separated using an Accelerated Solvent Extractor 350 (ASE). ASE cells (22 mL) were prepared with muffled glass fiber filters, 16 g deactivated silica gel and about 0.5 g of the sediment. The cells were flushed with *n*-hexane for the *n*-alkane fraction. After the extraction, an internal standard (hexatriacontane) was added to the samples to quantify the *n*-alkanes. Subsequently, they were dried in a centrifugal evaporator ('Rocket' by Genevac) and re-dissolved in isooctane before analysis. Analysis of the *n*-alkanes was carried out with an Agilent 7890B gas chromatography system with flame ionization detection (GC-FID) using a VF-200 column.

Lithium isotopes — indicators of soil formation. Lithium (Li) isotopes are used as a proxy for soil formation[30] and were analyzed for cores AU2 and SM5 (Fig. 3); the data were transferred to the respective stack numbers. The resolution of the Li isotope record is, however, not comprehensive enough to construct a complete stack such as that achieved for pollen and spores.

Sample preparation for Li isotope measurements was undertaken in a Class 10 cleanroom at the Wollongong Isotope Geochronology Laboratory, University of Wollongong, Australia. About 10 mg of ground sediment sample (typically < 63 µm fraction) was dissolved in 48% HF and 65% HNO_3 at 100 °C for > 12 h. After drying down, samples were re-dissolved in aqua regia at 130 °C for > 12 h to break down any fluorides. Samples were then re-dissolved in 1.5 mL 1 M HCl to perform ion exchange chromatography. Cation exchange columns were calibrated with natural seawater samples. After the chromatography procedure, the Li elution was dried down and taken up in 0.3 M HNO_3 for isotopic analysis on a MC ICP-MS at the University of Wollongong. Using wet plasma conditions, a 30 ppb single element Li tuning solution yielded a typical intensity of 1 V on ^{7}Li, while background was of the order 5–50 mV on ^{7}Li. The cones setup consisted of a Ni Jet sampler and X-skimmer and a PFA-100 microflow nebulizer (ESI, Omaha, NE, USA) with a flow rate of 90–150 µL/min with a high sensitivity insert (Thermo Scientific). A standard bracketing technique was applied using IRMM16 as primary standard for ^{7}Li/^{6}Li ratios. Synthetic standards Li7-N and Li6-N[80] were used to assess accuracy of isotopic ratio determination. Instrument blanks were measured between each standard and sample by introducing 0.3 M HNO_3. Blank intensities were then subtracted from each isotope. Corrected ^{7}Li/^{6}Li ratios were converted to δ^{7}Li values using L-SVEC as reference[80]. Results for Li7-N and Li6-N are: $\delta^{7}\text{Li} = 30.2 \pm 0.3$ ‰ (n = 22, 2SE) and -8.0 ± 0.2 ‰ (n = 16, 2SE), respectively. To verify the sediment sample dissolution and ion exchange chromatography protocols for Li isotope measurements, a granitic geochemical reference material JG-2 was processed with every sample batch of 10. The average δ^7Li value of JG-2 is 0.7 ± 1.0 ‰ (n = 5, 2SE). Measured Li isotope ratios for Li6-N, Li7-N, and JG-2 measured in this study are well within reported values.

Total procedure blanks (n = 3), measured on a Q ICP-MS, yielded 0.8 ng, 0.8 ng, and 0.2 ng of Li. The external reproducibility for Li isotope measurements of natural samples, calculated via the average of the 2-standard error (2SE) of two replicate samples, is estimated at 2.2‰.

Tephra. All ELSA cores covering the last 60,000 years (Supplementary Table S1) show a total of 7 visible tephra layers, each over 1-cm thick (Fig. 3). The thickness varies at different sites according to the distance to eruption centers and prevailing wind directions. Most of these tephra in the lake sediments were already correlated to known eruptions, namely the Laacher See (13,056 yr b2k), Eltville (24,720 yr b2k), Wartgesberg (28,100 yr b2k), Tephra with unknown eruption center (UT1, 30,300 yr b2k), Dreiser-Weiher (40,370 yr b2k), Meerfelder Maar (47,340 yr b2k), and Auel Maar (59,130 yr b2k)[20].

All the methods were in accordance with the relevant guidelines and regulations. The permission to collect pollen was given in the drilling permissions.

Data availability

All data is available in the main text or the supplementary materials.

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References

1. Sirocko, F. *et al.* Muted multidecadal climate variability in central Europe during cold stadial periods. *Nat. Geosci.* **14**, 651–658 (2021).
2. Sirocko, F. *et al.* The ELSA-vegetation-stack: reconstruction of landscape evolution zones (LEZ) from laminated Eifel maar sediments of the last 60,000 years. *Global Planet. Change* **142**, 108–135 (2016).
3. Sirocko, F. *et al.* Multi-proxy dating of Holocene maar lakes and Pleistocene dry maar sediments in the Eifel, Germany. *Quat. Sci. Rev.* **62**, 56–76 (2013).
4. Sirocko, F. *et al.* A late Eemian aridity pulse in central Europe during the last glacial inception. *Nature* **436**, 833–836 (2005).
5. Baker, A. G., Bhagwat, S. A. & Willis, K. J. Do dung fungal spores make a good proxy for past distribution of large herbivores?. *Quatern. Sci. Rev.* **62**, 21–31 (2013).
6. Davis, O. K. & Shafer, D. S. Sporormiella fungal spores, a palynological means of detecting herbivore density. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **237**, 40–50 (2006).
7. Doyen, E. & Etienne, D. Ecological and human land-use indicator value of fungal spore morphotypes and assemblages. *Veg. Hist. Archaeobotany* **26**, 357–367 (2017).
8. van Geel, B. & Aptroot, A. Fossil ascomycetes in Quaternary deposits. *Nova Hedwigia* **82**, 313–329 (2006).
9. Owen-Smith, R. N. *Megaherbivores: The Influence of Very Large Body Size on Ecology*. (Cambridge University Press, 1988).
10. Germonpré, M., Udrescu, M. & Fiers, E. The fossil mammals of Spy. in *Anthropologica et Præhistorica,* 41 (2012).
11. Hahn, J. *Gravettien-Freilandstationen im Rheinland.*
12. Bosinski, G. *Urgeschichte am Rhein*. (Kerns Verlag, 2008).
13. Münzel, S. C., Wolf, S., Drucker, D. G. & Conard, N. J. The exploitation of mammoth in the Swabian Jura (SW-Germany) during the Aurignacian and Gravettian period. *Quatern. Int.* **445**, 184–199 (2017).
14. Marković, S. B. *et al.* Danube loess stratigraphy: Towards a pan-European loess stratigraphic model. *Earth Sci. Rev.* **148**, 228–258 (2015).
15. Obreht, I. *et al.* A critical reevaluation of palaeoclimate proxy records from loess in the Carpathian Basin. *Earth Sci. Rev.* **190**, 498–520 (2019).
16. Grant, K. M. *et al.* Sea-level variability over five glacial cycles. *Nat. Commun.* **5**, (2014).
17. Moreno, A. *et al.* A compilation of Western European terrestrial records 60–8 ka BP: Towards an understanding of latitudinal climatic gradients. *Quatern. Sci. Rev.* **106**, 167–185 (2014).
18. Rasmussen, S. O. *et al.* A stratigraphic framework for abrupt climatic changes during the Last Glacial period based on three synchronized Greenland ice-core records: refining and extending the INTIMATE event stratigraphy. *Quatern. Sci. Rev.* **106**, 14–28 (2014).
19. Förster, M. W. & Sirocko, F. The ELSA tephra stack: Volcanic activity in the Eifel during the last 500,000 years. *Global Planet. Change* **142**, 100–107 (2016).
20. Förster, M. W., Zemlitskaya, A., Otter, L., Buhre, S. & Sirocko, F. Late Pleistocene Eifel eruptions: insights from clinopyroxene and glass geochemistry of tephra layers from Eifel Laminated Sediment Archive sediment cores. *J. Quatern. Sci.* 1–13 (2019).
21. Martrat, B. *et al.* Four climate cycles of recurring deep and surface water destabilizations on the Iberian Margin. *Science* **317**, 502–507 (2007).
22. Zolitschka, B. A 14,000 year sediment yield record from western Germany based on annually laminated lake sediments. *Geomorphology* **22**, 1–17 (1998).
23. Brunck, H., Sirocko, F. & Albert, J. The ELSA-Flood-Stack: A reconstruction from the laminated sediments of Eifel maar structures during the last 60000years. *Global Planet. Change* **142**, 136–146 (2016).
24. Dietrich, S. & Sirocko, F. The potential of dust detection by means of µXRF scanning in Eifel maar lake sediments. *E&G Quaternary Science Journal* **60**, 90–104 (2011).
25. Fuhrmann, F., Seelos, K. & Sirocko, F. Eolian sedimentation in central European Auel dry maar from 60 to 13 ka. *Quatern. Res.* **101**, 4–12 (2021).
26. Römer, W., Lehmkuhl, F. & Sirocko, F. Late Pleistocene aeolian dust provenances and wind direction changes reconstructed by heavy mineral analysis of the sediments of the Dehner dry maar (Eifel, Germany). *Global Planet. Change* **147**, 25–39 (2016).
27. Seelos, K., Sirocko, F. & Dietrich, S. A continuous high-resolution dust record for the reconstruction of wind systems in central Europe (Eifel, Western Germany) over the past 133 ka. *Geophys. Res. Lett.* **36**, (2009).
28. Dietrich, S. & Seelos, K. The reconstruction of easterly wind directions for the Eifel region (Central Europe) during the period 40.3 -12.9 ka BP. *Clim. Past* **6**, 145–154 (2010).
29. Dosseto, A. *et al.* Rapid response of silicate weathering rates to climate change in the Himalaya. *Faculty of Science, Medicine and Health - Papers: part A* 10–19 (2015) https://doi.org/10.7185/geochemlet.1502.
30. Rothacker, L. *et al.* Impact of climate change and human activity on soil landscapes over the past 12,300 years. *Sci. Rep.* **8**, (2018).

31. Francke, A. *et al.* Sediment residence time reveals Holocene shift from climatic to vegetation control on catchment erosion in the Balkans. *Global Planet. Change* **177**, 186–200 (2019).
32. Eglinton, T. I. & Eglinton, G. Molecular proxies for paleoclimatology. *Earth Planet. Sci. Lett.* **275**, 1–16 (2008).
33. Rommerskirchen, F., Plader, A., Eglinton, G., Chikaraishi, Y. & Rullkötter, J. Chemotaxonomic significance of distribution and stable carbon isotopic composition of long-chain alkanes and alkan-1-ols in C4 grass waxes. *Org. Geochem.* **37**, 1303–1332 (2006).
34. Poynter, J. G., Farrimond, P., Robinson, N. & Eglinton, G. Aeolian-Derived Higher Plant Lipids in the Marine Sedimentary Record: Links with Palaeoclimate. In *Paleoclimatology and Paleometeorology: Modern and Past Patterns of Global Atmospheric Transport* (eds. Leinen, M. & Sarnthein, M.) 435–462 (Springer Netherlands, 1989). https://doi.org/10.1007/978-94-009-0995-3_18.
35. Sikkema, R., Caudullo, G. & de Rigo, D. Carpinus betulus in Europe: distribution, habitat, usage and threats. in (2016).
36. Kubitz, B. Die holozäne Vegetations- und Siedlungsgeschichte in der - Westeifel am Beispiel eines hochauflösenden Pollendiagrammes - aus dem Meerfelder Maar. (2000).
37. Litt, *et al.* Correlation and synchronisation of Lateglacial continental sequences in northern central Europe based on annually laminated lacustrine sediments. *Quartern. Sci. Rev.* **20**, 1233–1249 (2001).
38. Bittmann, F. Reconstruction of the Allerød vegetation of the Neuwied Basin, western Germany, and its surroundings at 12,900 cal b.p. *Veget Hist Archaeobot* **16**, 139–156 (2007).
39. LoBuglio, K. F. Cenococcum. in *Ectomycorrhizal Fungi. Key Genera and Profile* (Springer, 1999).
40. Quiles, A. *et al.* A high-precision chronological model for the decorated Upper Paleolithic cave of Chauvet-Pont d'Arc, Ardèche, France. *Proc Natl Acad Sci USA* **113**, 4670–4675 (2016).
41. Hardt, J. Weichselian phases and ice dynamics of the Scandinavian Ice Sheet in northeast Germany: a reassessment based on geochronological and geomorphological investigations in Brandenburg. *E&G Quaternary Sci. J.* **66**, 101–102 (2017).
42. Wilczyński, J. *et al.* New radiocarbon dates for the late gravettian in Eastern Central Europe. *Radiocarbon* **62**, 243–259 (2020).
43. Wojtal, P., Wilczyński, J. & Wertz, K. Pavlovian hunters among bones. The animal remains (before 1990). *Dolní Věstonice II: Chronostratigraphy, Paleoethnology, Paleoanthropology* 105–128 (2016).
44. Terberger, T. & Street, M. Hiatus or continuity? New results for the question of pleniglacial settlement in Central Europe. *Antiquity* **76**, 691–698 (2002).
45. Förster, M. W. & Sirocko, F. The ELSA tephra stack: Volcanic activity in the Eifel during the last 500,000years. *Global Planet. Change* **142**, 100–107 (2016).
46. Hublin, J. J. The origin of Neandertals. *Proc. Natl. Acad. Sci.* **106**, 16022–16027 (2009).
47. Slimak, L. *et al.* Modern human incursion into Neanderthal territories 54,000 years ago at Mandrin, France. *Sci. Adv.* **8**, eabj9496 (2022).
48. Hajdinjak, M. *et al.* Reconstructing the genetic history of late Neanderthals. *Nature* **555**, 652–656 (2018).
49. Wißing, C. *et al.* Isotopic evidence for dietary ecology of late Neandertals in North-Western Europe. *Quatern. Int.* **411**, 327–345 (2016).
50. Pirson, S. *et al.* Chronostratigraphic context of the Middle to Upper Palaeolithic transition: Recent data from Belgium. *Quatern. Int.* **259**, 78–94 (2012).
51. Conard, N. J. A female figurine from the basal Aurignacian of Hohle Fels Cave in southwestern Germany. *Nature* **459**, 248–252 (2009).
52. Higham, T. *et al.* Testing models for the beginnings of the Aurignacian and the advent of figurative art and music: The radiocarbon chronology of Geißenklösterle. *J. Hum. Evol.* **62**, 664–676 (2012).
53. Nigst, P. R. *et al.* Early modern human settlement of Europe north of the Alps occurred 43,500 years ago in a cold steppe-type environment. *Proc. Natl. Acad. Sci.* **111**, 14394–14399 (2014).
54. Fu, Q. *et al.* The genetic history of Ice Age Europe. *Nature* **534**, 200–205 (2016).
55. Taller, A. & Conard, N. J. Transition or replacement? Radiocarbon dates from hohle fels cave (Alb-Donau-Kreis / D) and the passage from aurignacian to gravettian. *Archäologisches Korrespondenzblatt* **49**, 165–181 (2019).
56. Tallavaara, M., Luoto, M., Korhonen, N., Järvinen, H. & Seppä, H. Human population dynamics in Europe over the Last Glacial Maximum. *Proc. Natl. Acad. Sci.* **112**, 8232–8237 (2015).
57. Maier, A., Ludwig, P., Zimmermann, A. & Schmidt, I. The Sunny Side of the Ice Age: Solar Insolation as a Potential Long-Term Pacemaker for Demographic Developments in Europe Between 43 and 15 ka Ago: Special Issue: The Impact of Upper Pleistocene Climatic and Environmental Change on Hominin Occupations and Landscape Use, Part 1. *PaleoAnthropology* 35–51 (2022) https://doi.org/10.48738/2022.iss1.100.
58. Marchi, N. *et al.* The genomic origins of the world's first farmers. *Cell* **185**, 1842-1859.e18 (2022).
59. Reade, H. *et al.* Radiocarbon chronology and environmental context of Last Glacial Maximum human occupation in Switzerland. *Sci Rep* **10**, 4694 (2020).
60. Street, M. & Terberger, T. The last Pleniglacial and the human settlement of Central Europe: new information from the Rhineland site of Wiesbaden-Igstadt. *Antiquity* **73**, 259–272 (1999).
61. Lister, A. M. & Stuart, A. J. The extinction of the giant deer Megaloceros giganteus (Blumenbach): New radiocarbon evidence. *Quatern. Int.* **500**, 185–203 (2019).
62. Zimov, S. A. Pleistocene park: Return of the Mammoth's ecosystem. *Science* **308**, 796–798 (2005).
63. Street, M. & Turner, E. *The faunal remains from Gönnersdorf.* (2013).
64. Street, M. *et al.* Final Paleolithic and Mesolithic Research in Reunified Germany. 90 (2022).
65. Baales, M. & Street, M. Late Paleolithic Backed-Point assemblages in the northern Rhineland: current research and changing views. *Notae Praehistoricae* **18**, 77–92 (1998).
66. Weber, M.-J., Grimm, S. B. & Baales, M. Between warm and cold: Impact of the Younger Dryas on human behavior in Central Europe. *Quatern. Int.* **242**, 277–301 (2011).
67. Stockmarr, J. Tablets with Spores used in Absolute Pollen Analysis. *Pollen et Spores* **XIII**, 615–621 (1971).
68. Davis, O. K. Spores of the dung fungus Sporormiella: Increased abundance in historic sediments and before Pleistocene megafaunal extinction. *Quatern. Res.* **28**, 290–294 (1987).
69. Graham, R. W. *et al.* Timing and causes of mid-Holocene mammoth extinction on St. Paul Island, Alaska. *Proce. Natl. Acad. Sci.* **113**, 9310–9314 (2016).
70. Markova, A. K., Puzachenko, AYu., van Kolfschoten, T., van der Plicht, J. & Ponomarev, D. V. WITHDRAWN: Recent data on dynamics of mammoth and woolly rhinoceros ranges in Europe during the second half of the Late Pleistocene –Holocene. *Quatern. Int.* https://doi.org/10.1016/j.quaint.2012.11.017 (2012).
71. Arif, R. & Saleem, M. Isolation of coprophilous fungus sordaria fimicola from different areas of Lahore-Pakistan, and molecular characterization by ITS and RAPD-SCAR PCR. *Int. J. Agric. Biol.* **19**, 259–265 (2017).
72. Basumatary, S. K. & McDonald, H. G. Coprophilous fungi from dung of the greater one-horned Rhino in Kaziranga National Park, India and its implication to paleoherbivory and paleoecology. *Quatern. Res.* **88**, 14–22 (2017).
73. Ebersohn, C. & Eicker, A. Coprophilous fungal species composition and species diversity on various dung substrates of African game animals. Botanical Bulletin of Academia Sinica, (1992).
74. Dietre, B., Gauthier, É. & Gillet, F. Modern pollen rain and fungal spore assemblages from pasture woodlands around Lake Saint-Point (France). *Rev. Palaeobot. Palynol.* **186**, 69–89 (2012).

75. Aptroot, A. & van Geel, B. Fungi of the colon of the Yukagir Mammoth and from stratigraphically related permafrost samples. *Rev. Palaeobot. Palynol.* **141**, 225–230 (2006).
76. Ebersohn, C. & Eicker, A. Determination of the coprophilous fungal fruit body successional phases and the delimitation of species association classes on dung substrates of African game animals. *Botan. Bull. Acad. Sin.* (1997).
77. Gill, J. L. *et al.* Linking abundances of the dung fungus Sporormiella to the density of bison: implications for assessing grazing by megaherbivores in palaeorecords. *J. Ecol.* **101**, 1125–1136 (2013).
78. van Geel, B. *et al.* Mycological evidence of coprophagy from the feces of an Alaskan Late Glacial mammoth. *Quatern. Sci. Rev.* **30**, 2289–2303 (2011).
79. Rommerskirchen, F. *et al.* A north to south transect of Holocene southeast Atlantic continental margin sediments: Relationship between aerosol transport and compound-specific δ 13 C land plant biomarker and pollen records: HOLOCENE TRANSECT OF SE ATLANTIC MARGIN. *Geochem., Geophys. Geosyst.* **4**, (2003).
80. Carignan, J., Vigier, N. & Millot, R. Three secondary reference materials for lithium isotope measurements: Li7-N, Li6-N and LiCl-N solutions. *Geostand. Geoanal. Res.* **31**, 7–12 (2007).
81. Berger, A. & Loutre, M. F. Insolation values for the climate of the last 10 million years. *Quatern. Sci. Rev.* **10**, 297–317 (1991).

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Author contributions

F.S. coordinates the ELSA drillings and proposed and directed the research, F.D. counted pollen. S.B. counted the spores, F.S. and J.A. developed the stratigraphy of the ELSA-20 records, alkanes were measured in the laboratories of A.M.-G. and G.H. at the Max Planck Institute for Chemistry, Mainz. F.S., A.M.-G., and S.B. generated the figures. J.B. contributed a summary on the presence of humans in central Europe, T.T. provided background information on mammals and archeology. F.S., S.B., A.M.-G., A.D., J.B. and T.T. wrote the manuscript.

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Competing interests

The authors declare no competing interests.

Additional information

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Supplementary Materials for

Thresholds for the presence of Glacial Megafauna in central Europe during the last 60,000 years

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This file includes:

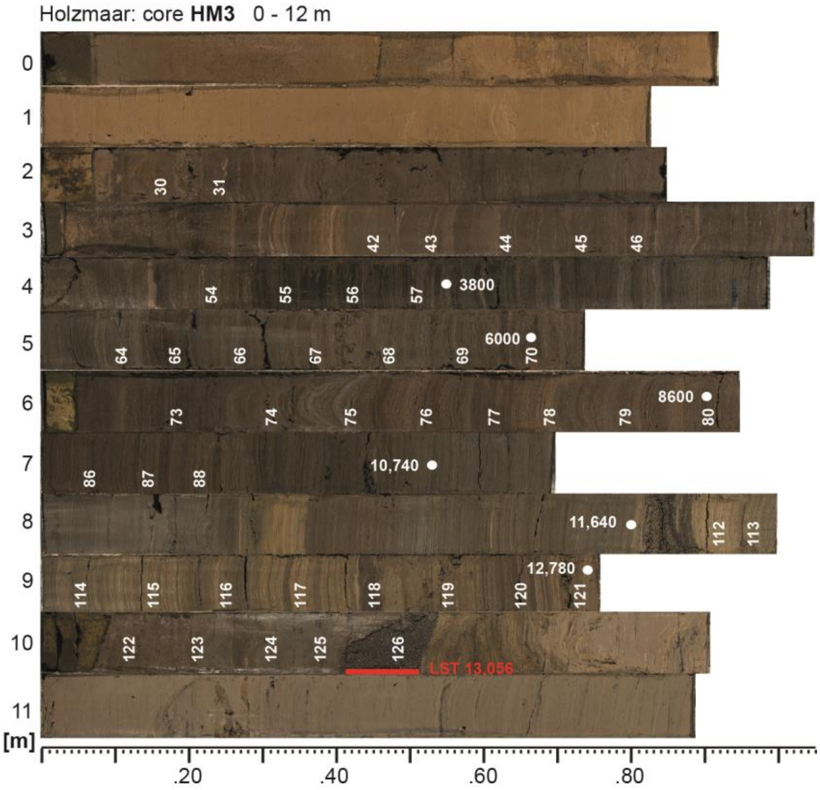
Supplementary Figures S1 to S10

Labels for Supplementary Tables S1 to S7

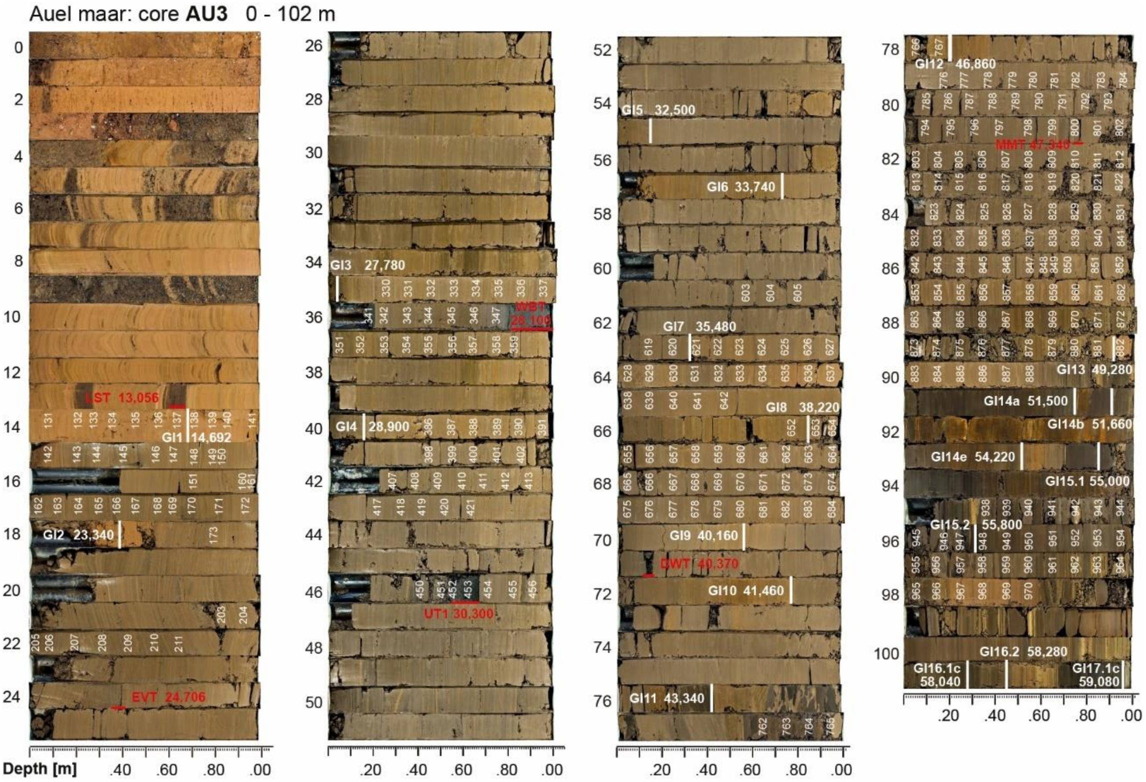
Other Supplementary Materials for this manuscript include the following:

Data S1 to S7 (separate files)

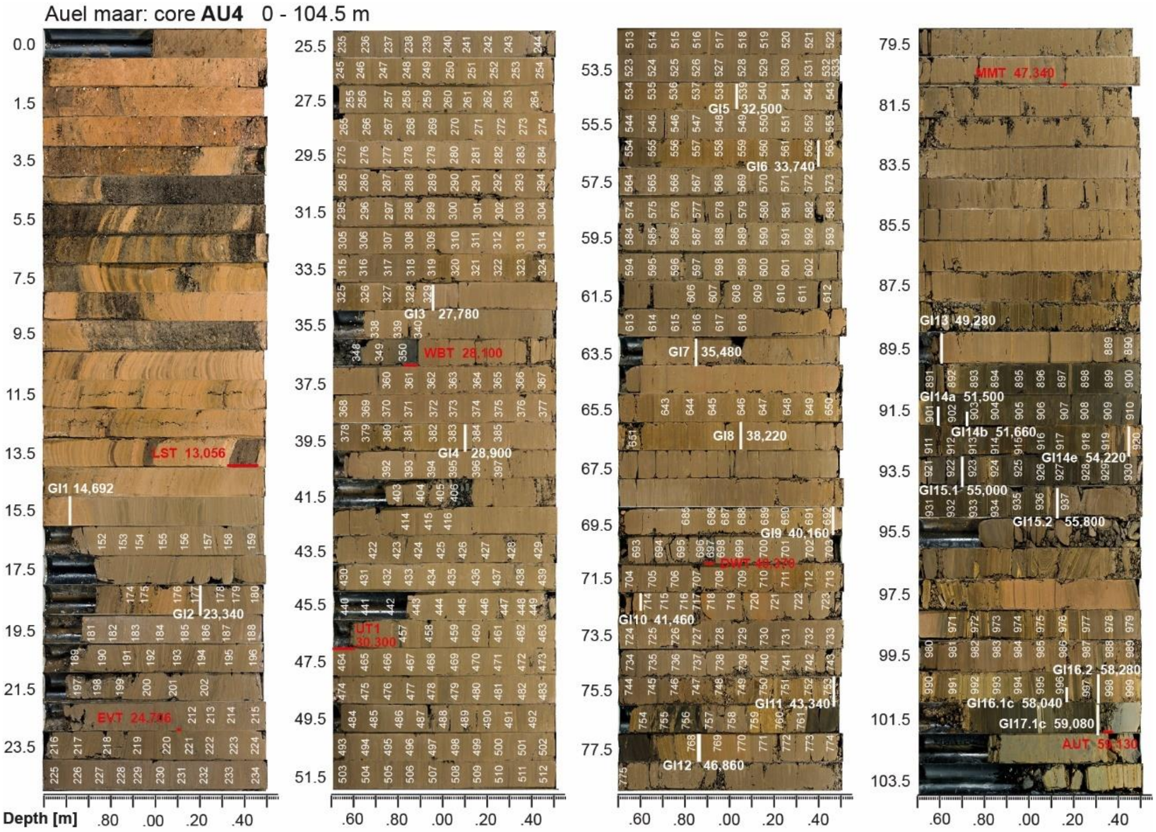
Supplementary Figure S1. Photos of core SMf from Schalkenmehren maar lake and core HM4 from Holzmaar lake. Stratigraphical marker of the ELSA-20 record are documented together with the ELSA-20-Stack sample numbers.



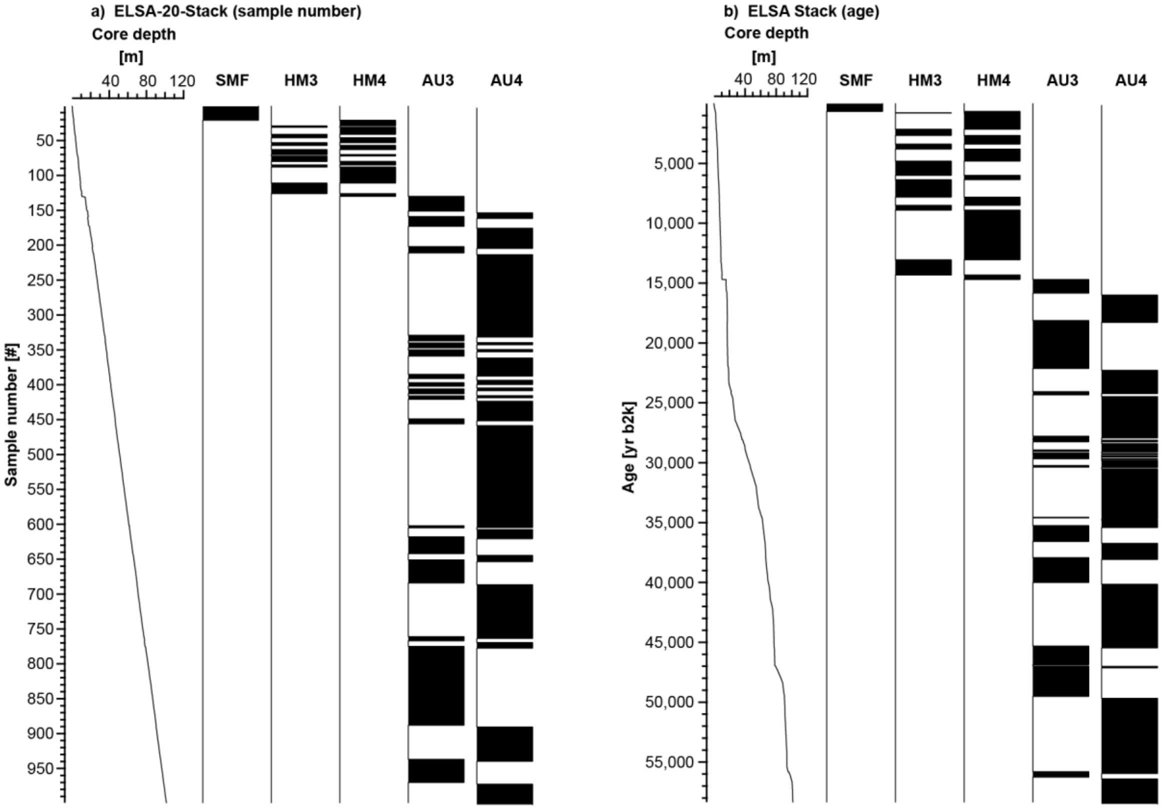
Supplementary Figure S2. Photos of core HM3 from Holzmaar lake. Stratigraphical marker of the ELSA-20 record are documented together with the ELSA-20-Stack sample numbers.



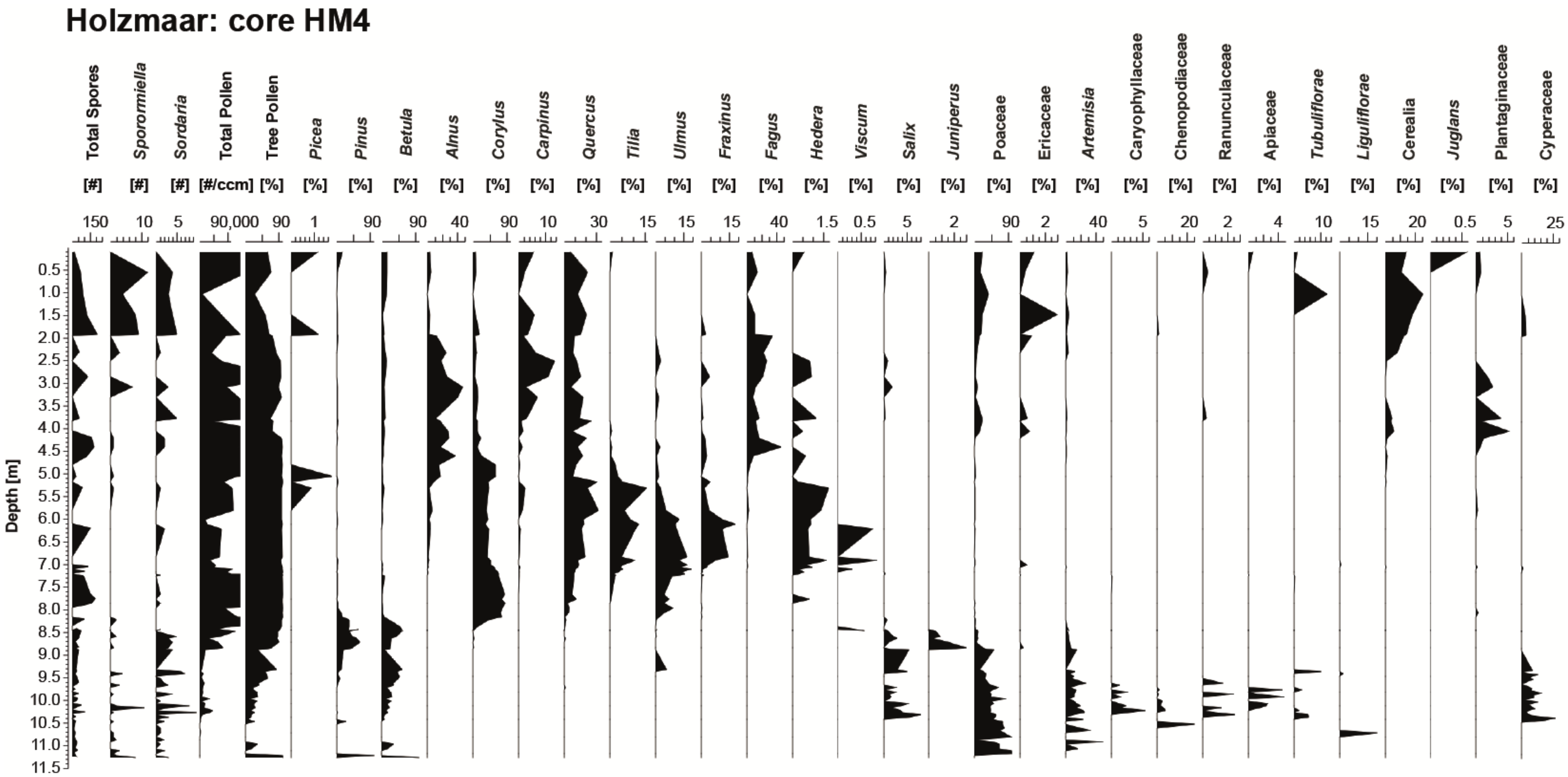
Supplementary Figure S3. Photos of core AU3 from the infilled maar of Auel. Stratigraphical marker of the ELSA-20 record are documented together with the ELSA-20-Stack sample numbers.



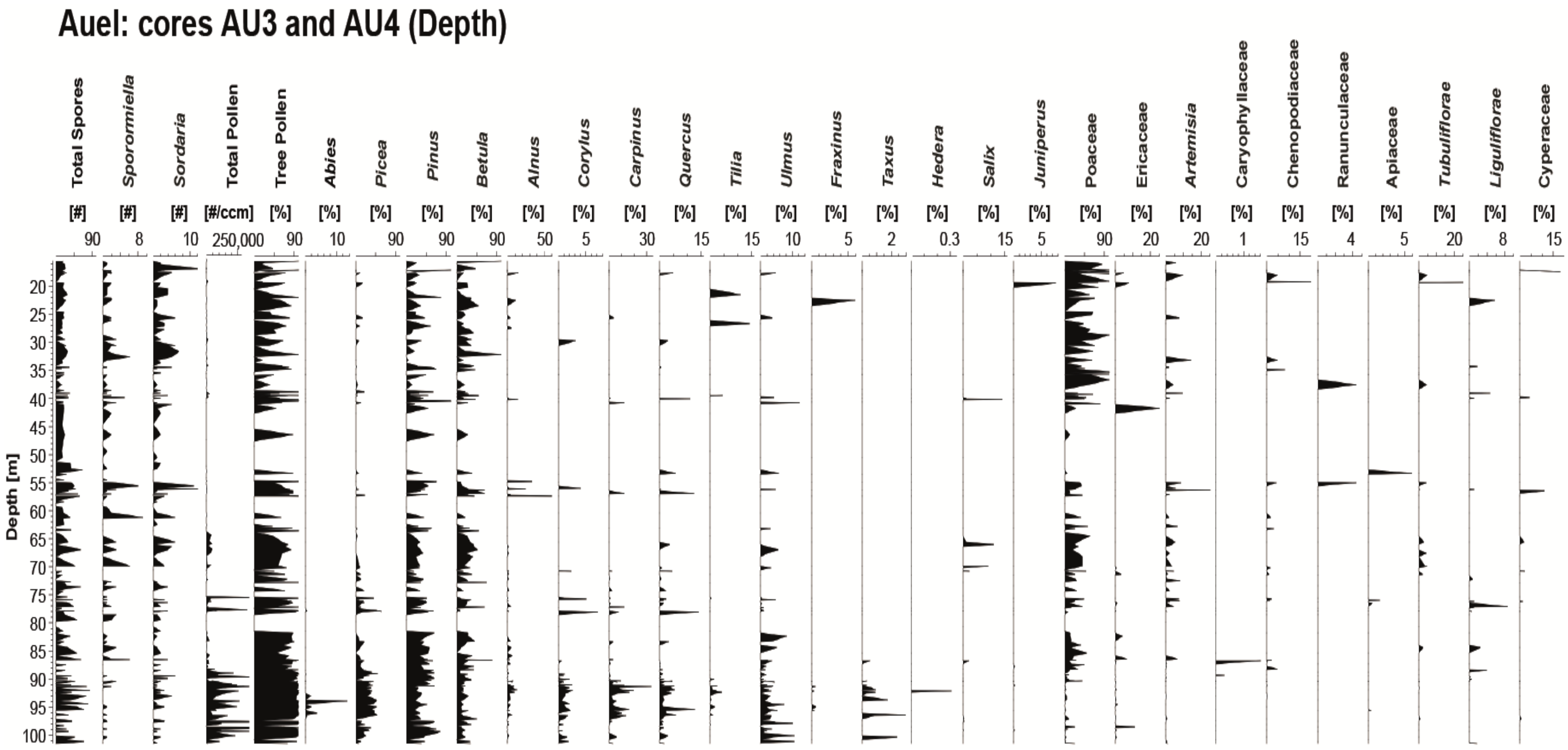
Supplementary Figure S4. Photos of core AU4 from the infilled maar of Auel. Stratigraphical marker of the ELSA-20 record are documented together with the ELSA-20-Stack sample numbers.



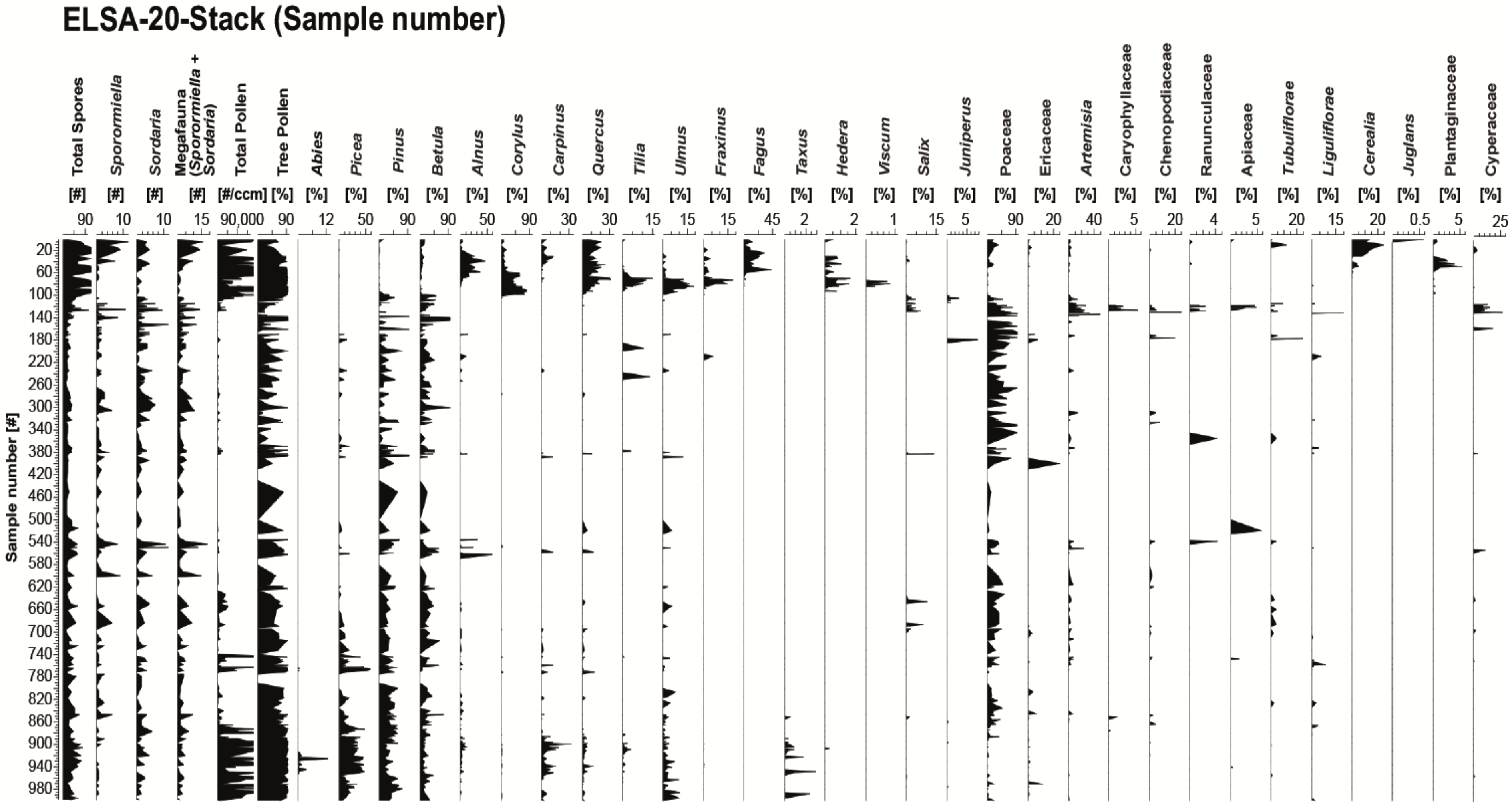
Supplementary Figure S5. Depth of ELSA-20-Stack samples in the sediment cores SMf, HM3, HM4, AU3, and AU4.



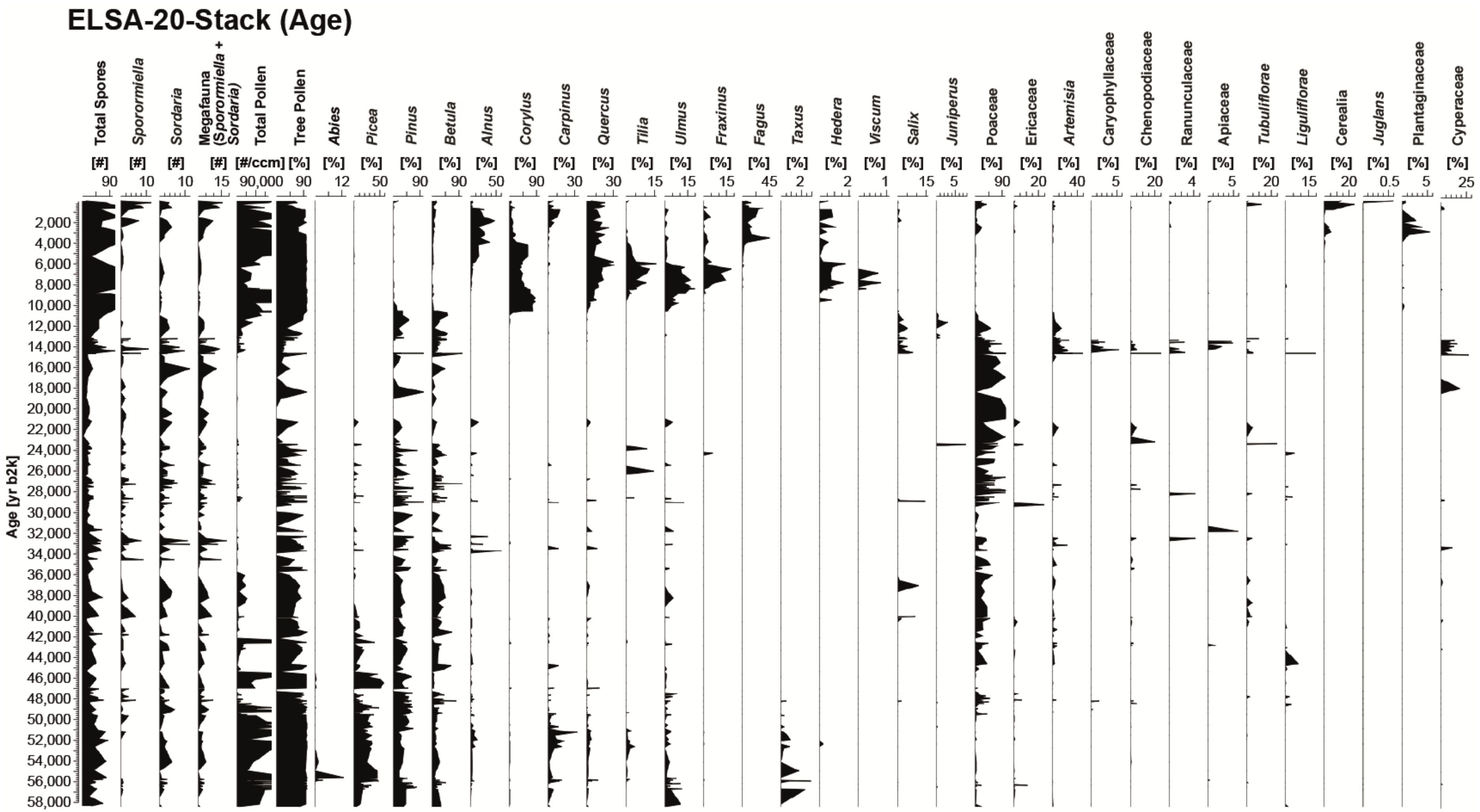
Supplementary Figure S6. Pollen concentrations and spore counts for the HM4 core from Holzmaar versus depth.



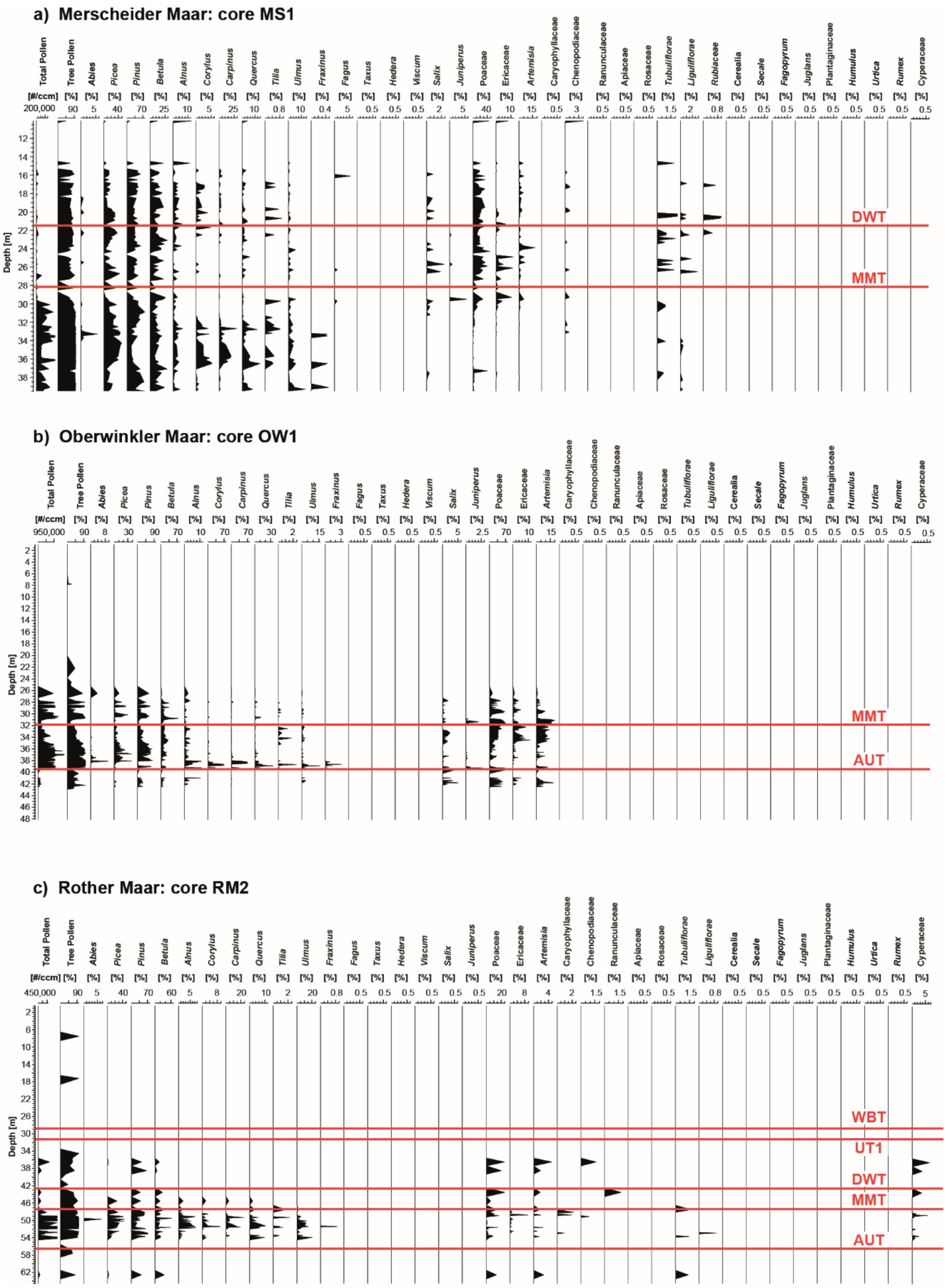
Supplementary Figure S7. Pollen concentrations and spore counts for the AU4 and AU3 core from Auel versus depth



Supplementary Figure S8. Pollen concentrations and spore counts for the ELSA-20-Stack versus Stack number. Shown are only samples with more than 20 pollen counted.



Supplementary Figure S9. Pollen concentrations and spore counts for the ELSA-20-Stack versus age. Composite of all counts from SMf, HM4, AU3, AU4.



Supplementary Figure S10. Pollen concentrations and tephra layers for MIS3/2 in the ELSA cores from Merscheider Maar, Oberwinkler Maar, and Rother Maar versus age. These low resolution records show the early MIS3 spruce forest and the same tephra[40] as found in Auel[1] and Dehner Maar[2]. Accordingly, ELSA-20 ages were applied for the age model of these records.

Supplementary Tables S1 to S7

Supplementary Table S1. ELSA Stack Sample Information. For each stack sample there are given the respective core depth, sampled core, and age in yr b2k. For the samples that were analyzed for *n*-alkanes or Lithium isotopes, the respective values are documented.

Supplementary Table S2. All counts on pollen and spores from Holzmaar core HM4. Data are shown versus age and core depth.

Supplementary Table S3. All counts on pollen and spores from Auel infilled maar core AU4. Data are shown versus age and core depth.

Supplementary Table S4. All counts on pollen and spores from Holzmaar core HM4 and Auel infilled maar cores AU3,4 transferred to the ELSA-20-Stack. For each sample number we show the respective age and the drill core depth from which the samples were taken.

Supplementary Table S5. Pollen values from samples with at least 15 pollen grains from Merscheider Maar core MS1 versus age and core depth.

Supplementary Table S6. Pollen values from all samples from Rother Maar core RM2 versus age and core depth.

Supplementary Table S7. Pollen values from all samples from Oberwinkler Maar core OW1 versus age and core depth.

scientific reports

Mammal extinction facilitated biome shift and human population change during the last glacial termination in East-Central Europe

Enikő Katalin Magyari[1,2,3]✉, Mihály Gasparik[4], István Major[3], György Lengyel[5], Ilona Pál[3], Attila Virág[1,6], János Korponai[7,8,9], Aritina Haliuc[10,11], Zoltán Szabó[2] & Piroska Pazonyi[1]

The study of local extinction times, together with the associated environmental and human population changes in the last glacial termination, provides insights into the causes of mega- and microfauna extinctions. In East-Central (EC) Europe, groups of Palaeolithic humans were present throughout the last glacial maximum, but disappeared suddenly around 15,200 cal BP. In this study cave sediment profiles dated using radiocarbon techniques and a large set of mammal bones dated directly by AMS ^{14}C were used to determine local extinction times. These were, in turn, compared to changes in the total megafauna population of EC Europe derived from coprophilous fungi, the Epigravettian population decline, quantitative climate models, pollen and plant macrofossil inferred climate, as well as to biome reconstructions. The results suggest that the population size of large herbivores decreased in the area after 17,700 cal BP, when temperate tree abundance and warm continental steppe cover both increased in the lowlands. Boreal forest expansion started around 16,200 cal BP. Cave sediments show the decline of narrow-headed vole and arctic lemming populations specifically associated with a tundra environment at the same time and the expansion of the common vole, an inhabitant of steppes. The last dated appearance of arctic lemming was at ~ 16,640 cal BP, while that of the narrow-headed vole at ~ 13,340, and the estimated extinction time of woolly mammoth was either at 13,830 (GRIWM) or 15,210 (PHASE), and reindeer at 11,860 (GRIWM) or 12,550 cal BP (PHASE). The population decline of the large herbivore fauna slightly preceded changes in terrestrial vegetation, and likely facilitated it via a reduction in the intensity of grazing and the concomitant accumulation of plant biomass. Furthermore, it is possible to conclude that the Late Epigravettian population had high degree of quarry-fidelity; they left the basin when these mammals vanished.

Despite the richness of vertebrate records from cave deposits and open air sites from the Late Pleistocene[1], twentieth century paleontological research did not take 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). It also failed to date systematically cave mammal bone stratigraphies for the last 40,000 years, a time period for which AMS ^{14}C dating would have been a perfect choice[2,3]. Only in recent years has a resurgence of

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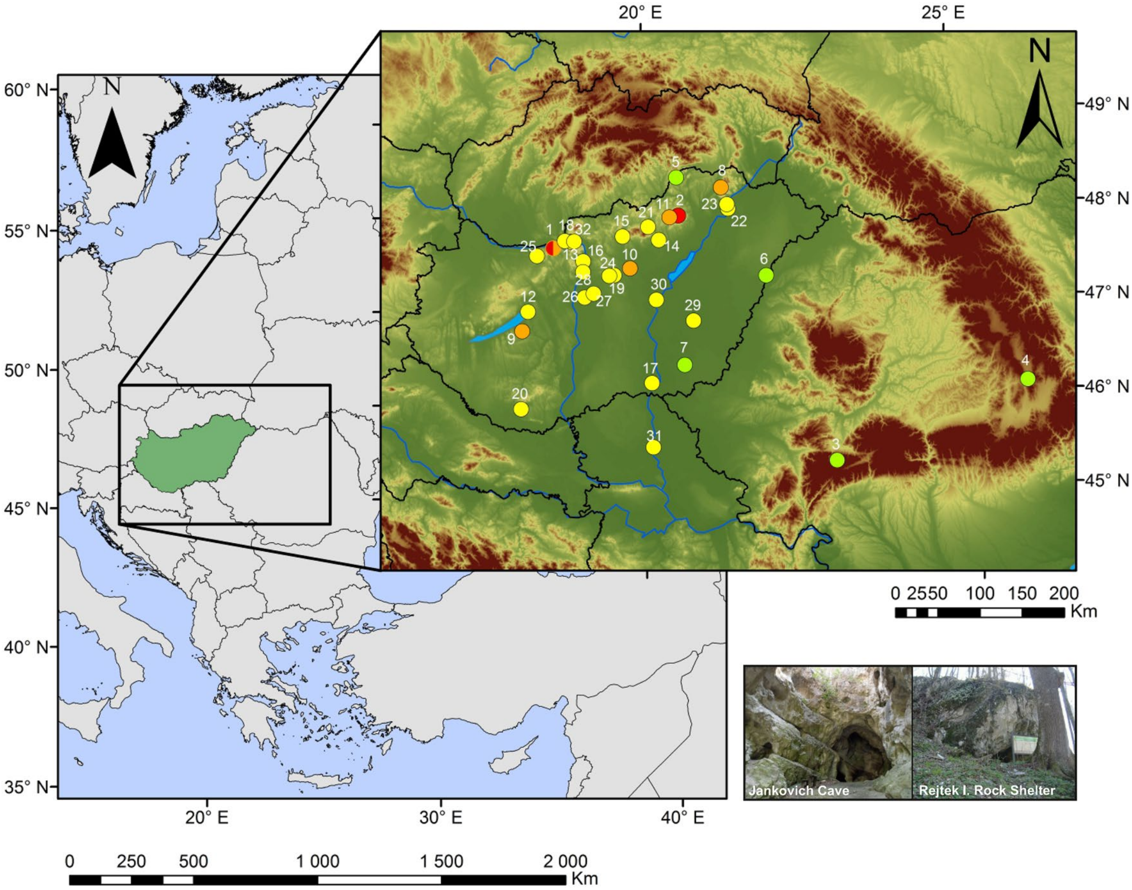

Figure 1. Location of the studied cave sites (red, 1–2), pollen records (green, 3–7), dated reindeer (*Rangifer tarandus*) (orange, 1, 8–11) and dated woolly mammoth (*Mammuthus primigenius*) bones (yellow, 12-32) in the Carpathian Basin (**a**) and in East-Central Europe (**b**). 1: Jankovich Cave; 2: Rejtek I Rock Shelter.; 3: Taul dintre Brazi[16]; 4: Lake St Anne[13]; 5: Kelemér Nagymohos[17]; 6: Kokad Mire[18]; 7: Kardoskút Fehér Lake[19]; 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. The software used to create the maps was ArcGIS 10.2.2 for desktop, version 10.2.2.3552. Software url: https://support.esri.com/en/products/desktop/arcgis-desktop/arcmap/10-2-2.; the photo of Rejtek I Rock Shelter was taken by Tivadar Czina under licence CC BY-SA 3.0, *source*: https://hu.wikipedia.org/wiki/Rejteki_1._sz._kőfülke; the photo of Jankovich Cave was taken by Mihály Gasparik.

Upper Weichselian megafauna research been seen, with researchers revisiting key localities, often associated with human occupation, and reassessing their dating[4–6]. As our understanding of Late Epigravettian human lifestyle, economy and hunting strategy increases, the clearer it becomes that the disappearance of mobile Epigravettian groups from the Carpathian Basin (CB) around 15,200 cal BP is related to changing environmental conditions, such as the rapid disappearance of their main quarry, the reindeer (*Rangifer tarandus*), the decimation of secondary quarries such as the wild horse (*Equus ferus*), not to mention the worsening visibility for hunting in a landscape subject to an increase in forest cover[7,8].

Here, the focus is on one species of megafauna, the woolly mammoth (*Mammuthus primigenius*), and several ungulate and rodent species that co-inhabited the CB in a fully developed glacial ecological setting, and what is more, one that is relatively well understood[9–14].

Using a large dataset comprising dated mammoth bones, two profiles of caves 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), a specific paleoecological hypothesis relating rapid climate change to population dynamics is put to the test, namely, that transitions from cold to warm intervals were briefly optimal for grazing megafauna, but these brief optima were followed by rapid regional extinctions[15]. The question of the order of faunistic and vegetation biome changes and its casual linkage is also examined.

Studied cave sites and the mammoth bone collections. The caves under consideration are in Northern Hungary, in the Pre-Carpathian hill region (Fig. 1). The Jankovich Cave is an archaeological site in the Gerecse Hills. In the present study the Late Upper Palaeolithic layer is in focus[20,21] that likely belongs to the Late

Epigravettian. Situated at 330 m a.s.l., its 88 m long chamber has been excavated repeatedly since 1913; Block II, excavated by László Vértes in 1956, was selected for examination (Suppl. Fig. 1). This revealed that microfauna adapted to a cold climate were replaced by temperate species[21], and was therefore assigned to the Pleistocene/Holocene boundary. 21 bone samples from 13 layers were selected for AMS ^{14}C dating (Suppl. Tables 1 and 2).

The Rejtek I Rock Shelter is situated in the Bükk Mts at 534 m a.s.l. (Fig. 1, Suppl. Fig. 2). Here, the AMS ^{14}C measurements were carried out on Profiles II (upper 4 layers) and III (layers 5–8)[22]. These two profiles had earlier been combined on the basis of depth[23], and faunistic and floristic changes were published accordingly (Suppl. Figs. 2 and 3; Suppl. Tables 1 and 3). Knapped lithics were found[24], charcoal, mollusc and bone assemblages were analysed[4,25,26]. 24 bone samples from 8 layers were selected for dating (Suppl. Tables 1 and 3). Priority was given to mammal species with missing or uncertain data on their last occurrence: e.g. steppe pika (*Ochotona pusilla*), arctic lemming (*Dicrostonyx torquatus*), narrow-headed vole (*Lasiopodomys* (*S.*) *gregalis*), reindeer (*R. tarandus*), and willow grouse (*Lagopus lagopus*).

The woolly mammoth was common in the CB during the Weichselian glaciation; *ca*. 400 specimens and 6 skeletons had been found in Hungary, but ^{14}C dates were only available for 8 specimens[27]. Within the scope of this study, 21 localities (Suppl. Table 4, Fig. 1) were selected for AMS ^{14}C dating.

The 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 dates were obtained in both caves below a depth of 1 m of sediment (layers 8–12 in Rejtek, layers 5–10 in Jankovich), while in the top meter, mixed Holocene and Pleistocene ages indicated significant disturbance (Suppl. Tables 1, 2 and 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 BP, while the Rejtek layers 8–12 span 13,450–9950 cal BP. The Pleistocene-Holocene transition could only be traced at Rejtek. The age-depth models (Suppl. Fig. 4) suggest that sediment accumulation rates were relatively even in both caves, *ca*. 0.5 mm yr^{-1}.

Major vole faunal changes in the Jankovich profile suggest that the common vole (*Microtus arvalis*), narrow-headed vole (*L.* (*S.*) *gregalis*) and arctic lemming (*D. torquatus*) were dominant after the last glacial maximum (LGM: 26–21 ka cal BP) up until 16,360 cal BP. This assemblage was replaced by common vole (*M. arvalis*) and bank vole (*Clethrionomys glareolus*), which achieved dominance by 15,540 cal 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 had ended by the onset of the Bølling/Allerød Interstadial (GI-1e: ~ 14,700 cal BP) (Fig. 2; Suppl. Fig. 5). The onset of the Holocene is characterised by an increase in the forest dwelling bank vole (*C. glareolus*). A transition from wooded steppe tundra to continental steppe may be inferred as taking place between 15,540 and 16,000 cal BP (Fig. 2). The Jankovich vole record implies that the dominance of the arctic lemming and tundra vole (*D. torquatus* & *M. oeconomus*) between 17,000 and 16,300 cal BP may well be connected to the HE-1 cooling (Suppl. Fig. 5). The steppe pika (*O. pusilla*) retreated after this interval (Suppl. Table 1).

The large mammalian fauna of Jankovich also indicates this climatic change: the cave bear (*Ursus spelaeus*), reindeer (*R. tarandus*), cave lion (*Panthera* (*Leo*) *spealea*), arctic fox (*Vulpes lagopus*) and horse (*Equus sp.*) that characterize the lower layers gradually disappear upwards in the stratigraphy. It should, however, be noted that the large mammalian bones were not directly dated using ^{14}C.

Macrofauna, vole and rodent relative frequency from Rejtek I (Fig. 2; Suppl. Fig. 6) demonstrate that accumulation started in the Allerød (~ GI-1b) and a major change is the shift in dominance from the common vole to the bank vole (*M. arvalis* – > *C. glareolus*) at 12,200–11,700 cal BP. This correlates with the Holocene transition. The relative frequencies of the European pine vole (*M. subterraneus*) and wood mouse (*Apodemus sylvaticus*) also increase indicating warming and forest cover increase. In the Allerød warm period, willow grouse (*L. lagopus*; dated to 14,610–15,190 cal 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 disappear in the Holocene layers (Fig. 2; Suppl. Fig. 6). This suggests a Late Glacial (LG) persistence of some species adapted to cold taiga, forest tundra and steppe habitats.

This cave sequence is exceptional in terms of the detailed charcoal record present in the same sediment layers as those in which the mammal bones were found. As shown in Suppl. Fig. 3, the dominant trees in the LG landscape of Rejtek were needle leaved: the charred remains of Norway spruce (*Picea abies*) and Arolla pine (*Pinus cembra*) were found together with Scots pine (*P. sylvestris*). From *ca*. 13,000 cal BP onwards, a dominance of mixed deciduous, maple (*Acer platanoides*), field elm (*Ulmus campestris*), hornbeam (*Carpinus betulus*) and beech (*Fagus sylvatica*) suggested a LG expansion of several early and late successional deciduous trees[4,25]. Particularly striking was the appearance of beech and hornbeam. These spread later at 300 m a.s.l. in the Bükk Mts, around 6500 cal BP[28,29], and heir LG presence supports isoensyme and chloroplast (cp) microsatellite DNA studies inferring possible cryptic populations in the N Hungarian Hills[30]. The mollusc fauna of Rejtek contained over 65% forest dwellers (Clausiliidae, *Cochlodina cerata*) in the LG and Early Holocene layers, indicating a forested landscape[4,31].

^{14}C dates suggest that the arctic lemming's (*D. torquatus*) population significantly decreased in the Gerecse Hills around 16,640 cal BP, followed by the narrow-headed vole (*L.* (*S.*) *gregalis*) around 13,340 cal BP, while the steppe pika (*O. pusilla*) survived into the Early Holocene; the latest detection time is around 11,015 cal BP at Rejtek (Suppl. Table 1; Fig. 3). Several reindeer (*R. tarandus*) bones were also dated; the latest date was from a stratigraphically consistent, undisturbed layer: ~ 15,195 cal BP (Suppl. Table 5; Suppl. Fig. 7). Taking into account other published data on reindeer ^{14}C dates in the CB (15 sites), the Phase model in OxCal[32] and the

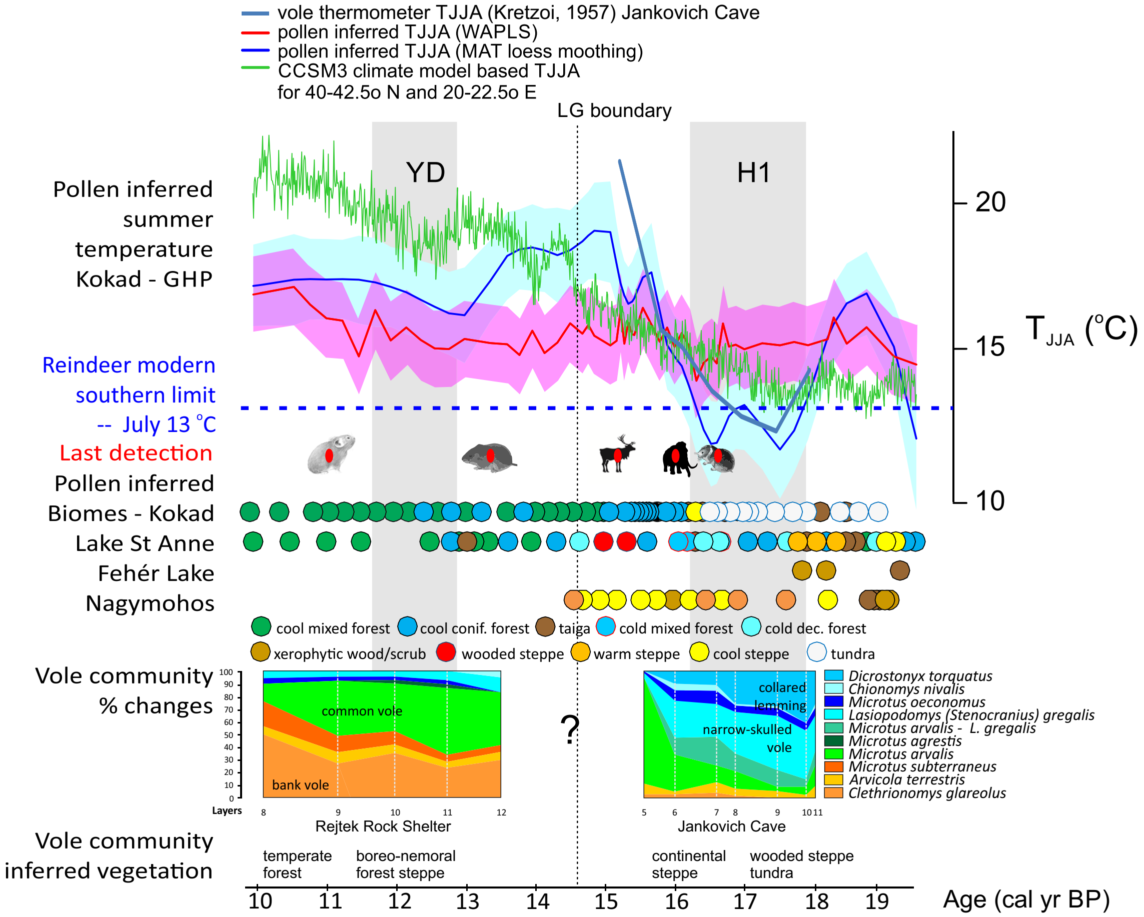

Figure 2. Vole community changes through time in two Carpathian Basin cave sediment profiles AMS ^{14}C dated within the scope of this study (Jankovich Cave, Rejtek Rock Shelter); vegetation inferred from the vole community; reconstruction of the biome on the basis of five pollen records from the Carpathian Region (for locations see Fig. 1); last detection times of micro- and macrofauna elements in this study (from left: *Ochotona pusilla*, *Lasiopodomys* (*S.*) *gregalis*, *Rangifer tarandus*, *Mammuthus primigenius*, *Dicrostonyx torquatus*), pollen inferred summer mean temperature reconstructions (WAPLS, MAT) on the basis of the Kokad Mire pollen records (redrawn and modified from Magyari et al.[18]) and CCSM3 climate model based summer mean temperature simulation for the Kokad grid cell from PaleoView; animal drawings on this figure were made in Corel Draw version 23.0.0.363 by the first author.

GRIWM model[33] were employed to estimate the last appearance of reindeer. The end boundary in the Phase model provides an estimate between 8300 and 14,480 cal BP, with a median at 12,550, while the GRIWM model places the extinction between 11,470 and 12,815 with an inverse weighted terminal age estimate of 11,860 cal BP (see Supplementary Material).

In the radiocarbon dating of the woolly mammoth (*M. primigenius*) bone assemblages from the CB (Suppl. Table 4; Suppl. Fig. 8), 12 of 40 bones had an insufficient collagen content, 16 samples were dated beyond 40,000 ^{14}C BP, and 12 provided dates suitable for calibration.

Combined with previously published dates from the CB (Suppl. Fig. 8), the 2σ calibrated age ranges using Intcal20[35] showed that the youngest woolly mammoth was from Csajág[36], dated to 16,180 (15,830–16,010) cal BP. There are eight bones dated to < 20 ka, nine between 20 and 30 ka, and twenty beyond 30 ka cal BP. Although the number of dated bones is a fraction of the bones available in museum collections, an absence between 22–24.5 ka and 27.4–32.5 ka cal BP is apparent. These data further suggest that woolly mammoth was common in the CB after the LGM, until 18 ka cal BP, though 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 a last appearance between 12,690 and 16,150 cal BP, with a median at 15,210 cal BP. The GRIWM model narrows down the confidence interval, but also estimates a considerably younger extinction time (13,717–13,960, terminal age 13,830 cal BP). If the problematic Zók site and burnt bones are removed from the Phase modelling (n=22), the estimated last appearance interval is still very similar (12,050–16,110 cal BP; median: 15,270).

Last glacial termination vegetation changes in pollen and plant macrofossil records. Pollen based biome reconstruction of four EC European localities (Fig. 2) suggests that the vegetation was diverse during and after the LGM, depending on elevation, water availability and soil type. Alluvial plains and mid eleva-

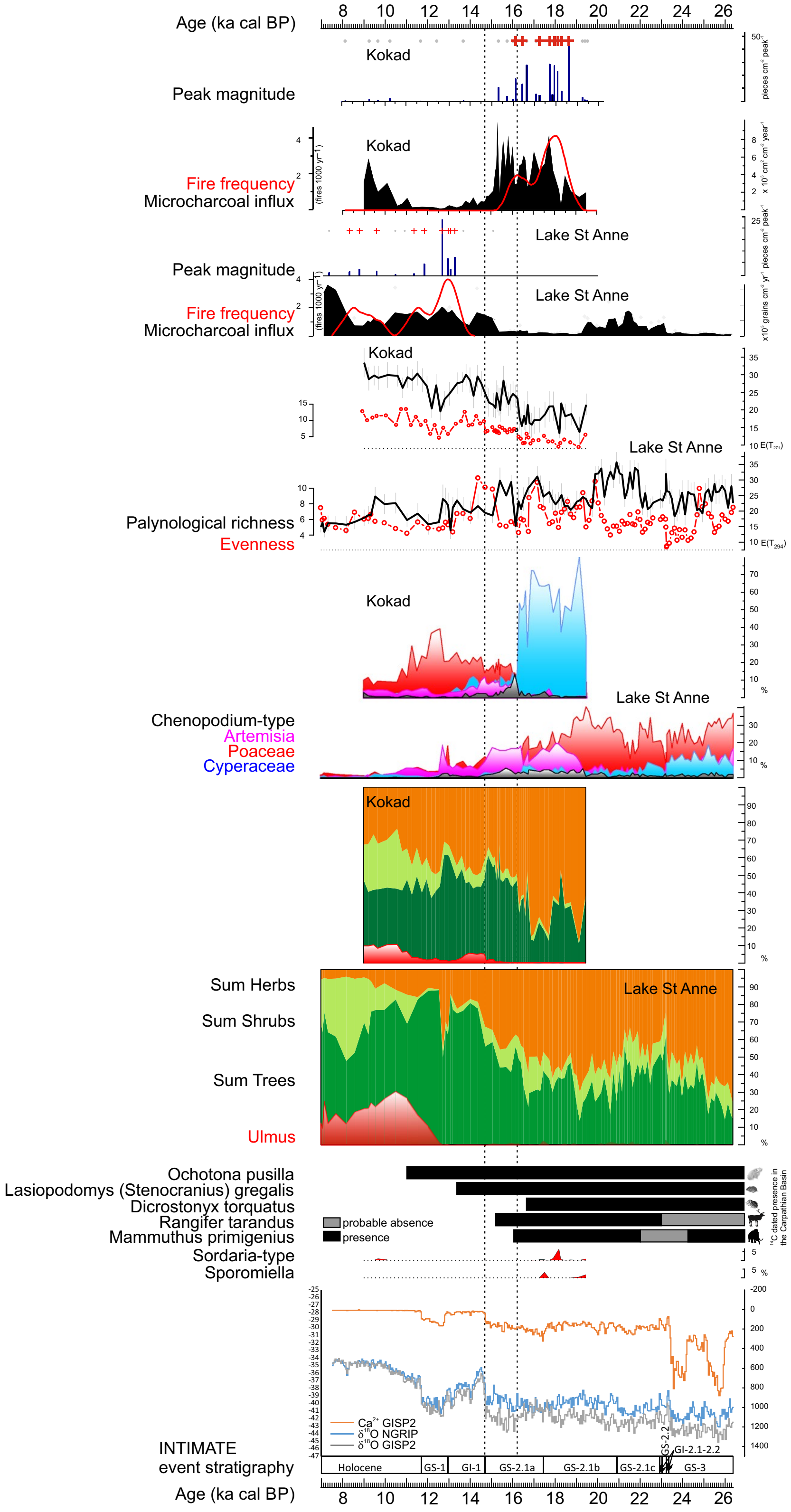

Figure 3. INTIMATE event stratigraphy plotted along the NGRIP and GISP2 $\delta^{18}O$ and Ca^{2+} ice core records from Greenland[34]; selected dung fungal spores (*Sporomiella*, HdV55a) indicating the presence of large bodied grazers in the Kokad pollen profile[18]; calibrated BP intervals of presence for selected mega- and microfauna elements in the Carpathian Basin dated within the 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.[18]) 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, microcharcoal influx, macrocharcoal inferred fire frequency curves, peak fire magnitudes and fire events (red crosses) from the same pollen sites. The methodology of macrocharcoal analyses is described in the Supplementary Material.

tion 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 xerophytic woodland and scrub and cold steppe biomes were also present (Fig. 2).

Biome shifts begin to prevail earliest between 17,000 and 16,000 cal BP. In the mountains, cold deciduous forest, cool coniferous forest and forest steppe replaced the dominant steppe and taiga biome of the preceding HE-1 cooling. A much more abrupt biome shift from tundra to cool coniferous forest took place at Kokad around 16,200 cal BP (Fig. 2)[18]; this was followed by a second biome shift to cool mixed forest at 14,740 cal BP, a biome that then 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 BP, suggesting the expansion of temperate deciduous trees during the LG interstadial (GI-1).

At the lowland Kokad site, grazing indicator fungi (*Sporomiella*, Sordariales and *Sordaria*-type (HdV55a)) were present on pollen slides. The disappearance of these fungi took place at 16,780 cal BP (Fig. 3)[18]. Around the same time, the micro- and macro-charcoal accumulation rate increased in the sediment and stayed high until *ca*. 15,000 cal BP, suggesting recurrent wildfires in the region between 17,700 and 15,000 cal BP (Fig. 3.).

Comparing selected pollen types, palynological richness (representing floristic diversity here), evenness (a measure of abundance distribution within the pollen assemblages), microcharcoal accumulation rate (indicative of regional fires) and macrocharcoal-based fire frequency and peak magnitude records (indicative of local fires), several differences become apparent between the lowland and mid mountain localities (Fig. 3). First, warming at ~ 16,200 cal BP and even at 14 700 cal BP did not lead to massive afforestation in the lowland; instead, a modest increase in forest cover was accompanied by the expansion of grass-steppes. A second striking difference is in fire history. The lowland site was characterised by increased fire activity from 17,800 cal BP until the LG onset (14,700 cal BP), when broad-leaved trees became dominant in this region. The onset of fire increase pre-dates the estimated disappearance of the megafauna, but 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 sequence tundra → cool steppe → cool coniferous forest steppe resulted in an increase in palynological diversity and evenness; at the mid mountain site, however, palynological diversity decreased when closed mixed leaved and taiga forests started to dominate from the LG onset (~ 14,700 cal BP). Taxa accumulation curves (Suppl. Figs. 9 and 10) also indicate a change in the local species pool at the LG onset. This has implications for the grazing megafauna as well: first, the least diverse floristically was the steppe tundra ($E(T) < 20$), while the forest steppe biomes were more diverse ($E(T) \sim 30$). On the basis of the radiocarbon dates from woolly mammoth and reindeer (Suppl. Figs. 7 and 8), a decline in these species is observed when locally tundra (steppe tundra) disappeared.

Figure 2 shows pollen-inferred July mean temperatures at Kokad using two different transfer functions[18]. While the WA-PLS reconstruction indicates that between 19,440 and 16,700 cal BP pollen-inferred summer mean temperatures were stable and fluctuated between 14.5 and 15.7 °C, the MAT based reconstruction yields lower values and a high amplitude fluctuation. A distinct cooling is present between 17,900 and 16,280 cal BP, with inferred summer mean temperatures between 7.5 and 12.7 °C. This interval coincides with HE-1 (17,850–16,200 cal BP), and the reconstructed temperature values follow the summer mean temperature values indicated by the vole fauna at the Jankovich Cave[21] (Fig. 2). This suggests that the MAT based reconstruction is likely to be realistic. Following this event, July mean temperatures increased rapidly to 16–18 °C. Both the vole 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[16,37–39].

Discussion

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

The 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. Fig. 8), fungal spores (*Sporomiella*, *Sordaria*-type (HdV55a), 1.4–230 spores cm^{-2} yr^{-1}) living in the dung of large grazing mammals confirm a population decrease from 17.2 ka cal BP that likely culminated around 16.2 ka cal BP, contemporaneous with the last dated mammoth, even though the final disappearance is modelled to 13.8–15.2 ka cal BP. As demonstrated by the Kokad micro- and macrocharcoal records, regional and local fires appeared 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. A correlation is also apparent between the last ^{14}C date for a mammoth and the transformation of the herbaceous vegetation at the Kokad locality. The picture is therefore less definite here than in North America, where fungal spore, charcoal and pollen studies have demonstrated that the population decrease of megaherbivores preceded the vegetation change[40]. In the CB grazing indicator fungal spores are less frequent in the LP and LG deposits, rendering this less conclusive; in addition, radiocarbon dates suggest coincidence of the change in vegetation and megaherbivore latest radiocarbon dates in case of the woolly mammoth. Overall, the data presented here suggest that a previously large herbivore population probably 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, depending largely on tree cover (Fig. 3). From regional summaries it is known that wildfires were generally more frequent during the Early Holocene in EC Europe, and in conifer forest dominated regions during the LG[9,41]. This increase in fires may be explained by orbital forcing (warmer than present summers, cold winters, seasonal drought stress); however, the same studies also concluded that once temperate broadleaved forest had become established, biomass burning was high at ~ 45% tree cover and decreased to a minimum at between 60 and 70% tree cover. These data corroborate the determination of biomass burning by tree compositional change and tree cover. It was the highest at medium needle-leaved tree cover in the region.

The microfaunal changes and the vegetation changes inferred from the vole community from Jankovich and Rejtek I are the first rigorously dated cave sequences that yield information about ecosystem changes during the last glacial termination in Northern Hungary. Their merit is that they demonstrate that the point at which faunal turnover took place was not the LG onset, but the post HE-1 warming occurring at ~ 16.2 ka cal BP (see Jankovich Cave record on Fig. 2 and Suppl. Figs. 5 and 6).

Such high-resolution microfaunal records are rare in Europe. In Hungary, two cave faunal assemblages were revisited recently[4,42], including Rejtek I and Petényi Cave in the Bükk Mts, where mollusc shells were used for dating the earlier sequences, which also contained undiagnostic Late Upper Palaeolithic artefacts, such as retouched bladelets. The dates based on mollusc shells are close to the oldest estimates given here (Suppl. Table 3), in the LG interstadial layers (11–12) of Rejtek I, and the mollusc ^{14}C ages are also older, while in the Early Holocene layers there is a good agreement between the bone collagen and mollusc carbonate based ^{14}C dates.

Overall, this discrepancy, plus the deposition hiatus that demonstrably took place during the LG interstadial (between ~ 14,530 and 9270 cal BP) in the Petényi Cave, and the older dates for some large grazer or predator bones in Rejtek I and Jankovich serve to warn researchers that the interpretation of various cave sediment fauna 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 and 14,530 cal BP) indicate the development of a transitional flora and fauna (boreonemoral forest dominated by spruce) in the Bükk Plateau[4,23,43] 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[44,45], Spain[46] and Ukraine[47]. In addition, a recent summary work[48] compares ecosystem changes at a regional scale over the last 50,000 years.

The faunal turnover at 16.2 ka cal BP identified in Jankovich Cave has also been detected in two French cave sequences (Peyrazet 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 starting at the end of HE-1. Several rodents that occur in temperate and forested habitats today (e.g. the 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 species adapted to cold (e.g. arctic lemming, narrow-headed vole) gradually disappeared[44,45]. The three radiocarbon dated reindeer bones from the Peyrazet Cave gave an age range 13,835–15,410 cal BP[44], i.e. slightly more recent than the results from Jankovich Cave, falling mainly within the Bølling interstadial. Similar faunal turnover and climatic changes were observed in the El Mirón Cave sequence[46], where an increase in forest species diversity was detected between 18 and 11 ka cal BP, while *Pliomys lenki* (an extinct Pleistocene vole) and some other species mainly disappeared at the end of the YD.

According to Puzachenko and Markova[48] the CB belongs to the Central European South region, where after the significant decrease in species richness of the LGM, the number of species was gradually restored to the value characteristic of the late MIS-3 between ~ 17.5 and 13 ka BP. If local last detection times from the Rejtek I and Jankovich are compared with the regional disappearance times reported, it is possible to 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 last detection times may, in all likelihood, be connected 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 indicates a different Pleistocene-Holocene faunal transition[47]. Only the large herbivore species became extinct from this assemblage, while most other taxa persisted from the Pleistocene into the Holocene without losses, a phenomenon likely to have been influenced by the Crimea's geographic position and milder climate. Its relevance to the CB lies in the vegetation and fauna of the south-eastern lowland areas that via the Iron Gate are directly connected to the Pontic Crimean territories and contain several common taxa[49]. Many of the Pontic species originated from this climatically relatively stable area, and as the differences of the faunal records demonstrate, it is likely that Pontic species migrated into the CB during the last glacial termination period[50].

Plaid ecosystems reverting to equilibrium ecosystem mosaics: key to steppe fauna survival. Sommer and Nadachowski[51] have demonstrated that faunal communities during the LGM contained a combination of cold and 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 influenced by delayed immigration. When the order of changes in different ecosystem components is examined[12,17,50], a similar situation applies to certain woody and herbaceous elements of the temperate forest and forest steppe flora.

According to the Plaids and Stripes Hypothesis[52], 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[53]. 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 such plaid settings characterised by disequilibrium. 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[54,55] on immature, and thus more productive, soils. In support of this hypothesis, the transformation of the plaid ecosystems towards a striped structure during the LG and Early Holocene can be easily traced on Eurasian biome simulation maps[56].

The pollen based biome reconstruction, microfaunal change and climate model simulations presented here all suggest that the rapid transformation of the plaid landscape took place from 16.2 ka cal BP in the CB, and the major element was the expansion of temperate and boreal woodland species and the overall gradual increase in woodland cover that did not favour mammoth and reindeer. On the other hand, if current and simulated plant biomes in the CB are examined, it is possible to 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 for edaphic and hydrological reasons[49].

This deviation from the regional trend probably had an overarching consequence during the Holocene climate stability, allowing the longer subsistence of mega-herbivore mammal species in the lowlands, as demonstrated by several studies[3,57,58]. Although climate change led to the replacement of the ungulate species spectrum due to partial afforestation, early warming around 16.2 ka cal BP was detrimental to the mammoth adapted to cold-steppe, tundra-steppe environments. 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 productivity[59], and therefore plaid ecosystems are pertinent.

Local herbivore extinctions in context of European extinction history.

Reindeer. It is known from range modelling that the global potential range of reindeer declined by 84% between 21 and 6 kyr BP[60]. This is explicable in terms of rapid climate change, particularly after HE-1. Starting from their modern July mean temperature tolerance of < 12–13 °C and a metabolic adaptation to < 15 °C[61], their distribution dynamics in the CB suggest that reindeer were common in the CB during the LGM (from *ca*. 23 ka cal BP) and the population had declined steeply by ca. 15.2 ka cal BP (Suppl. Table 5), with a modelled last appearance at ~ 11,860–12,550 cal BP. The range dynamics of reindeer in Europe summarized recently[62] showed only four context-dated reindeer findings from the CB, all of which were dated between 18 and 25 ka cal BP. Recently, the Zöld Cave from the central CB[8] 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, the dating results of several reindeer bones from Jankovich Cave presented here 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 their local extinction probably occurred later than assumed by Sommer et al.[62].

The present data suggest that the reindeer population declined considerably around 15.2 ka cal BP. Comparing this timing with the climate reconstruction inferred from pollen and chironomid, together with biome records (Figs. 2 and 3)[38], it is possible to conclude that reindeer persisted in the cool conifer forest steppe environment of the basin for about 1000 years, and their population decline predated the emergence of cool mixed (coniferous-deciduous) forests around 14.7 ka cal BP (Fig. 2; Suppl. Fig. 11). The species was abundant during the LGM and persisted during the subsequent period, as demonstrated by the relatively large number of Late Epigravettian sites in Hungary where reindeer bones are present.

In Southern Sweden, reindeer extinction 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 decline in the reindeer population cannot be demonstrated, although both elm (*Ulmus*) and hazel (*Corylus*) were already expanding regionally in the Great Hungarian Plain at 15.2 ka cal BP without a biome shift (Fig. 2). It is likely that rapidly increasing summer temperatures had a direct effect on the local reindeer population, and that this probably left the basin as a result of its metabolic adaptation to < 15 °C. As the climate reconstructions used herein demonstrate, not only were the lowlands certainly too warm for reindeer by 15.2 ka cal BP, but also the mid mountain regions (Fig. 2). Another striking feature of the plain is that during the abrupt biome shift from a tundra to cool coniferous forest biome, the lowlands and low hills of the CB remained partially steppe covered, and this characteristic of the landscape must have helped the survival of grazers if their metabolic/physiological adaptation made it possible. The timing of the reindeer's withdrawal from the CB agrees well with the dates of the youngest/latest Epigravettian campsites[8,63]. Even though the Epigravettian population also hunted horses by this time[8], the coincidence of these two events suggests quarry fidelity and environmental determinism.

Woolly mammoth. Available summaries on European proboscidean extinction times suggest that woolly mammoth (*Mammuthus primigenius*) was present in the ice-free parts of Europe during the Weichselian Glacial until 14 ka cal BP, when its populations collapsed due to warming[64]. Moreover, the endemic European mammoth population became extinct after 24 ka cal BP and was replaced by members of a Siberian mammoth genetic clade which had been colonizing Europe since 34 ka cal BP[65].

In 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 3[66], when ice-free conditions prevailed in the major valleys. Over 230 bones have been examined in Austria, and their distribution suggests that mammoth were 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. Fig. 8.), the onset of the latter period coincides with a massive dust accumulation period above Greenland (see Ca^{2+} on Fig. 3) followed by two short interstadials (GI-2.1 & GI-2.2). Regarding the earlier time interval, four Greenland interstadials fall within this (GI-3-4-5.1-5.2; Suppl. Fig. 8)[34], and it is known, mainly from loess mollusc studies, that the lowlands of the CB were covered by boreal parkland forests at these milder time intervals[67]. Furthermore, variations in glacial dust deposition on centennial–millennial timescales in the CB and Greenland were synchronous[68]. Even though the number of ^{14}C dated mammoth bones is still low, if the apparent low figures for the mammoth population or indeed its absence are valid, then it is likely that the warmer and more forested periods were disadvantageous to its populations in the CB. Moreover, the European mammoth population extinction after 24 ka cal BP likely also affected the CB, where on the basis of ^{14}C measurements that form part of this study, the Siberian clade's expansion is probable after 22 ka cal BP.

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 extinction[69], the diversity of extinction patterns observed on different continents has led to an increasing recognition of the potential synergistic role of climate change[60]. As demonstrated by Cooper et al.[70], in many cases the extinction of genetic clades coincided with rapid warming events in the absence of a human presence in North America. These events involved the rapid replacement of one species or population by a conspecific or congeneric one across a broad area. It appears that cold conditions were not an important driver of extinctions even in the presence of anatomically modern humans in Europe.

In the CB, Early Epigravettian groups were present during the LGM (GS-3–2.1c) and Late Epigravettian in the GS-2.1a-b and early GI-1 periods[7]. According to Lengyel et al.[71] Early Epigravettian (26–20 ka cal BP) hunter-gatherers subsisted on reindeer and the wild horse, with reindeer predominating. A marked change was detected in the dominant quarry at the Late Epigravettian sites (20–15.2 ka cal BP), when reindeer decreased, while the wild horse became dominant, and mammoth was present again. These changes suggest that the LGM reindeer population thinned out in the CB during the last glacial termination. It has also been demonstrated that a decrease in human population of the CB took place at the end of the Late Epigravettian[8]. So far only Lovas (14–13 ka cal BP)[72], and a stray find from Mezőlak (13.7–13.46 ka cal BP)[73,74] are known from Transdanubia that are contemporaneous with the Epi-Magdalenian Culture of Czechia[75] and the Arched Backed Point techno complex of Poland[76].

These findings attest to the fact that human groups with new persistence strategies appeared in the western CB about 1000 years after the mammoth, reindeer and wild horse hunters left. Lovas provided evidence for the hunting of the Eurasian elk (*A. alces*) and Red deer (*C. elaphus*) and the use of their bones for ochre mining[77,78]. From these still fragmentary data it is possible to conclude that the Late Epigravettian population that seems to have left the CB around 15 ka cal BP had strong quarry fidelity and hunting habits, with the result that it followed the megafauna elements. Supporting this argument are the recently dated Late Palaeolithic camp sites (13–11.7 ka cal BP) further north in Slovakia, and a few in Southern Poland[79], where the fauna is too poorly preserved to determine hunted species.

Conclusions

In this paper the hypothesis that transitions from cold to warm intervals were briefly optimal for grazing megafauna, followed by rapid extinctions has been tested[15]. The 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. The paleoclimate and biome reconstructions suggest that a major warming at 16.2 ka cal BP was, however, detrimental to these populations, probably due to the intolerance to increased warmth in the case of reindeer. It has also been demonstrated that in the CB, vegetation regime shifts inferred from pollen data coincided with or slightly postdated the local population decline of woolly mammoth and reindeer. Furthermore, wildfires played a role in the transformation of the vegetation at the last glacial termination, when the array of biome changes 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 the increasing number of well dated Late Epigravettian sites and their associated fauna in the CB are compared with the biome and climate reconstruction on the basis of pollen, it is possible to infer that the reason for the disappearance of the Epigravettian hunters was the diminishing population size of their dominant quarries, 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 more drastic faunal and human population changes in response to early warming after the LGM than more north-westerly and northerly locations in Europe.

It was found that cave faunas in general can be used to estimate local extinction times. Direct AMS ^{14}C measurements on the investigated species are required; large mammal bones from the same sediment layer often give deviating (older) ages to 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 which became extinct in the latest Pleistocene or in the Holocene. Since the aim was to determine the probable age of disappearance, preference was given to bones of the same species from all layers in the sequence, where possible.

Radiocarbon dating, age-depth modelling. The selected bones were first subjected to physical preparation, including surface removal using a Dremel device, followed by grinding and sieving. Then 600 mg of the 0.5–1 mm fraction was placed into a test tube to perform acid–base-acid treatment (ABA), using 0.5 M HCl and 0.1 M 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, a ~ 4 mg gelatine sample together with MnO_2 reagent was placed to a glass combustion tube, which was, after sealing, heated to 550 °C[80,81]. The CO_2 gas thus obtained was then purified and reduced to solid graphite, applying a customized sealed tube graphitization method[82]. The ^{14}C measurements were performed using the EnvironMICADAS AMS instrument at the ICER laboratory[83].

^{14}C ages were calibrated into calendar years using Calib Rev. v. 8.2html software and the Intcal20 calibration curve[35]. Age-depth modelling for the cave sediment sequences was performed with the Bacon package in R using Bayesian probability statistics[84]. 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[32,85]. 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 the determination of 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). An alternative model was also used to estimate extinction times of woolly mammoth and reindeer. The GRIWM model[33] inversely weights the contribution of each dated record to determine the terminal date. Equations and further details of the method are described in the Supplementary Material.

Re-analysis and re-plotting of the mammal bone assemblages. Bone assemblages were re-analysed for taxonomic inconsistencies by Piroska 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.[18] In brief, the European Modern Pollen Database (EMPD) was used as training set[86]. 209 terrestrial pollen types were used for the summer mean temperature reconstruction, and this 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. Quantitative pollen-based transfer functions were developed for T_{JJA} using weighted averaging-partial least squares (WA-PLS) regression[87] with five components. Leave-one-out cross-validation[88] was employed 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. The surface pollen data was transfomed to square-roots to reduce the noise of the data[89], a randomization t-test [90] was applied to select the most appropriate WA-PLS component for TJJA reconstructions, and sample-specific standard errors were calculated for the reconstructions, using a bootstrapping procedure with 1000 cycles[91]. The WA-PLS transfer functions and associated T_{JJA} reconstructions were performed using the RIOJA package in R[92]. The statistical significance of the WA-PLS based T_{JJA} reconstructions was assessed using an approach involving 999 randomizations developed by Telford and Birks[93], and these significance tests were conducted using the R package PALAEOSIG[93]. 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 pollen assemblages to modern assemblages. The similarity between each fossil and modern pollen assemblage is evaluated using the chord distance metric[94,95]. In this study, the six modern pollen spectra that had the smallest distance were considered 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 the Monte-Carlo method[94], the modern sample was considered a 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 the focus was 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 the pollen based TJJA reconstruction were also compared with the vole-thermometer based T_{July} reconstruction from the Jankovich Cave and Rejtek Rock Shelter[21,23]. 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[21,96]. The present-day optimum temperature for the distribution of certain vole-species is given in Jánossy and Kordos[23]. These are 15 °C for *Clethrionomys*, 17.5 °C for Arvicola, 21 °C for *Microtus arvalis*, 19 °C for *Microtus agrestis*, 10 °C for *Lasiopodomys* (*S.*) *gregalis*, 12.5 °C for *Microtus oeconomus* and 7.5 °C for *Dicrostonyx*. After the multiplication of the values of mean July temperature by 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, so its distribution is not zonal[21,23].

Biome reconstruction. For the pollen assemblage based biome reconstructions the technique of Prentice et al.[97] was used, as improved further by Tarasov et al.[98]. The first step was the assignment of the pollen taxa to plant functional types (PFT). The biome-PFT-taxon matrix published in Allen et al.[99] was used here. 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 of each biome. The next step is the calculation of biome affinity scores[97]. This equation sums up the square roots of pollen percentages within a PFT and sums 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 steppe[99]. In this paper, the stratigraphic plot of the main biome affinity scores and the assigned biomes is presented.

Data availability

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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References

1. Vörös, I. Large mammal remains from the Upper Palaeolithic site at Esztergom-Gyurgyalag. *Acta Archaeol. Hung.* **43**, 261–263 (1991).
2. Jánossy, D. *Pleistocene Vertebrate Faunas of Hungary. Journal of Chemical Information and Modeling* (Akadémiai Kiadó, 1986).
3. Kordos, L. A sketch of the vertebrata biostratigraphy of the Hungarian Holocene. *Földrajzi Közlemények* **101**, 144–160 (1978).
4. Sümegi, P., Rudner, E. & Törőcsik, T. Environmental and chronological reconstruction problems during the Pleistocene/Holocene transition in Hungary (Magyarország pleisztocén végi és kora holocén környezeti változások kronológiai, tér és időbeli rekonstrukciós problémái). In *Őskoros Kutatók IV. Összejövetelének Konferenciakötete* (ed. Kolozsi, B.) 279–298 (Hajdú-Bihar Megyei Múzeumok Igazgatósága, 2012).
5. Bösken, J. *et al.* Investigating the last glacial Gravettian site 'Ságvár Lyukas Hill' (Hungary) and its paleoenvironmental and geochronological context using a multi-proxy approach. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **509**, 77–90 (2018).
6. Wilczyński, J. *et al.* Mammoth hunting strategies during the Late Gravettian in Central Europe as determined from case studies of Milovice I (Czech Republic) and Kraków Spadzista (Poland). *Quat. Sci. Rev.* **223**, 105919 (2019).
7. Lengyel, G. Reassessing the middle and late upper palaeolithic in Hungary. *Acta Archaeol. Carpathica* **51**, 47–66 (2016).
8. Béres, S. *et al.* Zöld cave and the late epigravettian in eastern central Europe. *Quat. Int.* **587–588**, 158–171 (2021).
9. Feurdean, A. *et al.* Trends in biomass burning in the Carpathian region over the last 15,000 years. *Quat. Sci. Rev.* **45**, 111–125 (2012).
10. Kuneš, P. *et al.* Interpretation of the last-glacial vegetation of eastern-central Europe using modern analogues from southern Siberia. *J. Biogeogr.* **35**, 2223–2236 (2008).
11. Pazonyi, P. Mammalian ecosystem dynamics in the Carpathian Basin during the last 27,000 years. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **212**, 295–314 (2004).
12. Sümegi, P. *et al.* Climatic fluctuations inferred for the middle and late pleniglacial (MIS 2) based on high-resolution (~ca. 20 y) preliminary environmental magnetic investigation of the loess section of the Madaras brickyard (Hungary). *Cent. Eur. Geol.* **55**, 329–345 (2012).
13. Magyari, E. K. *et al.* Vegetation and environmental responses to climate forcing during the last glacial maximum and deglaciation in the East Carpathians: attenuated response to maximum cooling and increased biomass burning. *Quat. Sci. Rev.* **106**, 278–298 (2014).
14. Feurdean, A. *et al.* Climate variability and associated vegetation response throughout central and eastern Europe (CEE) between 60 and 8 ka. *Quat. Sci. Rev.* **106**, 206–224 (2014).
15. Mann, D. H. *et al.* Life and extinction of megafauna in the ice-age Arctic. *Proc. Natl. Acad. Sci. U. S. A.* **112**, 14301–14306 (2015).
16. Magyari, E. K. *et al.* Rapid vegetation response to Lateglacial and early Holocene climatic fluctuation in the South Carpathian Mountains (Romania). *Quat. Sci. Rev.* **35**, 116–130 (2012).
17. Magyari, E. K. *et al.* Late Pleniglacial vegetation in eastern-central Europe: are there modern analogues in Siberia?. *Quat. Sci. Rev.* **95**, 60–79 (2014).
18. Magyari, E. K. *et al.* Warm Younger Dryas summers and early late glacial spread of temperate deciduous trees in the Pannonian Basin during the last glacial termination (20–9 kyr cal BP). *Quat. Sci. Rev.* **225**, 105980 (2019).
19. Sümegi, P., Magyari, E., Dániel, P., Molnár, M. & Törocsik, T. Responses of terrestrial ecosystems to Dansgaard-Oeshger cycles and Heinrich-events: a 28,000-year record of environmental changes from SE Hungary. *Quat. Int.* **293**, 34–50 (2013).
20. Hillebrand, J. *Paleolithic History (Az őskőkor Története)* (Magyar Szemle Társaság, 1934).
21. Vértes, L., Kretzoi, M. & Herrmann, M. Neuere Forschungen in der Jankovich-Höhle. *Folia Archaeol.* **9**, 3–23 (1957).
22. Jánossy, D. Preliminary results of the paleontological investigations of a yet unknown rock shelter in the Bükk Mountains (A Bükk-hegység eddig ismeretlen kőfülkéjében végzett őslénytani ásatás előzetes eredménye, Répáshuta, Rejtek). *Karszt- és Barlkut. Tájékoztató* 72 (1963).
23. Jánossy, D. & Kordos, L. Pleistocene-Holocene Mollusc and Vertebrate Fauna of two caves in Hungary. *Ann. Hist. Musei Natl. Hungarici* **68**, 5–29 (1976).
24. Vértes, L. *Paleolithic and Mesolithic Remains in Hungary (Az Őskőkor és az Átmeneti Kőkor Emlékei Magyarországon)* (Akadémiai Kiadó, 1965).
25. Stieber, J. Oberpleistozäne Vegetationsgeschichte Ungarns im Spiegel anthrakotomischer Ergebnisse (bis 1957) (A magyarországi felsőpleisztocén vegetáció-története az anthrakotómiai eredmények (1957-ig) tükrében). *Földtani Közlöny* **97**, 305–317 (1967).
26. Jánossy, D. Vorläufige Ergebnisse der Ausgrabungen in der Felsnische Rejtek I. (Bükkgebirge, Gem. Répáshuta). *Karszt- és Barlangkutatás* **3**, 49–58 (1961).
27. Kovács, J. Radiocarbon chronology of late Pleistocene large mammal faunas from the Pannonian basin (Hungary). *Bull. Geosci.* **87**, 13–19 (2012).
28. Willis, K. J., Braun, M., Sümegi, P. & Tóth, A. Does soil change cause vegetation change or vice versa? A temporal perspective from Hungary. *Ecology* **78**, 740–750 (1997).
29. Magyari, E. Holocene biogeography of *Fagus sylvatica* L. and *Carpinus betulus* L. in the Carpathian-Alpine Region. *Folia Hist. Musei Matra.* **26**, 15–35 (2002).
30. Magri, D. Persistence of tree taxa in Europe and quaternary climate changes. *Quat. Int.* **219**, 145–151 (2010).
31. Füköh, L. Biostratigraphical investigation of the mollusc fauna of Rejtek I. rock-niche and Petényi Cave: Bükk Mountains, Hungary (Rejtek kőfülke és a Petényi-barlang (Bükk-hegység) Mollusca faunájának malakosztratigráfiai vizsgálata). *Folia Hist. Musei Matra.* **12**, 9–13 (1987).

32. Ramsey, C. B. & Lee, S. Recent and planned developments of the program OxCal. *Radiocarbon* **55**, 720–730 (2013).
33. Bradshaw, C. J. A., Cooper, A., Turney, C. S. M. & Brook, B. W. Robust estimates of extinction time in the geological record. *Quat. Sci. Rev.* **33**, 14–19 (2012).
34. Rasmussen, S. O. *et al.* A stratigraphic framework for abrupt climatic changes during the last glacial period based on three synchronized Greenland ice-core records: refining and extending the INTIMATE event stratigraphy. *Quat. Sci. Rev.* **106**, 14–28 (2014).
35. Reimer, P. J. *et al.* The IntCal20 Northern Hemisphere radiocarbon age calibration curve (0–55 cal kBP). *Radiocarbon* **62**, 725–757 (2020).
36. Katona, L., Kovács, J., Kordos, L., Szappanos, B. & Linkai, I. The Csajág mammoths (*Mammuthus primigenius*): late Pleniglacial finds from Hungary and their chronological significance. *Quat. Int.* **255**, 130–138 (2012).
37. Buczkó, K. *et al.* Responses of diatoms to the Younger Dryas climatic reversal in a South Carpathian mountain lake (Romania). *J. Paleolimnol.* **48**, 417–431 (2012).
38. Tóth, M. *et al.* A chironomid-based reconstruction of late glacial summer temperatures in the southern Carpathians (Romania). *Quat. Res.* **77**, 122–131 (2012).
39. Sümegi, P. *et al.* Radiocarbon-dated paleoenvironmental changes on a lake and peat sediment sequence from the central Great Hungarian Plain (Central Europe) during the last 25,000 years. *Radiocarbon* **53**, 85–97 (2011).
40. Gill, J. L., Williams, J. W., Jackson, S. T., Lininger, K. B. & Robinson, G. S. Pleistocene megafaunal collapse, novel plant communities, and enhanced fire regimes in North America. *Science* **326**, 1100–1103 (2009).
41. Feurdean, A. *et al.* Fire hazard modulation by long-term dynamics in land cover and dominant forest type in eastern and central Europe. *Biogeosciences* **17**, 1213–1230 (2020).
42. Sümegi, P. *et al.* Radiocarbon dated complex paleoecological and geoarcheological analyses at the Bodrogkeresztúr—Henye Gravettian site (Ne Hungary). *Archeometriai Műhely* **13**, 31–41 (2016).
43. Herrmann, M., Jánossy, D., Stieber, J. & Vértes, L. Ausgrabungen in der Petényi- und Pesko-Höhle (Bükk-Gebirge). *Folia Archaeol.* **8**, 3–22 (1956).
44. Royer, A. How complex is the evolution of small mammal communities during the Late Glacial in southwest France?. *Quat. Int.* **414**, 23–33 (2016).
45. Crégut-Bonnoure, E. *et al.* The karst of the Vaucluse, an exceptional record for the last glacial maximum (LGM) and the Late-glacial period palaeoenvironment of southeastern France. *Quat. Int.* **339–340**, 41–61 (2014).
46. Cuenca-Bescós, G., Straus, L. G., González Morales, M. R. & García Pimienta, J. C. The reconstruction of past environments through small mammals: from the Mousterian to the Bronze Age in El Mirón Cave (Cantabria, Spain). *J. Archaeol. Sci.* **36**, 947–955 (2009).
47. Kovalchuk, O. *et al.* Living in a time of change: late Pleistocene/Holocene transitional vertebrate fauna of Grot Skeliastyi (Crimea, Ukraine). *Hist. Biol.* https://doi.org/10.1080/08912963.2020.1769094 (2020).
48. Puzachenko, A. Y. & Markova, A. K. Evolution of mammal species composition and species richness during the Late Pleistocene—Holocene transition in Europe: a general view at the regional scale. *Quat. Int.* **530–531**, 88–106 (2019).
49. Varga, Z. Extra-Mediterranean refugia, post-glacial vegetation history and area dynamics in Eastern Central Europe. In *Relict Species: Phylogeography and Conservation Biology* (eds Habel, J. C. & Assmann, T.) 57–87 (Springer Berlin Heidelberg, 2010).
50. Magyari, E. K. *et al.* Holocene persistence of wooded steppe in the Great Hungarian Plain. *J. Biogeogr.* **37**, 915–935 (2010).
51. Sommer, R. S. & Nadachowski, A. Glacial refugia of mammals in Europe: evidence from fossil records. *Mamm. Rev.* **36**, 251–265 (2006).
52. Mann, D. H., Groves, P., Gaglioti, B. V. & Shapiro, B. A. Climate-driven ecological stability as a globally shared cause of Late Quaternary megafaunal extinctions: the Plaids and Stripes Hypothesis. *Biol. Rev.* **94**, 328–352 (2019).
53. Lister, A. M. & Sher, A. V. Ice cores and mammoth extinction. *Nature* **378**, 23–24 (1995).
54. Owen-Smith, N. R. *Megaherbivores: The Influence of Very Large Body Size on Ecology* (Cambridge University Press, 1988).
55. Guthrie, R. D. *Frozen Fauna of the Mammoth Steppe: The story of Blue Babe* (The University of Chicago Press, 1990).
56. Huntley, B. *et al.* Millennial climatic fluctuations are key to the structure of last glacial ecosystems. *PLoS One* **8**, e61963 (2013).
57. Vörös, I. Large mammalian faunal changes during the Late Upper Pleistocene and Early Holocene times in the Carpathian Basin. In *Pleistocene Environment in Hungary* (ed. Pécsi, M.) 81–102 (Geographical Research Institute HAS, 1987).
58. Németh, A. *et al.* Holocene mammal extinctions in the Carpathian Basin: a review. *Mamm. Rev.* **47**, 38–52 (2017).
59. Marchant, R., Brewer, S., Webb, T. I. & Turvey, S. T. Holocenedeforestation: a history of human–environmental interactions, climate change, and extinction. In *Holocene Extinctions* (ed. Turvey, S. T.) 213–234 (Oxford University Press, 2009).
60. Lorenzen, E. D. *et al.* Species-specific responses of Late Quaternary megafauna to climate and humans. *Nature* **479**, 359–364 (2011).
61. Herre, W. Rangifer tarandus—Ren, Rentier. In *Handbuch der Saugetiere Europas 2/II Paarhufer—Artiodactyla* (eds Niethammer, J. & Krapp, F.) 198–216 (Aula Publisher, 1986).
62. Sommer, R. S., Kalbe, J., Ekström, J., Benecke, N. & Liljegren, R. Range dynamics of the reindeer in Europe during the last 25,000 years. *J. Biogeogr.* **41**, 298–306 (2014).
63. Lengyel, G. & Wilczyński, J. (2018) The Gravettian and the Epigravettian chronology in eastern central Europe: a comment on Bösken et al. (2017). *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **506**, 265–269 (2018).
64. Sommer, R. S. Late Pleistocene and Holocene history of mammals in Europe. *Handb. Mamm. Eur.* https://doi.org/10.1007/978-3-319-65038-8_3-1 (2020).
65. Palkopoulou, E. *et al.* Holarctic genetic structure and range dynamics in the woolly mammoth. *Proc. R. Soc. B Biol. Sci.* **280**, 20131910 (2013).
66. Spötl, C., Reimer, P. J. & Göhlich, U. B. Mammoths inside the Alps during the last glacial period: radiocarbon constraints from Austria and palaeoenvironmental implications. *Quat. Sci. Rev.* **190**, 11–19 (2018).
67. Sümegi, P. *Loess and Upper Paleolithic Environment in Hungary: An Introduction to the Environmental History of Hungary* (Aurea, 2005).
68. Újvári, G. *et al.* Coupled European and Greenland last glacial dust activity driven by North Atlantic climate. *Proc. Natl. Acad. Sci. U. S. A.* **114**, E10632–E10638 (2017).
69. Haynes, G. Extinctions in North America's late glacial landscapes. *Quat. Int.* **285**, 89–98 (2013).
70. Cooper, A. *et al.* Abrupt warming events drove Late Pleistocene Holarctic megafaunal turnover. *Science* **349**, 602–606 (2015).
71. Lengyel, G. *et al.* The Epigravettian chronology and the human population of eastern Central Europe during MIS2. *Quat. Sci. Rev.* **271**, 107187 (2021).
72. Sajó, I. E. *et al.* Core-shell processing of natural pigment: upper Palaeolithic red ochre from Lovas, Hungary. *PLoS One* **10**, 1–18 (2015).
73. Horváth, T. & Ilon, G. Mezőlak-Szélmező-peatbog: an unusual prehistoric site (Mezőlak-szélmező-tőzegtelep: egy nem hétköznapi őskori lelőhely). *Archeometriai Műhely* **14**, 143–183 (2017).
74. Zalai-Gaál, I. Possibilites of the social-archaeological studies of the Neolithic. *Antaeus* **27**, 449–471 (2004).
75. Reade, H. *et al.* Magdalenian and Epimagdalenian chronology and palaeoenvironments at Kůlna Cave, Moravia, Czech Republic. *Archaeol. Anthropol. Sci.* https://doi.org/10.1007/s12520-020-01254-4 (2021).
76. Łanczont, M. *et al.* Late Glacial environment and human settlement of the Central Western Carpathians: a case study of the Nowa Biała 1 open-air site (Podhale Region, southern Poland). *Quat. Int.* **512**, 113–132 (2019).
77. Mészáros, G. & Vértes, L. A paint mine from the early Upper Palaeolithic age near Lovas (Hungary, county Veszprém). *Acta Archaeol. Acad. Sci. Hung.* **5**, 5–34 (1955).

78. Pathou-Mathis, M. Nouvelle analyse du metérial osseux du site de Lovas. *Praehistoria* **3**, 161–175 (2002).
79. Sobkowiak-Tabaka, I. & Diachenko, A. Approaching daily life at Late Palaeolithic camps: the case of Lubrza 10, Western Poland. *Prahistorische Z.* **95**, 311–333 (2020).
80. Molnár, M. *et al.* EnvironMICADAS : a mini 14C AMS with enhanced gas ion source. *Radiocarbon* **55**, 338–344 (2013).
81. Major, I. *et al.* Assessment and development of bone preparation for radiocarbon dating at HEKAL. *Radiocarbon* **61**, 1551–1561 (2019).
82. Rinyu, L. *et al.* Optimization of sealed tube graphitization method for environmental C-14 studies using MICADAS. *Nucl. Instrum. Methods Phys. Res. Sect. B Beam Interact. Mater. At.* **294**, 270–275 (2013).
83. Molnár, M. *et al.* Status report of the new AMS 14 C sample preparation lab of the Hertelendi laboratory of environmental studies (Debrecen, Hungary). *Radiocarbon* **55**, 665–676 (2013).
84. Blaauw, M. & Christeny, J. A. Flexible paleoclimate age-depth models using an autoregressive gamma process. *Bayesian Anal.* **6**, 457–474 (2011).
85. Kosintsev, P. *et al.* Evolution and extinction of the giant rhinoceros Elasmotherium sibiricum sheds light on late Quaternary megafaunal extinctions. *Nat. Ecol. Evol.* **3**, 31–38 (2019).
86. Davis, B. A. S. *et al.* The European modern pollen database (EMPD) project. *Veg. Hist. Archaeobot.* **22**, 521–530 (2013).
87. ter Braak, C. J. F. & Juggins, S. Weighted averaging partial least squares regression (WA-PLS): an improved method for reconstructing environmental variables from species assemblages. *Hydrobiologia* **269–270**, 485–502 (1993).
88. Birks, H. J. B., Line, J. M., Juggings, S., Stevenson, A. C. & ter Braak, C. J. F. Diatoms and pH reconstruction. *Philos. Trans. R. Soc. B* **327**, 263–278 (1990).
89. Prentice, I. C. Multidimensional scaling as a research tool in quaternary palynology: a review of theory and methods. *Rev. Palaeobot. Palynol.* **31**, 71–104 (1980).
90. van der Voet, H. Comparing the predictive accuracy of models using a simple randomization test. *Chemom. Intell. Lab. Syst.* **25**, 313–323 (1994).
91. Birks, H. J. B. Quantitative palaeoenvironmental reconstructions from holocene biological data. *Glob. Change Holocene* https://doi.org/10.4324/9780203785027 (2003).
92. Rioja, J. S. Analysis of Quaternary Science Data, R package version (0.8-5). (2012).
93. Telford, R. J. & Birks, H. J. B. A novel method for assessing the statistical significance of quantitative reconstructions inferred from biotic assemblages. *Quat. Sci. Rev.* **30**, 1272–1278 (2011).
94. Guiot, J. Methodology of the last climatic cycle reconstruction in France from pollen data. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **80**, 49–69 (1990).
95. Birks, H. J. B. Ecological palaeoecology and conservation biology: controversies, challenges, and compromises. *Int. J. Biodivers. Sci. Ecosyst. Serv. Manag.* **8**, 292–304 (2012).
96. Kordos, L. Climatostratigraphy of Upper Pleistocene vertebrates and the conditions of loess formation in Hungary. *GeoJournal* **15**, 163–166 (1987).
97. Prentice, I. C., Guiot, J., Huntley, B., Jolly, D. & Cheddadi, R. Reconstructing biomes from palaeoecological data: a general method and its application to European pollen data at 0 and 6 ka. *Clim. Dyn.* **12**, 185–194 (1996).
98. Tarasov, P. E. *et al.* Present-day and mid-Holocene biomes reconstructed from pollen and plant macrofossil data from the former Soviet Union and Mongolia. *J. Biogeogr.* **25**, 1029–1053 (1998).
99. Allen, J. R. M., Watts, W. A. & Huntley, B. Weichselian palynostratigraphy, palaeovegetation and palaeoenvironment; the record from Lago Grande di Monticchio, southern Italy. *Quat. Int.* **73–74**, 91–110 (2000).

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Author contributions

E.K.M. wrote the manuscript, was responsible for the pollen analyses, for the conceptualization, methodology, supervision, project administration, funding acquisition, review & editing; Z.S.Z. and J.K. took part in the visualisation and statistical analyses of the data; P.P. and M.G. analysed the bone assemblages, wrote part of the manuscript, took part in the conceptualization; I.M. was responsible for the stable and radioactive isotope analyses, wrote part of the original draft, reviewed & edited the manuscript; I.P. analysed pollen samples and took part in data visualisation; G.Y.L. was responsible for archaeological data acquisition, reviewed & edited the manuscript; A.V. took part in the sample collection, reviewed & edited the manuscript; A.H. did the statistical analysis of the the macrocharcoal records and plotted diagrams.

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Competing interests

The authors declare no competing interests.

Additional information

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