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Food web reconstruction of Barmaky, the oldest post-LGM hunter-gatherer site in north-western Ukraine

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The site of Barmaky currently marks the oldest Epigravettian occupation of north-western Ukraine shortly after the Last Glacial Maximum (LGM), dated to around 19 cal. ka BP. Stable isotope analyses of bone collagen from six terrestrial mammals and two bird species show a comparatively highly structured palaeo-food web. Characteristic are high δ^{15}N values in mammoth (*Mammuthus primigenius*) bone collagen compared with other herbivores and δ^{13}C values showing niche partitioning between mammoth and hare on the one hand and reindeer on the other. These findings may indicate differentiated herbivore niches, with different diets and habitats between herbivorous groups. Additionally, different mobility patterns could cause isotopic scatter in food webs. To better understand the context of early post-LGM mammoth behaviour, we compare the mammoth δ^{15}N values of Barmaky (19.0 cal. ka BP; 7.2±0.1‰) with those of Yudinovo (lower layer: 19.1/18.3–15.1 cal. ka BP and upper layer: 14.8–13.8 cal. ka BP; 7.3±1.0‰), Yeliseevichi (17.6 cal. ka BP; 5.7±0.8‰) and Mezhyrich (18.5–17.5 cal. ka BP; 4.3±0.8‰). At all sites, δ^{15}N values of mammoths are comparatively high, except for Mezhyrich and a single specimen from Barmaky. In comparison with sedentary hares, mammoths from Barmaky suggest a non-locally dominated δ^{15}N signal, while the mammoths from Mezhyrich show the local isotope signal. We also discuss the potential role of differences in temperature, precipitation and permafrost development for the different locations. Results from climate models indicate a gradient in temperature and precipitation with possible implications for food availability in the mammoth steppe.

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During the last glacial period, climate repeatedly alternated between cooler (stadial) and warmer (interstadial) conditions (Andersen *et al.* 2004; Rasmussen *et al.* 2014). During the Last Glacial Maximum (LGM, *sensu stricto* 24–19 cal. ka BP, Mix *et al.* 2001), severe climatic deteriorations were accompanied by changing ecosystems and environments in central Europe (Maier *et al.* 2021, 2022), which significantly affected the distribution of animals and thus subsistence patterns of Palaeolithic hunter–gatherer communities (Maier *et al.* 2023). However, small-scale differences are often not recorded in the supra-regional trend, which is why the reconstruction of local climatic and environmental conditions is crucial for understanding ecosystem development or human–animal interactions.

Beside other natural archives that record past environmental conditions, such as lacustrine (Meyers & Lallier-Vergès 1999; Mayr *et al.* 2017a, b) and terrestrial geochemical and sedimentological records (Marković *et al.* 2015; Lehmkuhl *et al.* 2016, 2021; Pötter *et al.* 2023) or pollen records (Duprat-Oualid *et al.* 2017; Stojakowits *et al.* 2021), animal bones represent a natural archive that is often well-preserved and abundant at Palaeolithic sites (Brock *et al.* 2010; Drucker *et al.* 2012; Bocherens *et al.* 2015). These mammal assemblages are widely used to investigate relationships between Palaeolithic humans and their prey as they represent a snapshot of the human–animal interactions at that time, even though the presence of animal bones is always somewhat biased by the selection of Palaeolithic humans (Reiss *et al.* 2023; Pasda *et al.* 2025).

Over the years, stable isotope analyses of bone collagen have become a powerful tool for the reconstruction of local palaeo-food webs and thus palaeoecological conditions (DeNiro & Epstein 1978, 1981; Bocherens *et al.* 2015). Reconstructing food webs relies on the principle that isotopic fractionation varies between animals at different trophic levels. In addition, isotopic differences are also influenced by dietary isotopic variability at temporal and spatial scales, which is well-reflected in animal collagen (DeNiro & Epstein 1978; Beijersbergen *et al.* 2021). In contrast to tooth dentin and enamel, bone collagen is a regenerating tissue and therefore reflects the average isotopic input of the animals' diet

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over a period of up to 10 years (Hedges *et al.* 2007; Drucker 2022).

The relative ^{13}C enrichment between bone collagen and the diet of a mammal is about 5‰ (e.g. Lee-Thorp *et al.* 1989; Ambrose & Norr 1993; Drucker 2022), while the fractionation between the consumer's collagen and the collagen of its prey lies between 0.8‰ and 1.3‰ (e.g. Bocherens & Drucker 2003; Fox-Dobbs *et al.* 2007; Krajcarz *et al.* 2016, 2018; Drucker 2022). The ^{15}N enrichment ranges between 3‰ and 5‰ per trophic level (e.g. DeNiro & Epstein 1981; Minagawa & Wada 1984; Schoeninger & DeNiro 1984; Bocherens & Drucker 2003; Fox-Dobbs *et al.* 2007; Krajcarz *et al.* 2018; Drucker 2022).

In general, both the δ^{13}C and the δ^{15}N values in a terrestrial mammal depend on various abiotic factors such as humidity and temperature. While the δ^{13}C values of bone collagen allow, via the herbivores' food sources, inferences about light intensity, CO_2 partial pressure and moisture (Peterson & Fry 1987; Bump *et al.* 2007; Kohn 2010), the δ^{15}N values can depend on nutritional as well as physiological factors (Peterson & Fry 1987; Van der Klift & Ponsard 2003). For instance, prolonged fasting (Hobson *et al.* 1993) or lactation (Bocherens *et al.* 1994; Fizet *et al.* 1995) can significantly affect the δ^{15}N values, while the consumption of mother's milk can lead to an increase in the ^{15}N content in body tissues of young animals (Fogel 1989; Bocherens *et al.* 1994; Jenkins *et al.* 2001).

During the last glacial period, steppe and tundra-like ecosystems, also referred to as the 'mammoth steppe' (Guthrie 2001), were prevalent in central and eastern Europe and are characterized by the great abundance of large herbivores, especially mammoths (e.g. Zimov *et al.* 1995, 2012; Bocherens 2003; Drucker *et al.* 2003; Bocherens *et al.* 2005, 2014, 2015; Drucker & Henry-Gambier 2005; Fox-Dobbs *et al.* 2008; Yeakel *et al.* 2013; Schwartz-Narbonne *et al.* 2019). The mammoth steppe developed in a changing landscape with continuous or discontinuous permafrost, depending on the geographical region and time period considered (Delisle *et al.* 2007; Blaser *et al.* 2010; Vandenberghe *et al.* 2014).

To date, a large number of studies have been conducted on bone collagen from different taxa of the mammoth steppe, especially for Marine Isotope Stage (MIS) 3 (59–29 cal. ka BP) and 2 (29–11.7 cal. ka BP; Voelker & Workshop Participants 2002), which have demonstrated a particular niche partitioning between different herbivorous and carnivorous taxa (Iacumin *et al.* 2000, 2006, 2010; Drucker *et al.* 2003, 2018; Stevens & Hedges 2004; Fox-Dobbs *et al.* 2008; Stevens *et al.* 2008; Bocherens *et al.* 2015; Krajcarz *et al.* 2016; Drucker & Fontana 2024). Characteristically, horse and mammoth are among the most ^{13}C-depleted, whereas reindeer are among the most ^{13}C-enriched herbivores, at least partly reflecting their high consumption of lichen (Bocherens *et al.* 2015). Mammoth typically had strikingly high δ^{15}N values, placing the woolly mammoth in a similar range to carnivorous taxa (e.g. Bocherens *et al.* 1994; Iacumin *et al.* 2000; Fox-Dobbs *et al.* 2008; Szpak *et al.* 2010; Bocherens 2015). This anomalously high δ^{15}N signature of the mammoths is still subject to scientific debate and has not been conclusively clarified. However, it has been demonstrated that physiological characteristics can largely be ruled out (Schwartz-Narbonne *et al.* 2015; Naito *et al.* 2016) and that the high δ^{15}N values can rather be attributed to dietary specialization and the occupation of a certain ecological niche (Bocherens 2003; Schwartz-Narbonne *et al.* 2019; Malikov *et al.* 2023). In the past, it has been shown that significant environmental changes that affected the base of terrestrial food webs could have had an impact on isotopic niche partitioning (Stevens *et al.* 2008; Schwartz-Narbonne *et al.* 2015; Drucker *et al.* 2018; Reiss *et al.* 2023), and local environmental conditions played an important role in δ^{15}N signatures of central European mammoths (Iacumin *et al.* 2000; Drucker *et al.* 2018).

In this study, we present the food web structure of Barmaky, an Epigravettian site from the East European Plain, to infer possible isotopic shifts due to local climatic and environmental changes. In this context, the isotopic composition of mammoth bone collagen from Barmaky will be compared with that from other Epigravettian sites from the broader region to contribute to a better understanding of the regional isotopic niches in the mammoth steppe of that time. We further discuss different mobility patterns of mammoths as an alternative explanation for inter-site isotopic variability.

Study site

The site of Barmaky (50°37.700′N, 26°17.579′E), north-west Ukraine, is located in the western part of the East European Plain (Fig. 1), on a loess plateau of the Volhynian-Lublin upland (Chabai *et al.* 2024).

Other post-LGM sites, such as Mezhyrich (49°37.500′N, 31°25.900′E), Yeliseevichi (53°8.633′N, 33°38.800′E) and Yudinovo (52°39.883′N, 33°16.183′E), are located in the wider region, with the latter two situated to the northeast of Barmaky (Fig. 1). These sites date to the post-LGM period (Tables 1, S1), which allows their faunal assemblages to be partially compared to the animal collagen data from Barmaky. With a weighted mean of radiocarbon dates of 19 000±60 cal. a BP (Tables 1, S1), Barmaky is so far the oldest post-LGM site in north-west Ukraine. It is also the oldest assemblage related to the Epigravettian in the territory of the mid-Dnieper basin and probably represents a palimpsest of repeated stays (Chabai *et al.* 2024). Mammoth makes up by far the largest part of the faunal remains, in terms of both numbers and weight. Bison and reindeer were represented in rather equal proportions, while horse and saiga are only represented with a few finds. The carnivores are represented by fox, wolf and bear (Chabai *et al.* 2024).

Fig. 1. Location of the study site Barmaky (red star) and other Epigravettian sites (black dots) in the East European Plain. Basemap: © Esri, USGS.

Material and methods

Bone material and collagen extraction

In our study, the find inventory includes large numbers of faunal remains, both herbivores and carnivores, that is woolly mammoth (*Mammuthus primigenius*), bison (*Bison* sp.), reindeer (*Rangifer tarandus*), horse (*Equus* sp.), hare (*Lepus* sp.), brown bear (*Ursus arctos*), arctic fox (*Vulpes lagopus*) and even aquatic birds, that is (European) shag (*Phalacrocorax aristotelis*) and (European) herring gull (*Larus argentatus*) (Table S2). For collagen extraction, we applied a slightly modified version of the method of Bocherens *et al.* (1991). About 0.25–1.0 g was carefully sawn from each animal bone using a rotary tool (Proxxon-Micromot, Germany) with a circular diamond blade. Samples were cleaned with sandpaper, soaked in deionized water for 30 min, cleaned in an ultrasonic bath for 10 s and dried at 40 °C overnight. Samples were then ground using a mortar and a pestle. 0.25–1.0 g of each powdered sample (0.3–0.7 mm grain size) was weighed in centrifuge tubes and soaked in 1 M HCl and placed on a rotator for 20 min to dissolve minerals by constant agitation. Subsequently, samples were repeatedly washed with distilled water and centrifuged (Heraeus Multifuge 3L-R; Thermo Electron Corporation, Waltham, MA, USA) at 1930 x *g* for 5 min, respectively, until a neutral pH was reached. For dissolution of humic acids, the pellets were soused with 0.125 M NaOH and left under the fume hood for 20 h. Thereafter, all samples were washed again with distilled water and centrifuged until pH was neutral. In the last step, the pellets were soaked in 0.01 M HCl (pH 2) and incubated for 10–17 h in a water bath (Julabo, SW23, Germany) at 95 °C to solubilize the gelatine. Finally, the dissolved gelatine was filtrated through MF-Millipore membrane filters (5.0 µm), using vacuum flasks and filter funnels, washed with deionized water, frozen and lyophilized.

Stable isotope analysis

Depending on the amount of extracted collagen, samples were analysed, whenever possible, in duplicates or triplicates at the stable isotope laboratory of the Institute of Geography at the Friedrich-Alexander-Universität Erlangen-Nürnberg (FAU). 240–260 µg of collagen was wrapped in tin capsules and combusted in an elemental

Table 1. Previously published radiocarbon dates derived from mammoth bone collagen for various Epigravettian sites in the East European Plain. All radiocarbon dates were re-calibrated with the IntCal20 curve (Reimer *et al.* 2020). All dates represent weighted means calculated from dates with reliable stratigraphic positions (Table S1) and for which isotope data from mammoth collagen are available. Coloured boxes represent ages directly dated on bones (blue boxes) and teeth/tusks (pink boxes) with the numbers indicating the respective $\delta^{15}N$ values.

Age (cal. ka BP)	19.1	19	18.9	18.8	18.7	18.6	18.5	18.4	18.3	18.2	18.1	18	17.9	17.8	17.7	17.6	17.5	17.4	17.3	17.2	17.1	17	References
Barmaky		🟦 7.2																					Chabai *et al.* (2019, 2024)
Yudinovo	🟦 7.7																						Iacumin *et al.* (2000)
Yudinovo	🟦 7.4																						Iacumin *et al.* (2000)
Yudinovo	🟦 7.4																						Iacumin *et al.* (2000)
Yudinovo	🟥 7.1																						Drucker *et al.* (2018)
Yudinovo								🟥 7.5															Palkopoulou *et al.* (2013)
Yudinovo										🟥 7.7													Palkopoulou *et al.* (2013)
Yudinovo											🟥 6.8												Palkopoulou *et al.* (2013)
Yudinovo											🟥 5.0												Palkopoulou *et al.* (2013)
Yudinovo												🟥 8.9											Palkopoulou *et al.* (2013)
Mezhyrich, pit #7							🟦 4.0																Haesaerts *et al.* (2015)
Mezhyrich, pit #7							🟦 3.9																Haesaerts *et al.* (2015)
Mezhyrich, pit #8										🟦 4.9													Haesaerts *et al.* (2015)
Mezhyrich, pit #8										🟦 3.1													Haesaerts *et al.* (2015)
Mezhyrich, pit #6											🟦 3.6												Haesaerts *et al.* (2015)
Mezhyrich, pit #6											🟦 2.9												Haesaerts *et al.* (2015)
Mezhyrich																	🟥 5.3						Soffer (1985), Haesaerts *et al.* (2015)
Mezhyrich																	🟦 4.7						Soffer (1985), Haesaerts *et al.* (2015)
Mezhyrich																	🟦 4.6						Soffer (1985), Haesaerts *et al.* (2015)
Yeliseevychi I																🟦 6.7							Iacumin *et al.* (2000)
Yeliseevychi I																🟦 6.1							Iacumin *et al.* (2000)
Yeliseevychi I																🟦 5.3							Iacumin *et al.* (2000)
Yeliseevychi I																🟥 5.2							Iacumin *et al.* (2000)
Yeliseevychi I																🟦 4.8							Iacumin *et al.* (2000)

analyser (Flash 2000; Thermo Scientific, Waltham, MA, USA) coupled via a CONFLO-IV interface (Thermo Scientific) to an isotope ratio mass spectrometer (Delta V Advantage; Thermo Scientific) in which the evolved sample gases CO_2 and N_2 were isotopically analysed.

Isotope results are reported as delta (δ) values in per mil (‰) according to the equation:

$$\delta = R_{\mathrm{Sample}}/R_{\mathrm{Standard}} - 1 \quad (1)$$

where R is the mass ratio of the heavier to the lighter isotope ($^{13}C/^{12}C$ or $^{15}N/^{14}N$) of the sample and the international standards Vienna Pee Dee Belemnite (VPDB) for carbon and atmospheric nitrogen (AIR) for nitrogen (Coplen 2011).

Samples were also analysed for their weight percentage carbon (wt%) and nitrogen (wt%) using the ratios between peak areas of the sampling gases and the sample weights. The elemental standards atropine and cyclohexanone 2.4-dinitrophenylhydrazone were used for calibration of element contents. The measurement error of the element concentrations was <5%. The elemental contents and the atomic C/N ratios calculated from them were used to check for chemical purity and collagen preservation.

Collagen preservation

As impurities or diagenetic overprinting may bias the isotope values of prehistoric bone collagen, its preservation was checked using the quality criteria of atomic C/N ratios, elemental contents and collagen yields. Atomic C/N ratios of pure, well-preserved collagen range between 2.9 and 3.6, which is why we discarded all samples with C/N ratios >3.6 (DeNiro 1985; Ambrose 1990; van Klinken 1999; Grupe *et al.* 2003; Coltrain *et al.* 2004; Bösl *et al.* 2006). Depending on the study considered, the minimum yield of extracted collagen should lie between 0.5 and 2 wt% (DeNiro & Weiner 1988; Ambrose 1990; Ambrose & Norr 1993; van Klinken 1999; Dobberstein *et al.* 2009). Regarding the elemental contents, the acceptable ranges for well-preserved collagen are 11–16 wt% for nitrogen and 35±9 wt% for carbon (van Klinken 1999).

Statistics

Statistical calculations were carried out with R studio (version R-4.2.2). Shapiro–Wilk tests were used to check for normal distribution of data (Dytham 2011). For all analyses performed, a significance level of 0.05 was chosen.

Stable Isotope Bayesian Ellipses in R (SIBER) modelling

The determination of isotopic niche widths of the different analysed animal taxa was performed using the Stable Isotope Bayesian Ellipses in R (SIBER) package (Jackson *et al.* 2011). This method is based on the calculation of two-variate ellipses and substitutes the previously common use of convex hulls, which were dependent on the sample size (Laymann *et al.* 2007; Jackson *et al.* 2011). The estimates of ellipses using a Bayesian approach provide a robust comparison between data sets with different sample sizes and therefore allow a direct comparison of isotopic niches in different communities (Jackson *et al.* 2011). We determined the convex hulls, that is the total area (TA) and the standard ellipse area (SEA, in ‰^{2}) and the standard ellipse area corrected by sample size (SEAc) of the taxa represented by $n \geq 3$. Our calculation of the SEA using a Bayesian probability estimation includes 40% of all potential specimens that would fit into the respective niches.

Climate modelling

The climate data presented here have been obtained from a terrestrial climate dataset for the past 60 000 years (Armstrong *et al.* 2019). The dataset was constructed from 42 discrete snapshot simulations utilizing a coupled general climate model, which were subsequently splined to a monthly time series for the entire period. The individual snapshot simulations were forced with well-constrained variations in orbital parameters, greenhouse gases and ice sheets for the respective time periods. Finally, the authors conducted a downscaling process via bilinear interpolation to a spatial grid of 0.5° resolution, incorporating bias correction for temperature and precipitation based on the Climate Research Unit (CRU CL v2.0) observational dataset from the University of East Anglia (New *et al.* 2002). Further technical details and information on the methodology employed in the creation of the climate dataset can be found in the original source (Armstrong *et al.* 2019). In this study, we employed monthly data for temperature and precipitation to construct mean annual temperature (MAAT) and mean annual precipitation sum (MAP) maps for snapshots representing a 100-year mean climate state at 1000-year intervals, with a reference point at 20, 19, 18 and 17 cal. ka BP. Furthermore, we calculated areal means of annual MAAT and MAP with varying running means to illustrate the decadal (10-year running mean), standard reference (30-year running mean) and centennial climate (100-year) variability. The time series are calculated over a rectangular box with boundaries at 20°E–45°E and 40°N–56°N. Finally, the permafrost boundaries were determined based on the MAAT thresholds for the coldest (18.4 cal. ka BP) and warmest (18.15 cal. ka BP) decades between 18.5 cal. ka BP and 18 cal. ka BP. These boundaries for continuous permafrost are defined as MAAT values below −7 °C, for discontinuous permafrost as MAAT values between −7 and −3 °C, and for sporadic permafrost as MAAT values between −3 and −1 °C (Nolzen 1996).

Results

Preservation and purity of bone collagen

Based on the quality criterion considered, a total of 12 samples were either outside of the range of acceptable and sufficient collagen preservation or other chemical characteristics, such as nitrogen or carbon contents (wt %) were either too high or too low (Table 2). Therefore, they neither underwent further analysis nor were they included in the data evaluation and discussion.

Isotopic data of bone collagen

All stable isotope results are shown in Fig. 2. Shapiro–Wilk test showed that the data were normally distributed (δ^{13}C: $W = 0.93696$, $p > 0.05$; δ^{15}N: $W = 0.9542$, $p > 0.05$). Mammoth and bison exhibit the lowest δ^{13}C mean values that range from −20.9±0.1‰ to −21.2±0.1‰, respectively. A single specimen of the European herring gull has the highest δ^{13}C value of −18.4±0.04‰. Among the mammals, reindeer show the highest δ^{13}C mean value of −19.3±0.3‰ followed by arctic fox (−19.7±0.1‰), brown bear (−19.8±0.03‰) and hare (−20.2±0.1‰) that lie in between (Fig. 2). Both single specimens of aquatic birds, that is European herring gull and European shag, exhibit the highest δ^{15}N values of 10.1‰ and 9.4‰, respectively. Mammoth (7.2±0.1‰) and bison (6.0±0.2‰) have also high δ^{15}N mean values. Among the herbivores, hare exhibits the lowest δ^{15}N mean value of 1.6±0.5‰. However, a single mammoth bone specimen exhibits an equally low δ^{15}N value (1.3±0.1‰). Interestingly, arctic fox (4.7±0.1‰) has a similar mean value to reindeer (4.9±0.5‰) and brown bear (5.2±0.2‰) (Fig. 2).

SIBER analyses revealed the highest total area for mammoth (4.34‰^{2}) followed by arctic fox (0.77‰^{2}) and hare (0.02‰^{2}) (Fig. 3). The SEA of mammoth is 2.17‰^{2} and the SEAc 2.44‰^{2}. Arctic fox exhibits a SEA of 0.56‰^{2} and a SEAc of 0.70‰^{2}, whereas hare shows the smallest ellipses with a SEA of 0.03‰^{2} and, corrected for sample size, a SEAc of 0.07‰^{2}.

Climatic development between 20 and 17 cal. ka BP

For the period considered herein, between 20 and 17 cal. ka BP, there is a slight increase in temperature towards 17 cal. ka BP (Fig. 4A). The precipitation distribution pattern is comparatively stable over time but shows a clear decreasing moisture gradient from west to east (Fig. 4B).

Modelled MAAT and MAP data and the influence on permafrost distribution also suggest local climate changes (Fig. 5). At the time of the occupation of Barmaky (19 cal. ka BP, Table 1), increased precipitation and temperature are evident (Figs 4, 5A), followed by a decrease between 18.6 and 18.4 cal. ka BP and another increase at approximately 17.8 cal. ka BP. A minor increase occurred in the precipitation pattern around 18.2 cal. ka BP (Fig. 5A). For the period from 19.3 to 17.3 cal. ka BP, the MAAT centennial average ranges

Table 2. List of chemical results of the analysed material. Given are the carbon and nitrogen composition, the C/N ratio, the weight percentage (wt%) of the collagen yield and the number of analyses per specimen (*n*). Samples marked with asterisk indicate values outside the range of well-preserved collagen and are thus not discussed any further due to their anomalous chemical composition; n.d. means ‘not determined’.

Sample ID	Species	C (%)	N (%)	C/N atomic	Yield (wt%)	*n*
N 114*	*Bison* sp.	44.2	10.8	4.8	2.3	2
ID 411*	*Bison* sp.	22.4	7.7	3.4	0.6	3
N 115	*Bison* sp.	36.2	13.3	3.2	0.6	3
ID 582*	*Bison* sp.	28.6	10.2	3.3	0.8	3
ID 238*	*Equus* sp.	12.1	4	3.5	0.7	3
ID 530	*Larus argentatus*	35.6	13.1	3.2	2.1	3
ID 196*	*Lepus* sp.	16.8	5.8	3.4	0.9	3
ID 181	*Lepus* sp.	32.9	11.6	3.3	5.6	3
N 177	*Lepus* sp.	36.6	13.5	3.2	2.2	3
ID 361	*Lepus* sp.	34.4	12.7	3.2	3.9	3
ID 11*	*Mammuthus primigenius*	15.6	5.2	3.5	1.2	3
N 113*	*Mammuthus primigenius*	25	8.9	3.3	4.4	3
N 11*	*Mammuthus primigenius*	21.5	7.3	3.4	1.6	3
N 119*	*Mammuthus primigenius*	76.9	2.7	33.2	2.8	3
N 121	*Mammuthus primigenius*	43.2	16.2	3.1	3.9	3
N 20	*Mammuthus primigenius*	33.4	11.2	3.5	n.d.	1
N 10	*Mammuthus primigenius*	40.9	14.8	3.2	2.8	3
N 13	*Mammuthus primigenius*	40.9	14.2	3.4	5.1	1
N 14	*Mammuthus primigenius*	41.6	14.9	3.3	3.8	2
N 16	*Mammuthus primigenius*	32.9	11.8	3.3	4.5	3
N 21	*Mammuthus primigenius*	38	13.8	3.2	7.4	3
ID 8	*Mammuthus primigenius*	37.1	13.4	3.2	3.1	3
ID 10	*Mammuthus primigenius*	39.5	14.4	3.2	2.8	3
ID 214	*Mammuthus primigenius*	38.2	13.8	3.2	1.6	3
ID 357	*Phalacrocorax aristotelis*	31.8	11.2	3.3	1.1	1
ID 222*	*Rangifer tarandus*	8.6	3	3.4	1.1	3
ID 416*	*Rangifer tarandus*	27	9.2	3.4	0.5	2
ID 513	*Rangifer tarandus*	39.4	14.6	3.1	4.6	3
ID 330	*Rangifer tarandus*	41	15.3	3.1	9	3
N 64	*Ursus arctos*	39.2	14.6	3.1	2.7	3
ID 3*	*Vulpes lagopus*	62.7	22.1	3.3	5.5	2
N 22	*Vulpes lagopus*	38.6	13.7	3.3	n.d.	2
N 112	*Vulpes lagopus*	40.1	13.9	3.4	n.d.	1
ID 273	*Vulpes lagopus*	36.2	13.1	3.2	2.6	3
ID 187-191	*Vulpes lagopus*	38.9	14	3.2	3.8	3
ID 367	*Vulpes lagopus*	41.7	15.5	3.1	5.6	3
ID 512	*Vulpes lagopus*	36.7	13.6	3.1	2	3

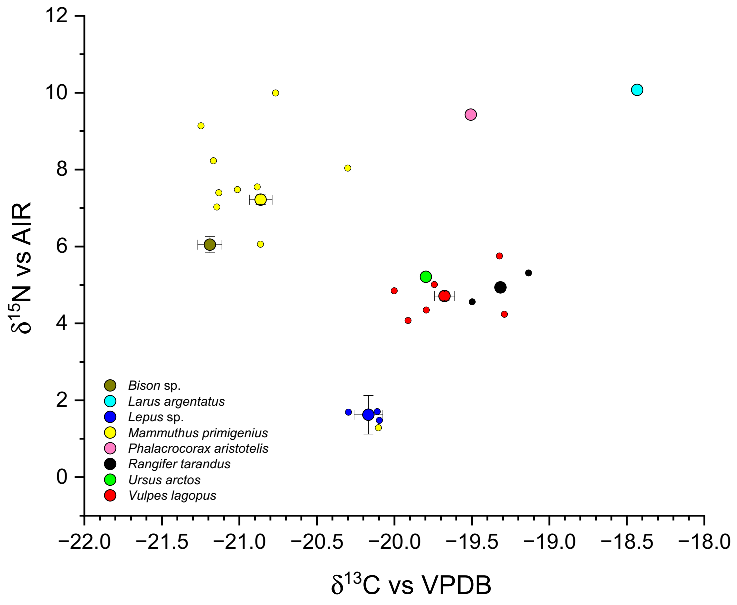
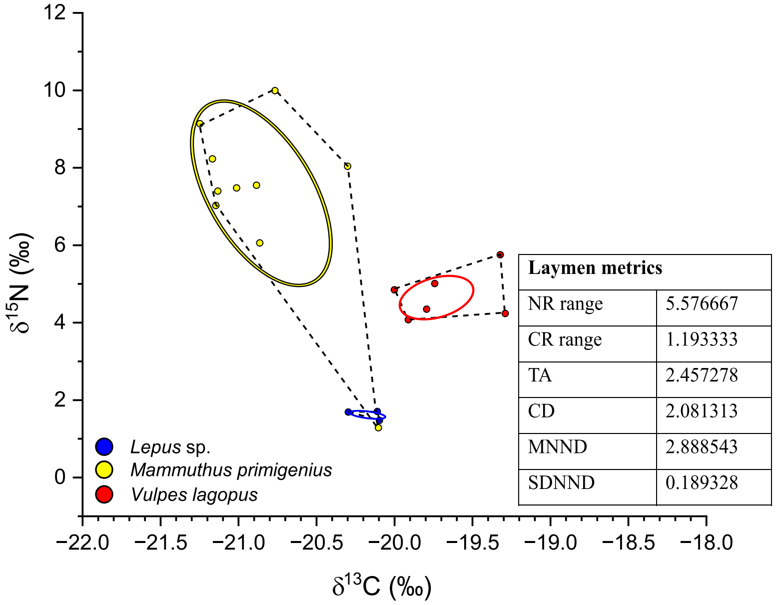


Fig. 2. Nitrogen vs. carbon stable isotope values of bone collagen from the Upper Palaeolithic site Barmaky. Mean values are represented as big circles, and whiskers represent the respective standard deviations. Small symbols indicate individual (multiple) measurements.



Laymen metrics	
NR range	5.576667
CR range	1.193333
TA	2.457278
CD	2.081313
MNND	2.888543
SDNND	0.189328

Fig. 3. Standard ellipse areas (SEAc) (solid ellipses) and convex hulls (dashed lines) of woolly mammoth, hare, and arctic fox. Abbreviations of Laymen metrics are as follows: CD = mean distance to centroid; CR = δ^{13}C range; MNND = mean nearest neighbour distance; NR = δ^{15}N range; SDNND = standard deviation of the nearest neighbour distance.

between approximately −4 and −3 °C, indicating discontinuous to sporadic permafrost in the area (Fig. 5B).

Discussion

Reconstruction of diet and habitat

The isotope-inferred food web of the Barmaky site reveals a niche partitioning that reflects differences in habitat and/or dietary behaviour (Stewart *et al.* 2003; Bocherens *et al.* 2015; Schwartz-Narbonne *et al.* 2015, 2019). The δ^{13}C clustering between mammoth and bison on the one side and reindeer on the other shows differences in terms of herbivorous dietary habits (Fig. 2). Reindeer, for instance, have the highest δ^{13}C values among the herbivorous taxa indicating the consumption of large amounts of lichen by this species (Finstad & Kielland 2011; Bocherens *et al.* 2015). Mammoths exhibit

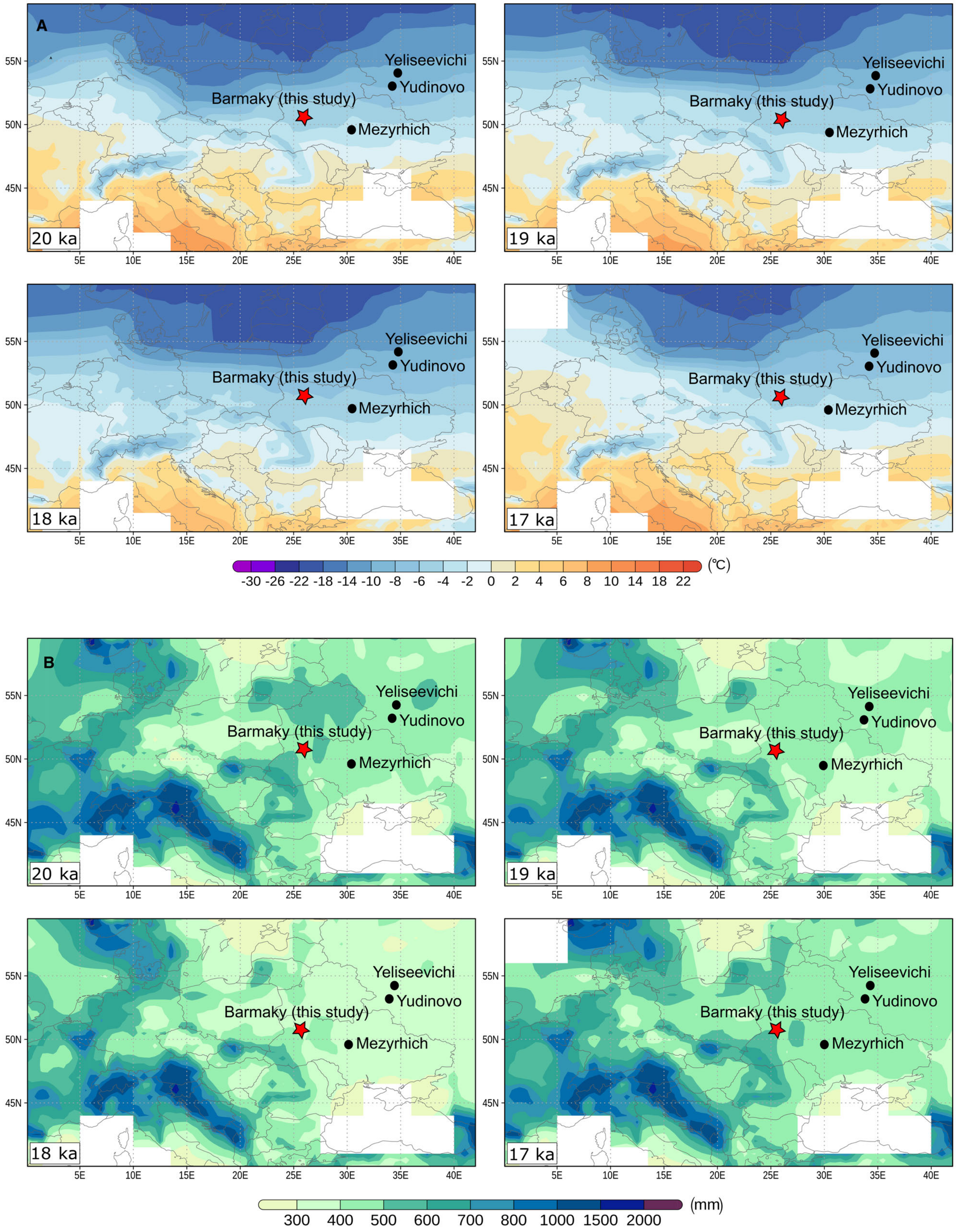


Fig. 4. Modelled climatic development. A. Mean annual air temperature (MAAT in °C). B. Mean annual precipitation sum (MAP in mm) from the time period 20–17 cal. ka BP in central Europe. White, spared parts represent large water bodies.

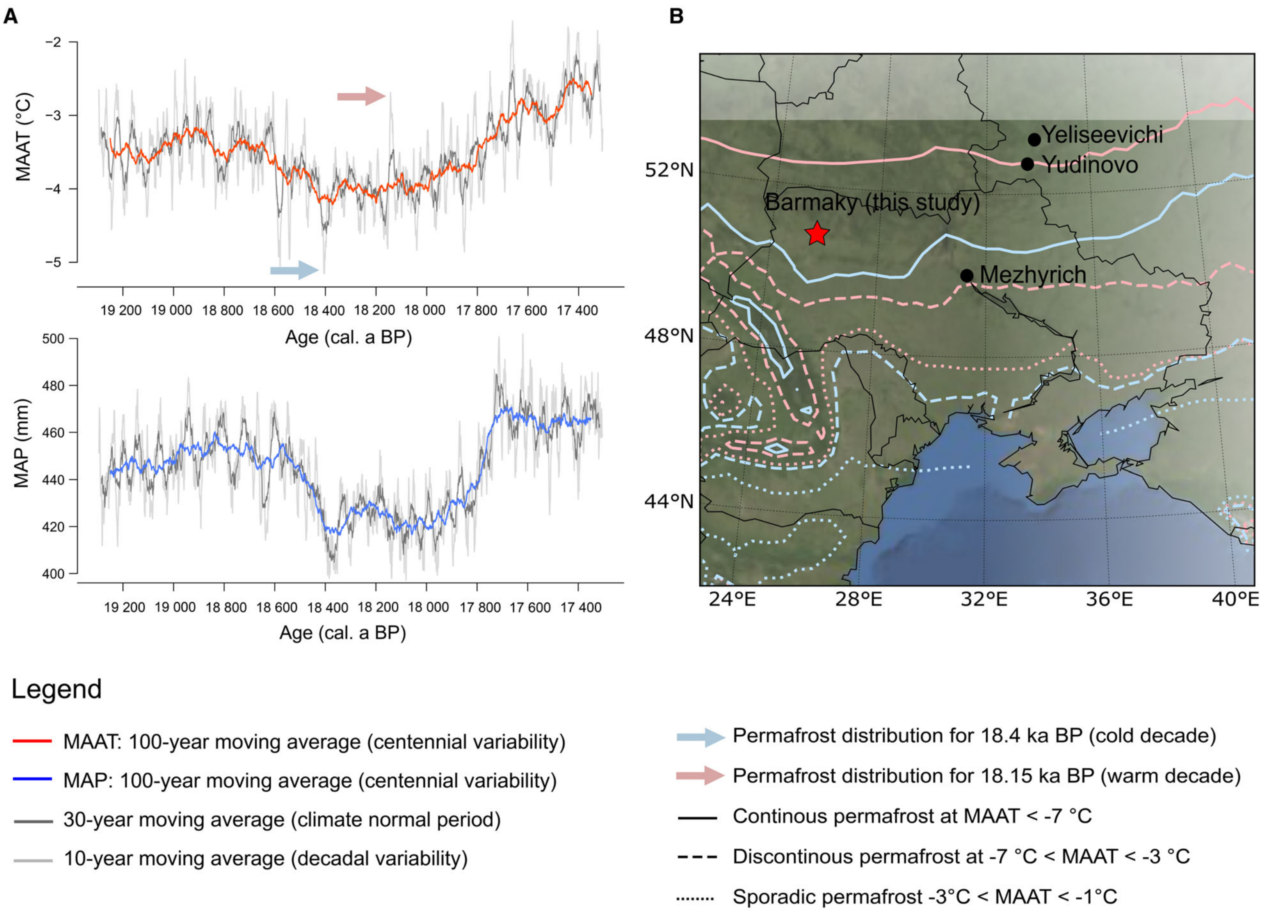


Fig. 5. A. Time series of mean annual temperature (MAAT, red, top) and mean annual precipitation sum (MAP, blue, bottom) for 19.3–17.3 cal. ka BP. MAAT and MAP are averaged over the area 20°E–45°E, 40°N–56°N. Blue and red arrows at 18.4 and 18.15 cal. ka BP indicate the times for permafrost distribution (10 year running mean) during a very cold and warm decade, respectively. B. Permafrost distribution for 18.4 cal. ka BP (blue, cold decade) and for 18.15 cal. ka BP (red, warm decade).

the lowest $\delta^{13}C$ values, which may either result from the consumption of grasses and sedges and/or the occupation of a more humid or riparian habitat (Guthrie 2001; Wooller *et al.* 2007; Drucker *et al.* 2008; Kirillova *et al.* 2016; Drucker 2022). A single data point of bison suggests a co-occupation of the mammoth niche. In general, the carbon isotope composition of plants is influenced by a variety of factors, such as humidity, CO_2 partial pressure, light intensity and temperature (Tieszen 1991; Bonafini *et al.* 2013). Whereas decreased $\delta^{13}C$ plant values result from reduced light, higher atmospheric CO_2 partial pressure and increased water availability, increased $\delta^{13}C$ plant values are the result of decreased temperatures, reduced water availability and a lower atmospheric CO_2 partial pressure (Pataki *et al.* 2003; Kohn 2010; Drucker 2022). Consequently, mammoths would have lived in more humid environments than, for example reindeer, feeding on the respective plant types. Shrubs, forbs and graminoids (grasses and sedges) exhibited the lowest $\delta^{13}C$ values in modern arctic realms (Fizet *et al.* 1995) and in combination with freshwater plants (Kirillova *et al.* 2016) have frequently been discussed as the main diet of mammoths in previous studies (e.g. Olivier 1982; Vereshchagin & Baryshnikov 1982; Tütken *et al.* 2007; Kosintsev *et al.* 2012; Metcalfe *et al.* 2013; Drucker 2022; Malikov *et al.* 2023). Based on tooth wear analyses, Eurasian mammoths show plasticity in diet between grazing and browsing (Rivals *et al.* 2010, 2012, 2015). They can be described as grass-dominated mixed feeders, whose wide dietary range indicates the adaptability of their feeding behaviour to the available plant resources (Rivals *et al.* 2012; Fig. 2). For instance, comparatively lower $\delta^{15}N$ values of mammoths from East Beringia compared to those from West Beringia were attributed to more mesophytic habitats and thus more ecologically diverse areas (Szpak *et al.* 2010; Malikov *et al.* 2023). Reindeer on the other hand would have lived in an edaphically drier habitat with less vegetation cover (Drucker *et al.* 2011) than mammoths. However, both taxa are also considered to be highly mobile animals, and thus, their isotopic values may just as well reflect isotopic signatures from geographically distinct environments (Britton 2010; Britton *et al.* 2011; Wooller *et al.* 2021). Hares exhibit an intermediate isotopic position between mammoths and reindeer and most probably reflect local site conditions as hares are non-migratory animals feeding mostly on herbs. Interestingly, arctic fox and brown bear do not show niche partitioning but rather share an isotopic niche. However, the brown bear is only represented by a single data point and therefore should be considered with caution. For a carnivorous species, arctic fox exhibits relatively low δ^{15}N values and is on the same isotopic level as reindeer and brown bear, the latter, at least during late Pleniglacial conditions, considered an omnivorous species (Matheus 1995; Hofreiter *et al.* 2004; Drucker *et al.* 2018). As foxes are often described as generalist feeders, their decreased δ^{15}N values may be the result of a diet based on micromammals with low δ^{15}N values, carrion, or an omnivorous diet (Baumann *et al.* 2020; Baumann 2023). In our study, when applying a linear dietary model, arctic foxes could have fed on the local hares as the collagen of foxes is enriched by about 3‰ in ^{15}N and by about 1‰ in ^{13}C compared to hares. The high δ^{15}N values of the single bird specimens most probably result from their limnic and/or marine feeding habits (Schoeninger & DeNiro 1984) and furthermore could also indicate migratory behaviour. At the same time, they also exhibit the highest δ^{13}C values. Except for the two bird taxa, which exhibit the highest δ^{15}N values of all animals investigated, the δ^{15}N values of mammoths are highest, even higher than those of the arctic fox (4.7±0.1‰). Exceptionally high δ^{15}N values in mammoths are a common phenomenon throughout Eurasia and the so-called mammoth steppe (Bocherens *et al.* 1994, 1997, 2001, 2011, 2015; Iacumin *et al.* 2000, 2010; Fox-Dobbs *et al.* 2008; Drucker *et al.* 2015; Reiss *et al.* 2023) and partly from MIS 2 (Drucker *et al.* 2003, 2018). The high δ^{15}N has been interpreted as the result of distinct dietary habits and the occupation of a special ecological niche where mammoth dung could have fertilized soils and plants (McKendrigk *et al.* 1980; Fraser *et al.* 2011; Drucker 2022). Coprophagy in mammoths could be another reason for high δ^{15}N values (van Geel *et al.* 2011; Metcalfe *et al.* 2013). The high variability in δ^{15}N values and large niche breadth of mammoths, as indicated by their SEAc (Fig. 3), however, could also be the consequence of individual mobility behaviour in geographically and climatically different regions. Individual δ^{15}N deviations, such as those seen in the Barmaky food web (Figs 3, 4), are a possible consequence of mobility behaviour or of feeding outside the isotopic niche (Drucker *et al.* 2018) or simply represent mammoths that lived predominantly in regions with isotopic signatures different from those of their death sites. In conclusion, the variability in δ^{15}N values of mammoths could be explained by their mobility behaviour, with high δ^{15}N values indicating non-local individuals and low δ^{15}N values pointing to individuals of more local origin. Interestingly, only one mammoth individual in the Barmaky record exhibits a similar isotopic composition as the sedentary hares. This indicates that this individual could have predominantly stayed around its death place, while most others may have stayed elsewhere for the ≥10 year turnover time of their bone collagen (Drucker 2022).

Palaeoenvironmental changes and the temporal and spatial variation of mammoth δ^{15}N

High δ^{15}N values in mammoths are a typical phenomenon for Late Pleistocene mammoth steppe populations (e.g. Bocherens *et al.* 1994, 1997, 2001, 2011, 2015; Iacumin *et al.* 2000, 2010; Fox-Dobbs *et al.* 2008) and are also partly evidenced for central Europe (Iacumin *et al.* 2000; Bocherens *et al.* 2015; Drucker *et al.* 2017, 2018) and the studied area (20°E–45°E, 40°N–56°N), including the Epigravettian sites Barmaky (this study) and Yudinovo (Iacumin *et al.* 2000; Drucker *et al.* 2018; Fig. 6). In contrast, exceptionally low δ^{15}N values were found in the mammoths from Mezhyrich, while the mammoths from Yeliseevichi had intermediate δ^{15}N values (Fig. 6B; Iacumin *et al.* 2000; Drucker *et al.* 2018). This could indicate

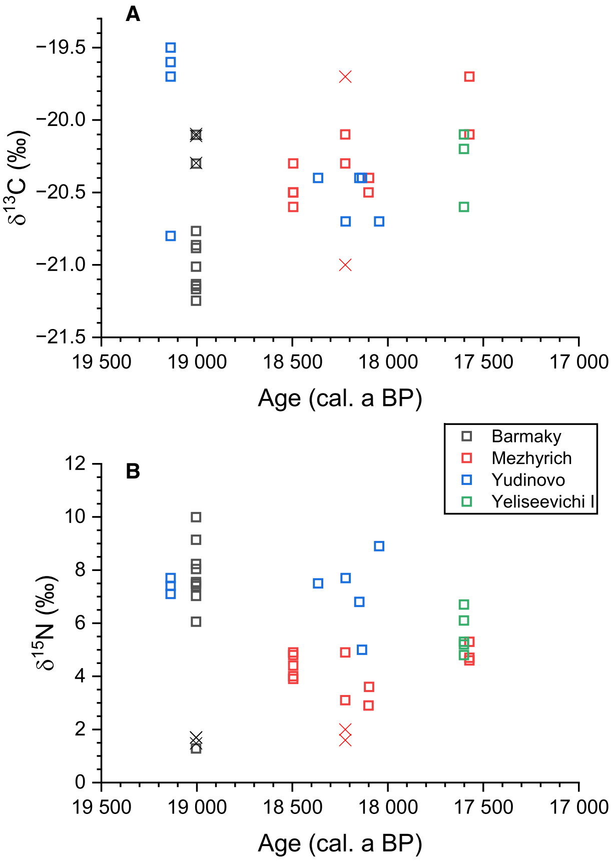


Fig. 6. Mammoth (open boxes) and hare (crosses) collagen isotope data from different Epigravettian sites in the East European Plain vs. age. A. δ^{13}C of bone collagen. B. δ^{15}N of bone collagen. Isotope values from Barmaky (this study) are compared to Yudinovo (Iacumin *et al.* 2000; Drucker *et al.* 2018), Mezhyrich (Iacumin *et al.* 2000; Drucker *et al.* 2014) and Yeliseevichi (Iacumin *et al.* 2000).

the loss of their specialized niche, as lower-than-usual δ^{15}N values in mammoth bone collagen indicate changes in the isotopic baseline due to changing environmental conditions (Drucker *et al.* 2018; Drucker 2022). A decline of isotopic niches from the late MIS 3 to the LGM is expressed by a drastic shift of δ^{15}N values at Lower Austrian sites (Reiss *et al.* 2023) and was caused by the climate deterioration during the long cooling phase of Greenland Stadial 3 (GS-3). At the site of Kammern-Grubgraben (24–20 cal. ka BP) in Lower Austria, this decline in niches was most pronounced in the δ^{15}N signature of mammoths (δ^{15}N of mammoth: 2.5±1.5‰), which, after the collapse of their specific niche, clustered in the same group as horses and hare. A decline in the mammoth niche has also been postulated for the Epigravettian site of Mezhyrich in the East European Plain (Drucker *et al.* 2018). At this site, mammoths also exhibited unusually low δ^{15}N values, which corresponded to those of the associated hares (Fig. 6B). This is in contrast to the Barmaky site, where the δ^{15}N values of mammoth and hare differ from each other with one exception. As an alternative explanation to the mammoth niche hypothesis, we suggest that the mammoths of Mezhyrich were killed in the vicinity of their main area of residence, whereas the mammoths of Barmaky spent most of their lives elsewhere than where they died. This may imply that the δ^{15}N baseline, which is determined by the δ^{15}N signature of the soil, was higher in the main residence area of the Barmaky mammoths than at their place of death. The δ^{15}N values of soils are controlled by temperature and precipitation in such a way that lower precipitation and/or higher temperatures lead to higher δ^{15}N values (Amundson *et al.* 2003). In summary, small-scale spatial changes in local hydrological and temperature gradients (Fig. 4) are a possible cause for δ^{15}N variability of the eastern European mammoths.

On a longer temporal scale, the sites have different climatic settings according to model results (Fig. 5). For instance, the site Mezhyrich was always located outside of the area of continuous permafrost, while the largely contemporaneous Yudinovo site (Iacumin *et al.* 2000; Drucker *et al.* 2018), located about 370 km further northeast, was always within the area of continuous permafrost (Fig. 5B). Such climatic differences should be reflected in the δ^{15}N values, but clearly more studies using more complete food webs are needed to substantiate this.

Conclusions

We analysed the food web of the Epigravettian site Barmaky, compared δ^{13}C and δ^{15}N of mammoth collagen to those of other Epigravettian sites in the East European Plain, and linked the results to modelled climate data from this specific area and period.

The Barmaky food web shows a characteristic structure with differences in the trophic ecology between herbivores, carnivores, and marine birds. A δ^{13}C clustering between the herbivorous species hare and mammoth on the one hand and reindeer on the other hand indicates a niche partitioning between both herbivorous groups associated with differences in diet and habitats along a local moisture gradient.

Mammoth collagen from our study shows high nitrogen isotope values, which partly agree with the regional sites Yudinovo and Yeliseevichi, but not with Mezhyrich, with the exception of a single outlier from Barmaky. Comparison with sedentary hares from Barmaky and Mezhyrich suggests that the mammoths from Mezhyrich are consistent with the local isotopic signature, whereas the mammoths from Barmaky diverge from the local herbivore signature and may have spent most of their lives away from their place of death.

The isotopic niche widths of the SIBER analyses indicate greater habitat diversity and an overlap with the hare's niche for mammoths at Barmaky, which also underlines their potential migratory behaviour. Even though the migratory behaviour of mammoths is very likely, it cannot be clarified with δ^{15}N and δ^{13}C analyses alone but should be complemented by using other isotopic techniques such as ^{87}Sr/^{86}Sr in future studies.

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Author contributions. – LR and LS carried out collagen extractions. LR evaluated and visualized the isotope data and wrote the original draft. AM, CM, VC, KP and PL contributed substantially to the text. KP taxonomically identified the study material. CM carried out stable isotope analyses. PL carried out climate model data analysis and visualized the climate model results. AM and VC initially designed the study and provided the study material. All authors reviewed and approved the manuscript.

Data availability statement. – All relevant data are available in Tables 1, 2, S1, S2. Detailed information on how to obtain the climate data from Armstrong *et al.* (2019) can be found at https://www.paleo.bristol.ac.uk/ummodel/scripts/papers/Armstrong_et_al_2019.html.

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Supporting Information

Additional Supporting Information to this article is available at http://www.boreas.dk.

Table S1. Previously published radiocarbon dates for Barmaky, Mezhyrich, Yudinovo and Yeliseevichi.

All radiocarbon dates were recalibrated with the IntCal20 curve (Reimer *et al.* 2020). Probability and reliability are given for weighted means with 1 = reliable stratigraphic position; 2 = the origin of the sample is not documented; 3 = unreliable sample; 4 = supposed to be reliable stratigraphic position; layers definition proposed by Khlopachev (2019), 5 = SPb-1768; two different dates are mentioned under this lab number: 12 950±140 and 12 943±100; 6 = ЛЕ-3303; also mentioned as the lower layer with the date 13 380±160 (Khlopachev 2019); 7 = ЛЕ-3302; also mentioned as the lower layer with the date 14 980±110 (Khlopachev 2019); 8 = ЛЕ-3401; also mentioned as the lower layer with the date 12 980±320 (Khlopachev 2019). Weighted mean dates are printed in bold. Coloured rows indicate the connection between individual dates and isotope data of mammoth with blue = directly dated bone; pink = directly dated tooth/tusk; red = dates in Drucker *et al.* (2018) not connected to nitrogen and carbon stable isotopes of mammoth, and green = nitrogen and carbon stable isotopes of mammoth not connected to individual dates.

Table S2. Summary of all samples analysed.