



PARAMETERS OF RANGE SIZE DIVERSITY OF EUROPEAN MAMMALS IN THE EEM INTERGLACIAL (MIS 5E) AND GS 2.1 STADIAL (MIS 2)

ANDREY YU. PUZACHENKO

Institute of Geography RAS, Staromonetnyi lane. 29, 119017, Moscow, Russia; e-mail: andreypuzak@gmail.com.

Puzachenko, A. Yu. (2024): Parameters of range size diversity of European mammals in the Eem interglacial (MIS 5e) and GS 2.1 stadial (MIS 2). – *Fossil Imprint*, 80(2): 401–423, Praha. ISSN 2533-4050 (print), ISSN 2533-4069 (on-line).

Abstract: Information on mammal remains from 665 sites/localities was used to estimate the range of size diversity of European species in the Eem interglacial (MIS 5e) and the GS 2.1 stadial (MIS 2). Review of faunal composition and comparison of the rank distributions of the occurrence of species remains across sites allowed determination of the composition of groups of typical and indicator species for each of the time intervals. Entropy, dominance index and self-organization index were calculated from the rank distributions of the occurrence of large, small and medium-sized herbivorous, carnivorous and representatives of the order Eulipotyphla. The parameters of the non-linear function describing the increase in the average number of species that can be found in 1, 2, 3, etc. randomly selected sites were calculated. The relationship between the parameters of these functions and between them and species richness is shown. The paper discusses hypotheses about the relationship between parameter variations and changes in range size ratios in different mammal groups during the Eem interglacial and at the end of the Last Glacial Maximum.

Key words: Europe, Mammalia, Late Pleistocene, Eem interglacial, GS 2.1, species ranges diversity

Received: June 23, 2024 | Accepted: September 20, 2024 | Issued: December 20, 2024

Zoobank: <http://zoobank.org/urn:lsid:zoobank.org:pub:27569C57-D54D-4543-AB3F-35D45B325873>

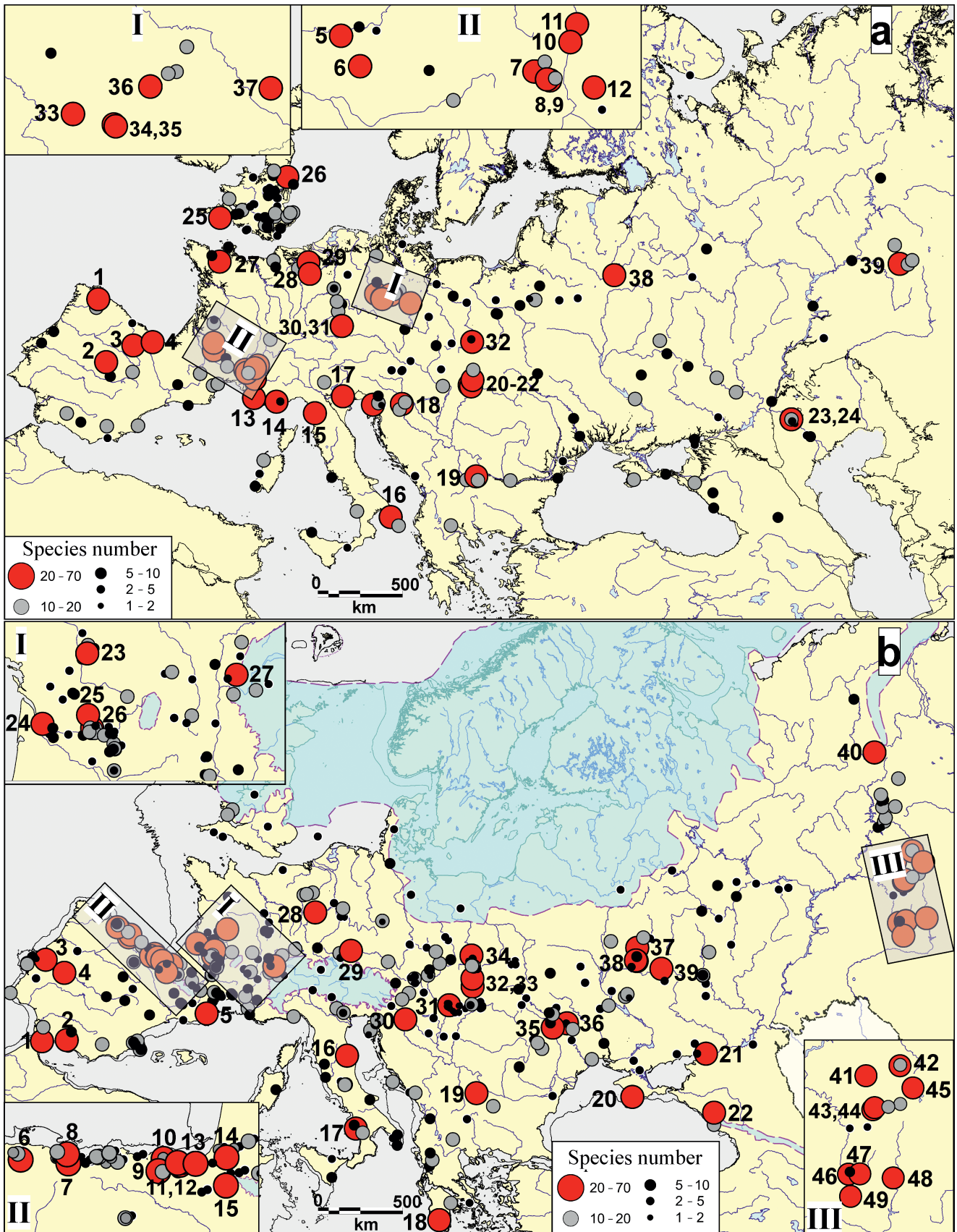
Introduction

The problem of predicting the evolution of modern ecosystems in the context of changing planetary physical conditions and anthropogenic impacts in part is caused by the uncertainty in our understanding of the general mechanisms of ecosystem response in the past. Species richness and derived biodiversity variables are fundamental parameters of the state of ecosystems, reflecting the complexity of their organization and their relative resilience to fluctuations in environmental conditions (Butchart et al. 2010, Barnosky et al. 2012). The study of fossil mammalian faunas allows reconstruction of evolutionary patterns of their composition and diversity in the past (Grayson et al. 1996, Hernández Fernández 2006, Semken et al. 2010, Kahlke 2014, López-García et al. 2016, Royer et al. 2016, Markova et al. 2019). The results of these studies provide a basis for understanding natural limits of mammalian adaptive capacity and for selecting qualitative and quantitative parameters that reflect the response of faunas to historical changes in environmental conditions. At the same time, researchers overlook the fact that the transformation of ecosystems is accompanied by changes in the ranges of the species that make them up. This is not just a matter of range reduction or expansion, but also

of range subdivision, changes in the shape of boundaries, etc. Quantitative characteristics of the historical variability (diversity) of mammalian ranges at the level of faunas have still not been investigated thoroughly. This topic falls within the scope of palaeobiogeography.

As far as Europe is concerned, the material on the fossil mammalian fauna I have is most complete in the case of the Late Pleistocene (MIS 5 – MIS 2) (Markova et al. 2019, Puzachenko et al. 2021). At that time, the following climatic events took place in Europe: the end of the Riss glaciation (= Wolston, Saale, Dnieper) and the beginning of the last Riss-Würm interglacial (= Ipswich, Eem, Mikulino), with an optimum of about 126 thousand years ago (MIS 5e); the last Würm glacial cycle (= Devens, Veichsel, Valdai (MIS 5d – MIS 2, 109.0–11.7 ka BP), with the Last Glacial Maximum (LGM) at 26–20 ka BP, which ended with the beginning of the Holocene interglacial. The most contrasting conditions for European Late Pleistocene ecosystems were therefore during the Eem interglacial and the LGM.

This work is a continuation of the studies on Pleistocene mammal fauna of Europe, carried out by the authors with colleagues over the last two decades (Markova and Puzachenko 2018, 2021, Puzachenko et al. 2021, 2022, Puzachenko and Markova 2019, 2020, 2023; and the



Text-fig. 1. European sites dated to Eemian interglacial (MIS 5e; a) or Greenland Stadial 2.1 (MIS 2; b) and list of sites with 20 or more species. a: 1 – Valdavara 3 (Vaquero et al. 2018), 2 – Villacastín (Arribas 1994a, b), 3 – Galería de las Estatuas (Arsuaga et al. 2017, Demuro et al. 2019), 4 – Lezetxiki, level VII (Falguères et al. 2005, Garcia-Ibaibarriaga et al. 2018), 5 – Vaufrey, Grotte XIV (Brugal and Jaubert 1991, Hernandez et al. 2014), 6 – Coudoulous II, couche 7 (Brugal et al. 2001, Thery-Parisot et al. 2008), 7 – Abri-des-Pêcheurs (Moncel 2010, Moncel et al. 2015), 8 – Orgnac 3, level 5a (Hanquet 2011), 9 – Baume Flandin (Moncel 2005, Moncel et al. 2008), 10 – Payre (Daujeard et al. 2011, Foury et al. 2016), 11 – Baume Moula-Guercy (Crégut-Bonnoure et al. 2010, Valensi et al. 2012), 12 – Grand Abri aux Puces (Slimak et al. 2010), 13 – Cèdres (Defleur et al. 1990, Valladas et al. 1999), 14 – Lazaret, complex E (Valensi and Abbassi 1998, Valensi and Psathi 2004, Michle et al. 2009), 15 – Montignoso (Rustioni et al. 1999),

references in them). Previously, the authors conducted studies on the evolution of mammalian faunal assemblage composition on the scale of particular geographical regions of Europe, and at varying time intervals of the Middle – Late Pleistocene and Holocene. In this study, I show that it is possible to obtain quantitative estimates of important parameters of mammalian diversity across the European subcontinent, despite the inherent uncertainties that typically accompany palaeontological data.

To demonstrate this possibility, a number of diversity parameters of species' range size were estimated and compared for the Eem interglacial and LGM mammal faunas in Europe, using only data on species occurrences. The next aim of the work was to select the most informative quantitative parameters characterizing the variation in the spatial distribution of species at the chosen temporal scales, and to formulate hypotheses in a biogeographical perspective.

Regional setting and time intervals

The study area covers the European sub-continent (Text-fig. 1), from the Atlantic coast in the west to the Urals in the northeast. The eastern border of the sub-continent conventionally draws along the Volga River. The southern border runs along the northern Caucasus, the Black Sea coast and further west along the Mediterranean coast to Gibraltar. It is the part of a temperate zone characterized by the west-east transition from maritime to temperate continental climate.

Harting (1875) first recognized the Eemian interglacial from boreholes near the town of Amersfoort, the

Netherlands, and named it after the local Eems River. In the parastratotype of the Eemian interglacial in the Amsterdam terminal section, it was dated by U-series to 118 ± 6.3 ka BP (Kukla et al. 2002). In the north of Eastern Europe, similar uranium-thorium dates were obtained for the Mikulino interglacial deposits studied in the Cheremoshnik key section (Upper Volga basin, Russia): $114.2 + 11.6/- 9.2$ ka BP and $115.5 + 15.8/- 11.6$ ka BP (Rusakov et al. 2015). In the south of Eastern Europe, a lagoon and marine sequence with Karangatian molluscs and small mammal fauna was described in the Eltigen section (eastern Crimea) and dated by $^{230}\text{Th}/\text{U}$ to 127 ± 8.9 ka BP (Cycle I) (Dodonov et al. 2000, Markova 2000). The North Greenland Eemian Ice Drilling Site provided the duration of the Eemian interglacial (130–115 ka BP) and the chronological position of its optimum (126 ka BP) (Dahl-Jensen et al. 2013). Thus, the interglacial condition correlates with the MIS 5e sub-stage. The mean annual air temperature was not probably different from today, or slightly higher, during the optimum period. The climate was probably wetter in the west, and drier in the east and northeast of Europe than today (Markova and Puzachenko 2018, Dabkowski and Limondin-Lozouet 2022).

Here and below are radiocarbon dates calibrated using OxCal 4.4 software and the IntCal20 calibration curve (Reimer et al. 2020). A gradual increase in the Scandinavian Ice Sheet from northwest to southwest, south, and southeast directions accompanied the transition to the LGM (~29–28 ka BP) from the onset of MIS 2 in Europe (Mix et al. 2001, Svendsen et al. 2004, Ehlers and Gibbard 2008, Velichko et al. 2011, Ehlers et al. 2013, Batchelor et al. 2019). The climate situation in Europe in the LGM was markedly different from today, with distinct regional features (Bush and Philander 1999, Ludwig et al. 2016, Višnjević et

16 – Avetrana (Pandolfi et al. 2013, Salari et al. 2019, Kotsakis et al. 2020), 17 – Caverna degli Orsi (Berto and Rubinato 2013), 18 – Krapina (Döppes et al. 2008, Musil 2010a), 19 – Kozarnika (Popov and Marinska 2007, Tillier et al. 2017), 20 – Horváti-lik (Pazonyi and Kordos 2004), 21 – Por-lyuk (Jánossy 1986, Luzzi et al. 2019), 22 – Kalman Lambrecht Cave (Jánossy 1964, 1986, Musil 2010a), 23 – Cherny Yar (Titov and Golovachev 2017, Golovachev and Titov 2019), 24 – Bueraki 2 (Kirillova and Svitoch 1994), 25 – Joint Mitnor Cave (Sutcliffe 1960, Stuart 1986, Curren and Jacobi 2001), 26 – Kirkdale Cave (Boylan 1981, McFarlane and Ford 1998), 27 – Mont-Dol (Simonet and Monnier 1991, Monnier et al. 2016), 28 – Scladina, unit 5 (Cordy 1992, Abrams et al. 2014, Blain et al. 2014), 29 – Zemst (Germonpré 2003), 30 – Biedermann travertine (Dietrich and Berckhemer 1983), 31 – Biedermanhöhle, Stuttgart Untertürkheim (Wenzel 1998, Kolfshoten 2000), 32 – Bišnik Cave (Cyrek et al. 2010, Socha 2014), 33 – Burgtonna I–III (Kahlke 1995, Kolfshoten 2000), 34 – Taubach (Kahlke 1961, Heinrich and Jánossy 1977, Bratlund 1999), 35 – Weimar-Ehringsdorf (Kahlke 1958, Schäfer et al. 2007), 36 – Neumark-Nord 2/2 (Kolfshoten 2002, Kindler et al. 2020), 37 – Schönfeld (Kolfshoten 2000), 38 – Borisova Gora (San'ko and Motuzko 1991), 39 – Barsuchii Dol Cave (Kuzmin et al. 2017, Kosintsev et al. 2022). b: 1 – Gorham's Cave (Waechter 1951, Cooper 1996, Stringer et al. 2008), 2 – Boquete de Zafarraya (Lecervoisier 2003, Wood et al. 2013), 3 – Caldeirão (Povoas et al. 1992, Davis 2002, Zilhão et al. 2021), 4 – Maltravieso-Chimeneas (López-García et al. 2013, Bañuls-Cardona et al. 2014), 5 – L'Arbreda (Zilhão 2006, López-García et al. 2015), 6 – Cueva de las Hienas (Laplana et al. 2018, Jones et al. 2021), 7 – El Mirón (López-García et al. 2013), 8 – La Riera (Altuna 1986, Jones et al. 2020), 9 – Arlanpe (García-Ibaibarriaga et al. 2013, Alonso et al. 2013), 10 – Santimamiñe (Castaños 1984, Rofes et al. 2014), 11 – Amalda (Straus and Straus 1990), 12 – Urutiaga (Altuna 1972), 13 – Aitzbitarte III, IV (Altuna and Mariezkurrena 2011, Pemán 2011), 14 – Isturitz (Bouchud 1952, Costamagno et al. 2016), 15 – Zatoya (Almuzara and Maestu 2001), 16 – Grotta della Ferrovia (Ceregatti et al. 2023), 17 – Grotta della Serratura (Kotsakis et al. 2003), 18 – Kalamákia (Lecervoisier 2003, Harvati et al. 2013), 19 – Kozarnika (Guadelli et al. 2005, Popov and Marinska 2007), 20 – Suren-1 (Demidenko and Noiret 2012, this study), 21 – Kamennaya Balka 1, 2 (Baigusheva and Titov 2007, Agadzhanov 2009), 22 – Mezmaiskaya Cave (Baryshnikov et al. 1996), 23 – Taillis-des-Coteaux (Soler et al. 2007), 24 – Roc de Marcamps (Delpech 1983, Jürgensen et al. 2017), 25 – Combe Saunière I (Castel et al. 2006), 26 – Laugerie-Haute (Delpech 1983, 2012), 27 – Colombière (Hanquet 2011), 28 – Oetrange (Ferrant and Friant 1937, Fabre 2010), 29 – Spitzbubenhöhle (Königswald 1983, Stampfli 1983), 30 – Vindija (Miracle et al. 2010), 31 – Bivak (Jánossy et al. 1957, Jánossy 1986), 32 – Dzeravá skála (Horáček 2005, Musil 2010b), 33 – Oblazowa (Lorenz 2013, Nadachowski and Valde-Nowak 2015), 34 – Deszczowa (Stefaniak et al. 2009), 35 – Duruitoarea Veche (David and Pascor 2012), 36 – Cosăuți I (David and Pascor 2012), 37 – Yudinovo (Markova 1995, Germonpré et al. 2008), 38 – Novgorod-Siversky (Rekovets 1985), 39 – Byki 1, 7 (Chubur 2001, Akhmetgaleeva and Burova 2021, Markova and Puzachenko 2021), 40 – Medvezh'ya (Bachura and Kosintsev 2007), 41 – Bobylek (Razhev et al. 2005, Danukalova et al. 2020), 42 – Dyrovaty Kamen (Sadykova 2002, Ulitko 2006), 43 – Prizhim 2 (Smirnov et al. 1990), 44 – Serpievskaya 1 (Danukalova and Yakovlev 2006), 45 – Ustinovo (Smirnov et al. 1990), 46 – Imanay Cave (Fadeeva et al. 2023), 47 – Kul'jurt-Tamak (Nekhoroshev and Girya 2004, Yakovlev 2014), 48 – Syrtinskaya (Kuzmina 2009), 49 – Maksyutovo (Danukalova et al. 2011).

al. 2020). The annual mean surface temperature was lower than at present by ~8.5 °C. There was probably a strong west-east temperature gradient. In the west of Europe, zonal atmospheric circulation prevailed, as it does today. In the south of Europe, western transport and cyclonic movements were more frequent, and in Central and Eastern Europe, southern and eastern air masses predominated. The rainfall was higher in Western Europe, especially in the southwest, compared to today (Lofverstrom 2020).

The time interval considered here coincides with the Greenland Stadial GS 2.1 (2.1c–2.1b) (Rasmussen et al. 2014) and the R1–R2 retreat phases of the Scandinavian Ice Sheet (Boulton et al. 2001), i.e., ~22.4–17.0 ka BP. The timing of the coldest interval and the position of the temperature minimum in the European region differs, depending on the proxy data used: the NGRIP oxygen isotope ($\delta^{18}\text{O}$) series (Rasmussen et al. 2014) or the marine benthic $\delta^{18}\text{O}$ series (Lisiecki and Raymo 2005, Lisiecki and Stern 2016). In the first case, the minimum falls in the GS 3 interval, 27.54–23.34 ka b2k (= before 2,000 A.D.; Vinther et al. 2006), but in the second one, it falls in the range between 22 and 17 ka BP or even between 20 and 18 ka BP. The maximum cooling may have occurred sometime after the maximum expansion of the ice cover (Clark et al. 2009), which was also asynchronous along different parts of the Scandinavian Ice Sheet boarder (Boulton et al. 2001, Demidov et al. 2006, Batchelor et al. 2019, Makkaveyev et al. 2020).

Material and methods

This study used data for mammal species from 665 sites/localities confidently dated to either the MIS 5e interglacial or the GS 2.1 stadial by various methods (Text-fig. 1, Tab. 1). A full description of the database is provided in the

Table 1. Description of the dataset used in this study (see Text-fig. 1).

Group of mammal	Number of sites/localities		
	MIS 5e	GS 2.1	Total
Total	222	442	665
Large herbivorous^a	191	411	602
Carnivorous^b	137	258	396
Small herbivorous^c	127	229	356
Eulipotyphla	56	88	144
Microchiroptera	12	15	27
Number of sites with 20 or more species	39	49	88

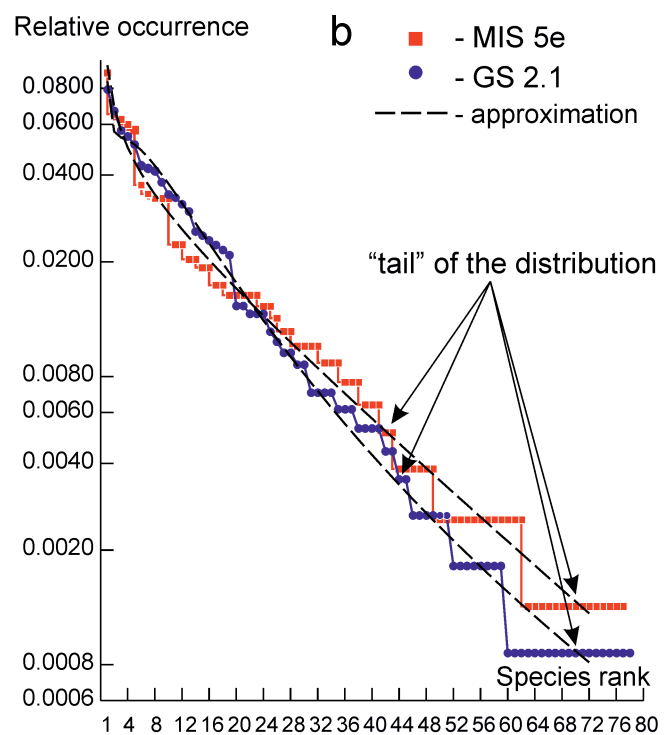
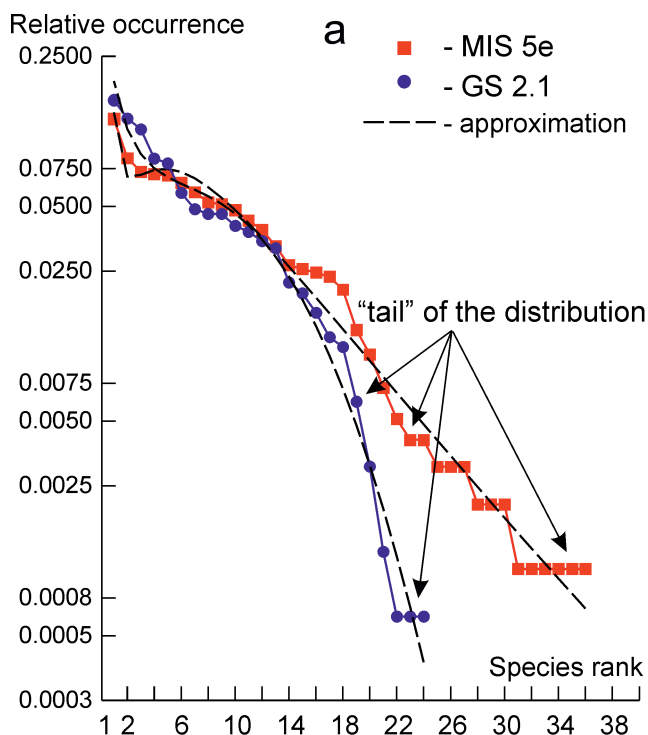
^aPrimates, Elephantidae, Camelidae, Rhinocerotidae, Suidae, Equidae, Hippopotamidae, Bovidae, Cervidae

^bCanidae, Ursidae, Hyaenidae, Felidae, Mustelidae

^cLagomorpha, Rodentia

electronic Supplementary Data. For the last interstadial, some uncertainty in dating is accepted, such as dates based on the composition of faunal assemblages, or significant variations in dates obtained by instrumental methods. Therefore, local faunas that conventionally assigned to the “early-first half” of MIS 5 were also included in the analysis.

Only about 13 % of sites contained information on 20 or more taxa, i.e., well-characterized local faunas. Microchiroptera were observed in only 4 % of the localities, so this group was excluded from the analysis. It is worth noting that there is a rather obvious disproportion in the occurrence of remains of representatives of the “large herbivorous” and “carnivorous” groups, which I conditionally identify here for convenience, in comparison with “small and medium-sized mammals” (Lagomorpha, Rodentia, and Eulipotyphla).



Text-fig. 2. Rank distributions of relative occurrence of large (a) and small or medium-sized (b) herbivorous mammals in MIS 5e interglacial and GS 2.1 stadial in Europe.

I distinguished several groups of species: the most abundant (widespread) species, indicator species, rare and sporadic species (“singletons”) for the MIS 5e sub-stage or the GS 2.1 stadial. If species were recorded in both time intervals (MIS 5e or GS 2.1), a frequency of localities with the indicator species should be significantly different in one of them (at least more/less ± 1 standard deviation).

I used only the frequencies of localities where species occurred, and did not estimate the abundance of their remains. The distributions of the number of occurrences of species from different groups were analyzed. To do this, I ranked species by frequency of occurrence, from the most common to those recorded only once. The most common species has rank 1, followed by rank 2 and so on. This leads to a rank distribution (see example in Text-fig. 2).

The theoretical justification for the existence of rank distributions, including species abundance distributions as well as different models for their approximation, have been discussed for a long time (see the review of the problem in Magurran 2004, McGill et al. 2007). This study assumes that the within the identified groups, species occurrence is proportional to the size of their ranges in MIS 5e or GS 2.1. The presence of highly tolerant species with ranges covering most of the region under consideration are expressed by the high dominance of one or more first ranks of distribution. A flat ranking distribution indicates the dominance of species with medium-sized ranges relative to the total area of Europe, and long-tailed distributions – a significant proportion of species with small compact or fragmented small ranges: highly specialized species, with special environmental requirements, sub-regional endemics, critically endangered species or species whose main range is outside Europe.

A quantitative general assessment of the rank distribution properties listed can be obtained using traditional diversity indices: Simpson’s index of dominance (D) (Simpson 1949) calculated as

$$\left[\sum_i^{\text{SPN}} n_i (n_i - 1) \right] / N(N - 1)$$

(unbiased form); Shannon’s index (entropy) (H) (Shannon 1948):

$$- \sum_i^{\text{SPN}} n_i / N \log_2 n_i / N - (\text{SPN} - 1) / 2N$$

(unbiased form); redundancy or index of self-organization (R) – 1 – “equitability or Pielou’s evenness” = 1 – H / $\log_2(\text{SPN})$ (Shannon 1948, von Foerster 1960), where SPN is species number, n_i – number of localities with species i , N – total number of localities.

The Simpson’s dominance (D) reflects the contribution to the rank distribution of species with very wide ranges. The entropy quantifies the diversity of species’ range sizes and the contribution of species with small ranges. The index of self-organization ($0 \leq R \leq 1$) shows how far is the particular rank distribution from equal random continuous uniform distribution ($R = 0$), i.e., the hypothetical case where the ranges of all species are approximately equal. In general, R increases as the tail of the distribution lengthens and the first ranked species dominate.

I selected randomly the number of localities (LCN) from the sample, and calculated the number of detected species

(SPN) there. Let us accept the hypothesis that the number of species in Europe did not change significantly over the time intervals considered, i.e., was limited – “equilibrium/stationary” hypothesis. In this case, one can assume the existence of the relationship “species – localities number relationship” (SLR), which is close to the “species – sample number relationship” and “species – area relationship” or “species– area curve”, well known in island biogeography and community ecology in general (Lomolino 2001, Schiener 2003).

Examples of such curves for the mammalian fauna of the region of Central Europe at the end of MIS 3 (~38–29 ka BP) were previously showed in Puzachenko et al. (2022). A formula similar to Arrhenius’ power curve (Arrhenius 1921): $\text{SPN} = A(\text{LCN})^z$ best described the relationship between the mean number of species and the number of localities. Constant A is the average number of species per randomly selected locality, depending on average species richness within a geographical region. Formally, z characterizes the rate of accumulation (growth) of species richness, and in the log-transformed version of Arrhenius’ formula, it is the tangent of the slope angle of the line describing the growth of the number of species from the number of sites/localities. In our interpretation, constant z – is the parameter depending on the distribution of species ranges within a region. Its value is inversely related to the degree of range overlap, reaching a value of 1 in the hypothetical case where species ranges do not overlap. In the “equilibrium/stationary” hypothesis, both constants are at the same time parameters of the number of species ranges in a region (equal to species richness) and the distribution of their size, which in turn is related to the overlap of ranges in geographical space. In other words, they represent diversity invariants for the region under study over a fixed time interval.

I found out that usage of the traditional formula resulted in an underestimation of mean SPN for the LCN interval 2(3)–6(7). In other words, diversity accumulation showed significant non-linearity. Therefore, in addition to the Arrhenius model, I tested other variants of SLR models: Gleason model (Gleason 1925): $\text{SPN} = A + z \ln(\text{LCN})$; the logistic curve (Archibald 1949): $B/(A + \text{LCN}^{-z})$; the logarithmic-power model, which I introduced here empirically without rigorous mathematical justification: $\text{SPN} = A + B [\ln(\text{LCN})]^z$.

The dominance of the localities with remains of large and medium-sized mammal classes is due to generally weaker relative knowledge of micromammals (Tab. 1), so each group of mammals was studied separately. At the same time, there is a certain convention in the definition of these groups themselves, which could potentially introduce some bias into the results of the analysis. In addition, some of the almost unresolvable uncertainties associated with palaeoenvironmental reconstructions should be taken into account. Another source of uncertainty is uneven geographical distributions of occurrences. For example, the vast majority of locations in Central, Western and Southern Europe are associated with karst and mountainous areas, i.e., places where caves are often found. In contrast, on the plains, in Eastern Europe, the density of sites is much lower, but the absence of records within the presumed range of the species does not prove that the animals avoided these areas.

Table 2. List of the most abundant, indicator and some most rare and endemic species in Europe in the Eem interglacial (MIS 5e) and the GS 2.1 stadial (MIS 2).

Group of animals	Most abundant species		Indicator species		Some most rare and endemic species	
	MIS 5e	GS 2.1	MIS 5e	GS 2.1	MIS 5e	GS 2.1
Large herbivorous	<i>P. antiquus</i> , <i>E. ferus</i> , <i>C. elaphus</i> , <i>B. primigenius</i> , <i>Bison</i> sp.	<i>M. primigenius</i> , <i>E. ferus</i> , <i>R. tarandus</i> , <i>C. elaphus</i> , <i>B. priscus</i> , <i>Bison</i> sp.	<i>P. antiquus</i> , <i>M. intermedius</i> , <i>S. hemitoechus</i> , <i>S. kirchbergensis</i> , <i>H. amphibious</i> , <i>D. dama</i> , <i>M. giganteus</i>	<i>M. primigenius</i> , <i>E. ferus</i> , <i>O. moschatus</i> , <i>R. tarandus</i>	<i>S. hundsheimensis</i> , <i>H. penlandi</i> , <i>P. mnaidriensis</i> , <i>C. knoblochi</i> , <i>H. mediterraneus</i> , <i>R. pyrenaica</i> , <i>C. caucasica</i>	<i>P. cazioti</i> , <i>O. orientalis</i> , <i>C. caucasica</i>
Carnivorous	<i>C. lupus</i> , <i>V. vulpes</i> , <i>C. spelaea</i> , <i>U. arctos</i>	<i>C. lupus</i> , <i>V. vulpes</i> , <i>V. lagopus</i> , <i>U. arctos</i>	<i>C. spelaea</i> , <i>U. spelaeus</i> , <i>P. spelaea</i> , <i>U. rossicus</i> , <i>U. thibetanus</i>	<i>G. gulo</i> , <i>V. lagopus</i>	<i>A. majori</i> , <i>A. antiqua</i> , <i>M. foinea</i> , <i>M. zibellina</i>	<i>U. kudarensis</i> , <i>C. sardous</i> , <i>A. majori</i> , <i>L. latra</i>
Small herbivorous	<i>A. sylvaticus</i> , <i>A. amphibious</i> , <i>M. arvalis</i> , <i>M. agrestis</i> , <i>C. glareolus</i>	<i>L. timidus</i> , <i>A. amphibious</i> , <i>A. oecconomus</i> , <i>M. arvalis</i> , <i>L. gregalis</i> / <i>anglicus</i>	<i>H. brachyura</i> , <i>G. glis</i> , <i>A. sylvaticus</i> , <i>A. bursae</i> , <i>L. lagurus</i> , <i>C. glareolus</i> , <i>M. agrestis</i> , <i>T. subterraneus</i>	<i>L. timidus</i> , <i>M. bobac</i> , <i>D. torquatus</i> , <i>C. nivalis</i> , <i>A. oecconomus</i> , <i>L. gregalis</i> / <i>anglicus</i>	<i>L. corsicanus</i> , <i>T. cuvieri</i> , <i>S. fulvus</i> , <i>S. telum</i> , <i>A. mystacinus</i> , <i>P. sungorus</i> , <i>P. episcopalus</i> , <i>L. lemmus</i> , <i>M. guentheri</i> , <i>T. mariaclaudiae</i> , <i>T. vaufreyi</i>	<i>P. sardus</i> , <i>O. nufescens</i> , <i>S. caucasica</i> , <i>S. telum</i> , <i>T. henseli</i> , <i>T. atapuerquensis</i> , <i>T. dagestanicus</i> , <i>A. middendorffi</i>
Eulipotyphla	<i>E. europaeus</i> , <i>T. europaea</i> , <i>S. araneus</i> , <i>S. minutus</i>	<i>E. europaeus</i> , <i>T. europaea</i> , <i>S. araneus</i> , <i>S. minutus</i>	<i>C. suaveolens</i>	<i>S. minutissimus</i>	<i>T. tyrrenica</i> , <i>Galemys</i> sp., <i>S. thaleri</i> , <i>S. daphnaenodon</i> , <i>S. isodon</i>	<i>T. caeca</i> , <i>T. caucasica</i> , <i>T. tyrrenica</i> , <i>A. similis</i> , <i>S. samniticus</i> , <i>S. runtonensis</i>

The Scandinavian ice sheet covered large areas of Europe during the Late Pleistocene. As the glaciers advanced, they destroyed the older sediments of the Eem interglacial and destroyed any evidence of animal habitation north of about 50 degrees. Finally, many or even most sites, especially from the second half of the Late Pleistocene, are associated in one way or another with the presence of hominids. Thus, it is possible that these are mainly evidences of human dispersal across Europe, which may not only misinterpret reconstructions of species ranges, but also influence the occurrence of remains of game species.

For processing of the data, I used the software products STATISTICA v. 8.0 (StatSoft, Tulsa, OK, USA) and PAST v. 4.16 (Hammer et al. 2001).

Results and discussion

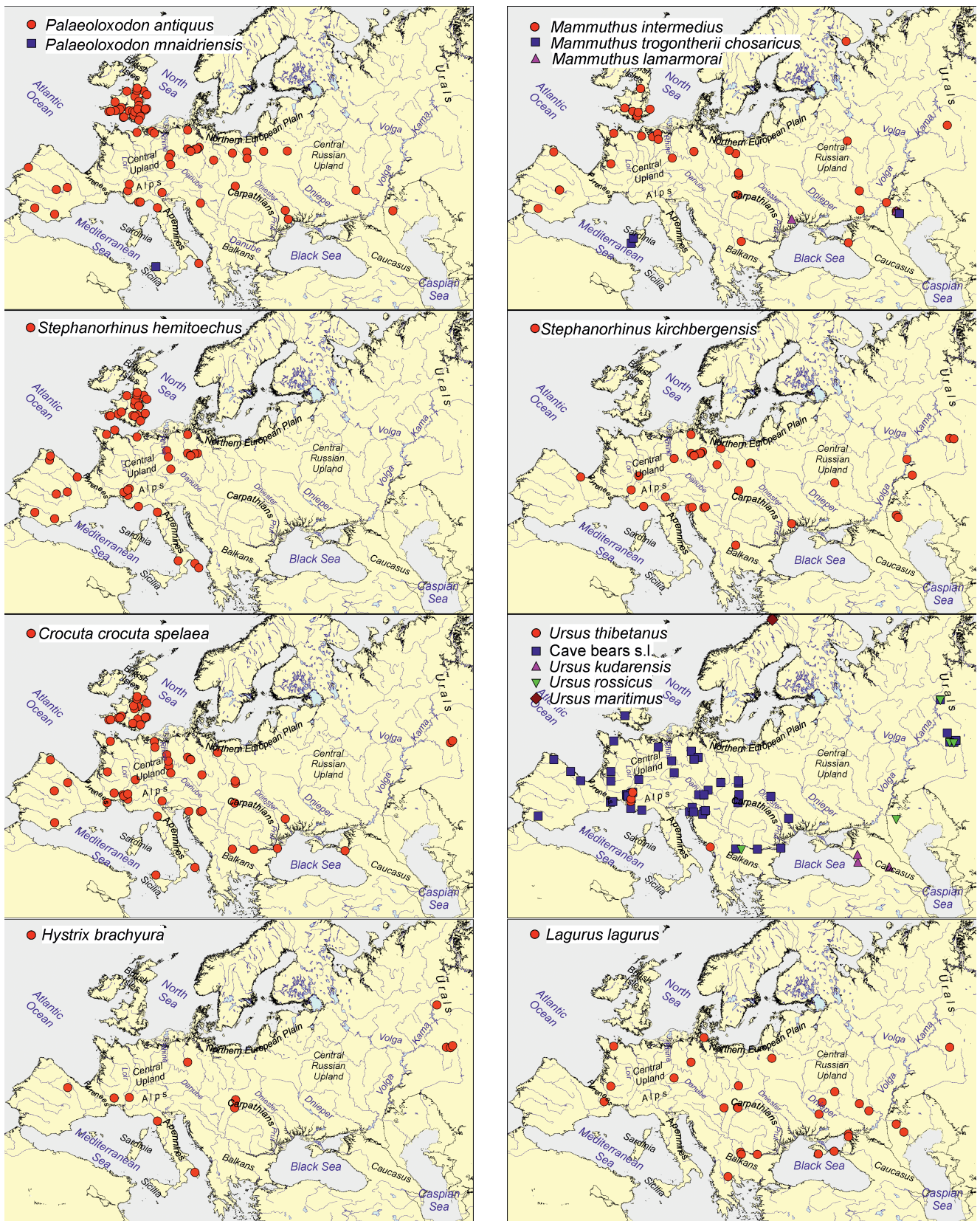
Brief overview of the European faunas MIS 5e and GS 2.1

The majority (>82 %) of European mammal species remained present in the area throughout the Late Pleistocene, despite qualitative changes in global climate.

The most severe changes between the Eem interglacial and the end of the LGM, inclusive, occurred in the group of large herbivorous mammals. This group lost 16 taxa, or about 41 %, if Asian species *Camelus knoblochi* and *Elasmotherium sibiricum* are excluded. The immigration of the woolly mammoth and the musk ox could not compensate for such a significant loss of biodiversity. The wave of extinctions after MIS 5e spread to species that were mostly Middle or even Early Pleistocene relics, and to endemic island species from Sardinia and Corsica (*Palaeoloxodon* sp., *Hippopotamus* sp., *Stephanorhinus* sp., *Haploidoceros mediterraneus*, *Hemitragus* sp.).

In the group of carnivorous mammals, 3 species (about 9 %) became extinct (*Aonyx antiqua* (= *Cyrnaonyx antiqua*), *Ursus thibetanus*, *Ursus rossicus*). An additional 7 species, including pantherines, cave bears s. l. and cave hyenas, became extinct in Europe at the end of the LGM or shortly after, or had their ranges drastically reduced.

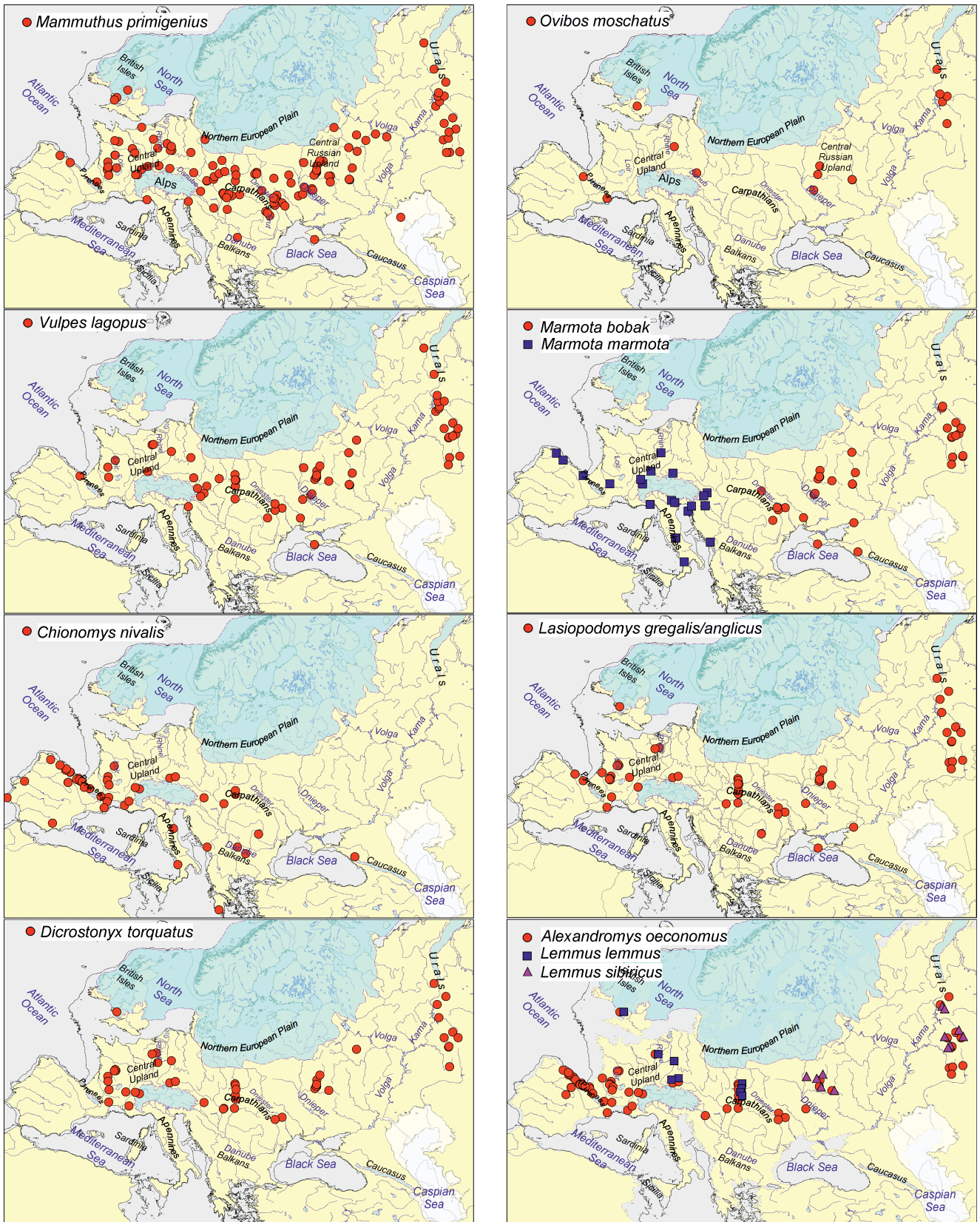
The data I have on the occurrence of small and medium-sized mammals may not be accurate. For example, our database for GS 2.1 lacks occurrences of the Corsican hare (*Lepus corsicanus*), European edible dormouse (*Glis glis*), great jerboa (*Allactaga major*), Günther's and Gerbe's vole (*Microtus guentheri*, *Microtus pyrenaicus*), midday jird (*Meriones meridianus*) and Altai vole (*Microtus obscurus*). There is little doubt that these species were present in southern and southeastern Europe at the end of the LGM. The absence of information on the Granada hare (*Lepus granatensis*), the montane water vole (*Arvicola scherman*), *Terricola atapuerquensis* and some other species in MIS 5e also can be interpreted as insufficient study of the group as a whole. Species that are certain or very likely to have disappeared from the European fauna by the end of the LGM include *Trogontherium cuvieri*, *Spermophilus citelloides*, *Terricola mariaclaudiae*, *Terricola vaufreyi*, and *Pliomys episcopalus*. Data on the distribution of Eulipotyphla species are even less reliable. Therefore, we cannot claim that any species on the list are truly extinct in the interval MIS 5e – GS 2.1.



Text-fig. 3. Localities with remains of some of most abundant and indicator species of Eem interglacial (MIS 5e) in Europe.

Table 2 presents the lists of species classified as (1) most abundant, (2) indicator species, which mark MIS 5e or GS 2.1 time, and (3) rare (the latter list is partial). For the Eem interglacial, indicator species include *Palaeoloxodon antiquus*, *Mammuthus intermedius*, *Stephanorhinus kirchbergensis*, and *Lagurus lagurus* (Text-fig. 3). The ranges of

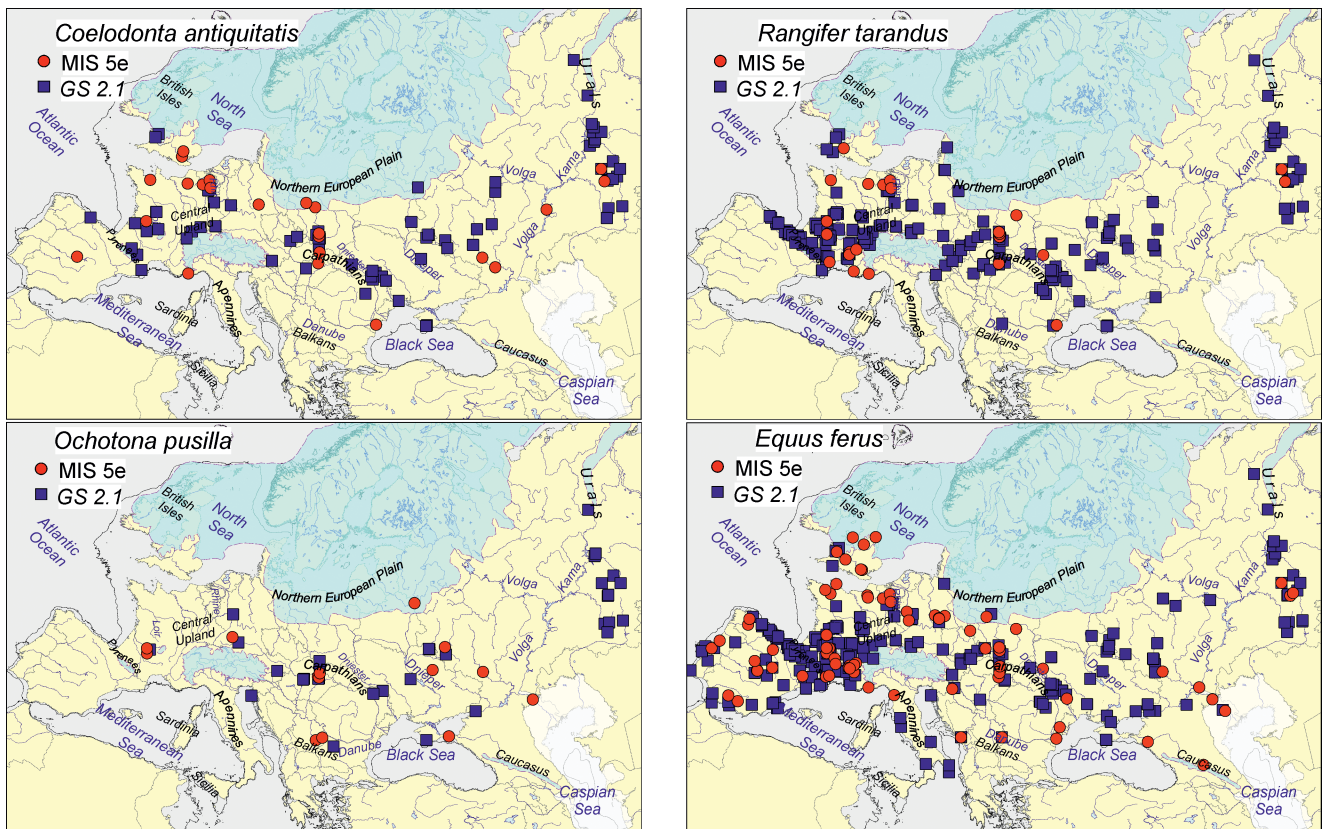
these species probably covered most of the subcontinent. The group of species with large ranges also includes *Megaloceros giganteus*, *Clethrionomys* (= *Myodes*) *glareolus*, *Microtus agrestis*, *Terricola subterraneus*. Indicators of an interglacial condition, widespread only in the western and/or western and central parts of Europe, are as follows: *Hippopotamus*



Text-fig. 4. Localities with remains of some indicator species from end of Last Glacial Maximum (GS 2.1) in Europe.

amphibius, *Stephanorhinus hemitoechus*, *Dama dama*, *Ursus spelaeus* s. l., *Hystrix brachyuran*, *Glis glis*, *Apodemus sylvaticus*, *Allocricetus* (= *Cricetulus*) *bursae* (unless it is classified as the gray hamster; Horáček and Lebedová 2022), and *Crociodura suaveolens*. The indicator group includes the Asian black bear, for which the MIS 5e

interglacial was the last time it was present in the fauna, and whose population occupied a very small area in southern Europe. The current list includes forest, forest-steppe and steppe species (narrow-nosed rhinoceros, “Choullans mammoth” *Mammuthus intermedius*, and steppe lemming). This combination in the interglacial mammal assemblage



Text-fig. 5. Localities of *Coelodonta antiquitatis*, *Equus ferus*, *Rangifer tarandus* and *Ochotona pusilla* in Eem interglacial (MIS 5e) and end of Last Glacial Maximum (GS 2.1) in Europe.

of Europe is consistent with ideas about the heterogeneous structure of the temperate forest belt of Europe at that time, and marked an increase in aridity from west to east, from the Atlantic Ocean (Markova and Puzachenko 2018, Pearce et al. 2023).

Key European indicators for GS 2.1 and the LGM as a whole include woolly mammoth, musk ox, wolverine, Arctic fox, Eurasian collared lemming (*Dicrostonyx torquatus*), European snow vole (*Chionomys nivalis*), bobak marmot (*Marmota bobak*), narrow-headed vole (*Lasiopodomys gregalis/anglicus*) and several others (Tab. 2, Text-fig. 4). Among the species characteristic of the final stage of the *Mammuthus-Coelodonta* Faunal Complex (Kahlke 2014), one can also distinguish a large group whose ranges cover most of Europe, mainly its western half (*Capra* sp., *Rupicapra* sp., *Lemmus lemmus*) or eastern parts (*Marmota bobak*, *Lemmus sibiricus*). Some species commonly included in the *Mammuthus-Coelodonta* Faunal Complex were not included in the group of indicator species. For example, the woolly rhinoceros (*Coelodonta antiquitatis*) and the steppe pika (*Ochotona pusilla*) were widespread in Europe in MIS 5e (Text-fig. 5). However, their range expansion and increase in abundance was quantitative rather than qualitative during the end of the LGM. On the other hand, the reindeer (*Rangifer tarandus*) and especially the caballoid horse (*Equus ferus*) were also well represented in European localities dated to MIS 5e (Text-fig. 5), but by the end of the LGM their abundance was significantly higher than during the interglacial time. This was the basis for including these species in the list of GS 2.1 indicators.

Biodiversity parameters

The results of previous studies on species richness dynamics in the Late Pleistocene of Europe, focused on the regional scale, showed a significant decrease in SPN precisely in the GS 2.1 stage, compared not only to the isotopic stage MIS 3 (when SPN was maximum), but also to the preceding period of the MIS 2 stage (Puzachenko and Markova 2019). Apparently, at that time at the final part of the LGM, environmental conditions maximally unfavorable for mammals formed, especially in the areas close to the ice sheet edge. At the same time, the species richness of mammals estimated at longer intervals of the Late Pleistocene, at the level of isotopic stages, did not show a significant difference between MIS 5e and MIS 2; at the level of individual regions, it could have been even lower during the interglacial time (Puzachenko and Markova 2020, Puzachenko et al. 2022). As mentioned above, the number of taxa recorded in GS 2.1 was significantly lower than in MIS 5e for large herbivores and predatory mammals (Tab. 3). In the group of small and medium-sized herbivores, the differences between interglacial and glacial periods were not significant. The material for comparing species richness in the Eulipotyphla group is, in my opinion, not representative.

It should be emphasized again that the obtained diversity parameters of faunal complexes for the corresponding rank distributions relate to the occurrence of sites containing remains of different species. Note that the analysis of rank distributions is of particular interest from the point of view of evaluating the measurement of diversity and assessing the state of systems in terms of equilibrium-stationarity-non-

Table 3. Diversity parameters calculated from rank distributions of selected mammal groups for the faunas of the Eem interglacial (MIS 5e) and the GS 2.1 stadial (MIS 2).

Group of animals	SPN		H, bit			D			R	
	MIS 5e	GS 2.1	MIS 5e	GS 2.1	t-test, <i>p</i>	MIS 5e	GS 2.1	t-test, <i>p</i>	MIS 5e	GS 2.1
Large herbivorous	36	23	4.35	3.88	9.9, <0.001	0.06	0.084	-7.2, <0.001	0.159	0.141
Carnivorous	31	26	4.09	3.96	1.61, 0.11	0.079	0.088	-1.64, 0.10	0.166	0.158
Small herbivorous	76	78	5.45	5.31	1.54, 0.12	0.034	0.035	-0.18, 0.86	0.13	0.155
Eulipotyphla	20	24	3.62	3.82	-1.39, 0.165	0.112	0.098	1.09, 0.28	0.164	0.168
Full fauna	115	102	5.8	5.43	7.92, <0.001	0.026	0.035	-7.4, <0.001	0.154	0.187

stationarity (Magurran 2004). However, that topic is beyond the scope of this study.

Entropy (H) is positively correlated with SPN ($r = 0.991$, $p < 0.001$) and negatively with the dominance index D ($r = -0.933$, $p = 0.001$). According to *t*-criterion, statistically significant differences of H and D in MIS 5e and GS 2.1 were obtained only for the group of large herbivores and for the total fauna. The meaningful relationship between entropy and the dominance index is because the rank distributions of species occurrence (e.g. in Text-fig. 2) in MIS 5e compared to GS 2.1 tended to be flatter in the range from rank 1 to about 10 (species with relatively large ranges), and had longer tails of rare species with small ranges. The Shannon index is more sensitive to the abundance of rare and single taxa. The number of the latter largely determines the overall value of species richness.

The self-organization index (R) shows no correlation with the entropy or dominance index. Formally, it indicates how far the observed distribution deviates from a uniform, random distribution. In our case, the deviation from such distribution can be interpreted as the deviation from the approximate equality of home ranges of all species.

For large herbivores and carnivores, higher R values are observed for interglacial assemblages, and for small herbivores – for glacial assemblages (Tab. 3). The increase in the index is probably due to the disappearance of a number of taxa with small ranges from the first two groups (some species became definitely extinct during MIS 3, early MIS 2, and some island endemics survived into the Holocene), and to the increase in the range of species such as woolly rhinoceros, reindeer and Arctic fox. For the large herbivore group, the abundance of species with ranks 1 to 3 (i.e., species with large ranges) is significantly higher, and that of species with ranks 14 and above is significantly lower in GS 2.1, compared to the similar interglacial distribution (Text-fig. 2a). In general, this biogeographical restructuring of ranges leads to a certain simplification of the spatial distribution pattern of mammals in these groups.

In the rank distribution of the group of small and medium-sized herbivores, the frequencies of species with ranks greater than 20 decrease in the GS 2.1 stadial (Text-fig. 2b) (as in the case of large herbivores, but to a lesser extent). At the same time, the frequencies of species with medium ranges, with ranks 6 to 19, become higher than in the distribution for MIS 5e. These differences in the patterns of the two distributions are reflected in the higher value of the R index in GS 2.1 against the background of a non-significant difference between the interglacial and glacial for species richness, entropy and dominance index.

“Species – localities number relationship” (SLR)

Note that a satisfactory statistical approximation to the SRL was obtained for all mammal groups and for both time intervals (Tab. 4). This supports the hypothesis of at least a stationary state of the geographical structure of mammal ranges in Europe during both MIS 5e and GS 2.1. In this study, I tested three functions known from the literature and proposed a new one. According to statistical criteria, all four approximations are similar and allow description of 78–54 % of the variability in the number of species found in 1, 2, 3... sites “randomly” selected from the total sample of sites containing remains of representatives of a given mammal group. Analysis of the plots (Text-fig. 6) of the regression lines passing through the points corresponding to the mean SPN values showed certain advantages of the logistic curve (Archibald 1949) and the logarithmic power model, at least for the interval of the number of sites from 1 to 11. It should be emphasized that it does not automatically follow that these functions are optimal for other initial data. For example, the Arrhenius model quite satisfactorily described the SRL for the mammalian fauna that existed in central Europe at the end of the MIS 3 stage (36.0–28.5 ka BP) (Puzachenko et al. 2022).

The parameters A, B, z correlated with the diversity parameters were calculated for the rank distributions. For the logarithmic power model, the correlation coefficient between parameters A and H (entropy) is 0.90, and between parameters B and H it is 0.96.

Parameter A provides an estimate of the average number of species per randomly selected site, and is therefore meaningfully related to the average level of species richness per unspecified area unit for the European territory. The parameter is a more accurate estimate of species richness than simply the sum of species found in Europe (SPN). Although it is difficult to estimate precisely, let us assume that one hypothetical site could accumulate the remains of species that lived in its vicinity over the area of about 10 km by 10 km (for large mammals) and 2 km by 2 km (for small mammals). Under these assumptions, and without considering animal size classes in the MIS 5e interglacial, 1 large herbivorous species could be found in an area of 20 km², 1 carnivorous species in an area of 25 km², and 1 small herbivorous species in an area of about 8 ha. Similar estimates for GS 2.1 conditions are 1 species per 25 km² for large herbivorous, one species per about 30 km² for carnivorous, and one species per 9 ha for of small herbivorous. It should be emphasized that these estimates refer to species richness only, and not to species population densities.

Table 4. Parameters of the “species – localities number (LCN) relationship” (SLR) for the sets of where species of a particular group of mammals were found in the Eem interglacial (MIS 5e) and the GS 2.1 stadial (MIS 2) (Text-fig. 3).

SLR model	A		B		z		LCN ₅₀		Explained variance (r ²)	
	MIS 5e	GS 2.1	MIS 5e	GS 2.1	MIS 5e	GS 2.1	MIS 5e	GS 2.1	MIS 5e	GS 2.1
Large herbivorous										
A(LCN) ^z	6.0 ± 0.15	4.5 ± 0.09	–	–	0.52 ± 0.013	0.52 ± 0.011			0.77	0.70
A + z ln(LCN)	5.0 ± 0.18	3.8 ± 0.11	–	–	6.21 ± 0.126	4.55 ± 0.082	8	5	0.78	0.71
B/(A + LCN ^{-z})	0.24 ± 0.019	0.23 ± 0.018	6.5 ± 0.25	4.9 ± 0.15	-1.01 ± 0.078	-0.98 ± 0.06			0.78	0.71
A + B[ln(LCN)] ^z	5.2 ± 0.21	3.9 ± 0.12	5.7 ± 0.28	4.1 ± 0.17	1.11 ± 0.055	1.13 ± 0.047			0.78	0.71
Carnivorous										
A(LCN) ^z	4.6 ± 0.20	3.8 ± 0.13	–	–	0.55 ± 0.025	0.60 ± 0.019			0.54	0.64
A+zln(LCN)	3.9 ± 0.25	3.2 ± 0.16	–	–	4.8 ± 0.17	4.54 ± 0.121	11–12	8	0.55	0.63
B/(A+LCN ^{-z})	0.24 ± 0.043	0.16 ± 0.038	5.03 ± 0.34	4.06 ± 0.18	-0.99 ± 0.144	-0.89 ± 0.11			0.57	0.64
A+B[ln(LCN)] ^z	4.0 ± 0.28	3.5 ± 0.17	4.3 ± 0.37	3.7 ± 0.25	1.13 ± 0.105	1.27 ± 0.082			0.56	0.64
Small and medium-sized herbivorous										
A(LCN) ^z	7.2 ± 0.32	5.8 ± 0.23	–	–	0.67 ± 0.023	0.69 ± 0.021			0.67	0.70
A+zln(LCN)	4.8 ± 0.48	4.2 ± 0.32	–	–	11.10 ± 0.317	9.41 ± 0.243	14–15	21–22	0.65	0.69
B/(A+LCN ^{-z})	0.09 ± 0.026	0.089 ± 0.024	6.93 ± 0.44	5.7 ± 0.29	-0.92 ± 0.107	-0.94 ± 0.09			0.67	0.71
A+B[ln(LCN)] ^z	6.4 ± 0.53	5.3 ± 0.34	7.6 ± 0.63	6.6 ± 0.47	1.47 ± 0.092	1.46 ± 0.084			0.67	0.71
Eulipotyphla										
A(LCN) ^z	3.1 ± 0.17	2.65 ± 0.15	–	–	0.59 ± 0.036	0.65 ± 0.033			0.56	0.62
A+zln(LCN)	2.5 ± 0.23	2.05 ± 0.20	–	–	3.52 ± 0.185	3.62 ± 0.15			0.56	0.61
B/(A+LCN ^{-z})	0.19 ± 0.061	0.14 ± 0.04	3.27 ± 0.28	2.68 ± 0.021	-0.98 ± 0.207	-1.01 ± 0.17	8	12	0.57	0.62
A+B[ln(LCN)] ^z	2.8 ± 0.28	2.3 ± 0.22	2.99 ± 0.34	2.91 ± 0.20	1.24 ± 0.141	1.32 ± 0.128			0.57	0.62

Parameter B shows the maximum possible increase in species richness with increasing number of sites. In addition to entropy, it naturally correlates negatively with the dominance index ($r = -0.98$). In other words, the greater the proportion of species with large ranges in the fauna, and the greater the average range overlap, the slower the increase in accumulated species diversity as the number of sites increases.

The shape of the curve is mainly determined by a logarithmic function describing the slowing down of the increase in species richness with increasing number of sites. Parameter z, which is greater than 1 and less than 2 in all cases, also affects the shape of this curve, slightly correcting the effect of the logarithmization of the LCN. Together, these two parameters determine the rate at which species accumulate with LCN.

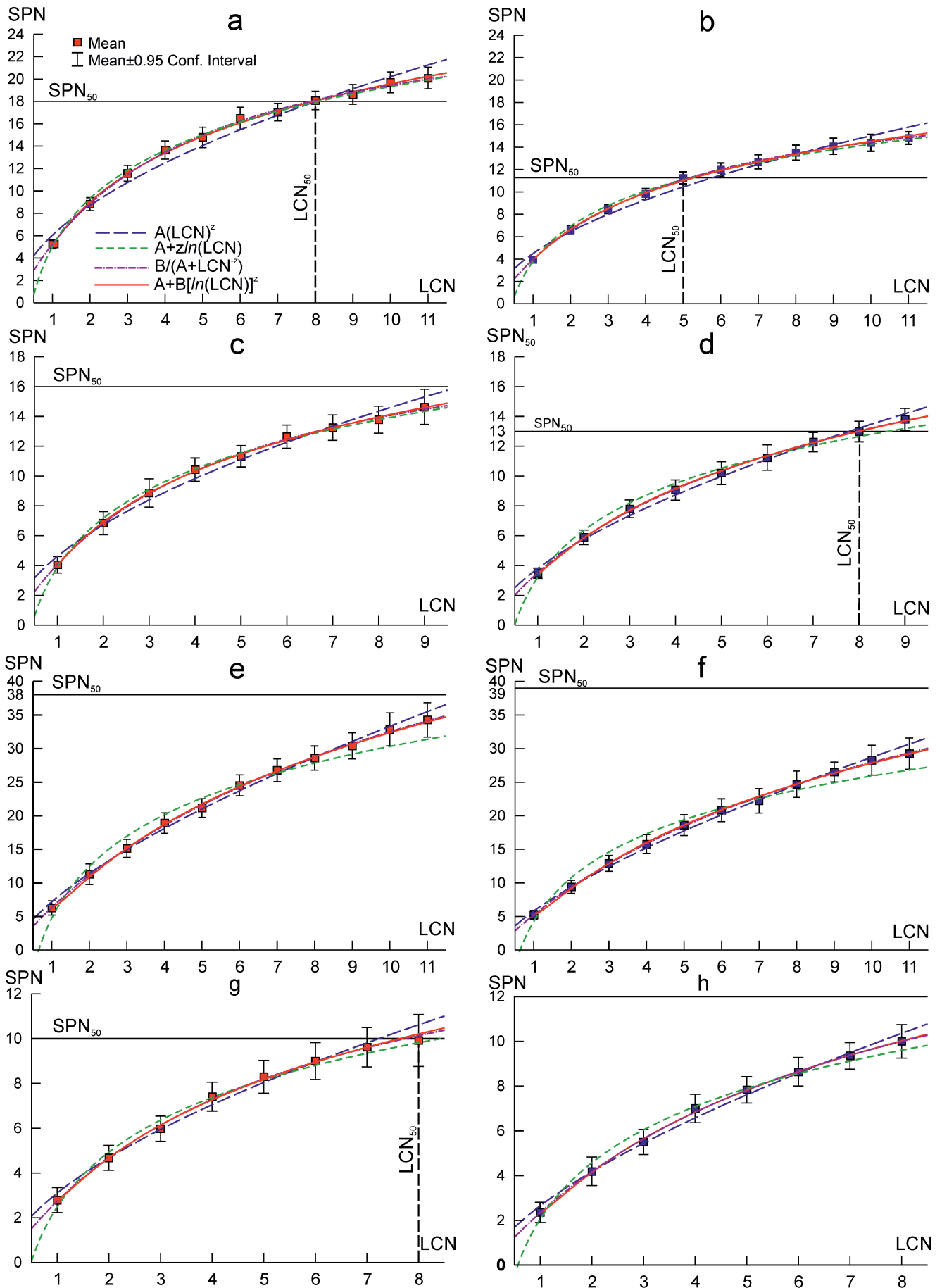
Parameter z shows statistically significant correlations with parameter LCN₅₀ ($r = 0.79$, $p = 0.02$). The latter parameter corresponds to the average number of sites containing 50 % of the species in the fauna (Text-fig. 6). Thus, as z increases, the number of sites required to estimate 50 % of the species richness also increases. However, this dependence cannot be described as a strict one. A major drawback of the logarithmic power model, as well as other exponential and power functions previously proposed to approximate the species area/individuals ratio, is that they grow indefinitely, which is clearly at odds with the finite number of species inhabiting a given area in a given segment of the time scale. In the case of the logistic function (Archibald 1949), parameter B correlates most strongly with

the dominance index ($r = -0.89$, $p = 0.04$), then with H and SPN ($r = 0.78$ and 0.71 , $p = 0.02$ and 0.05 , respectively). Parameter B is the elevation of the curve, while A and z together affect the curvature (Scheiner 2003). The B/A ratio is the asymptote for species richness. Calculation using parameter values from Tab. 4 shows that in our case, the logistic function significantly underestimates species richness for both the interglacial and the end of the LGM.

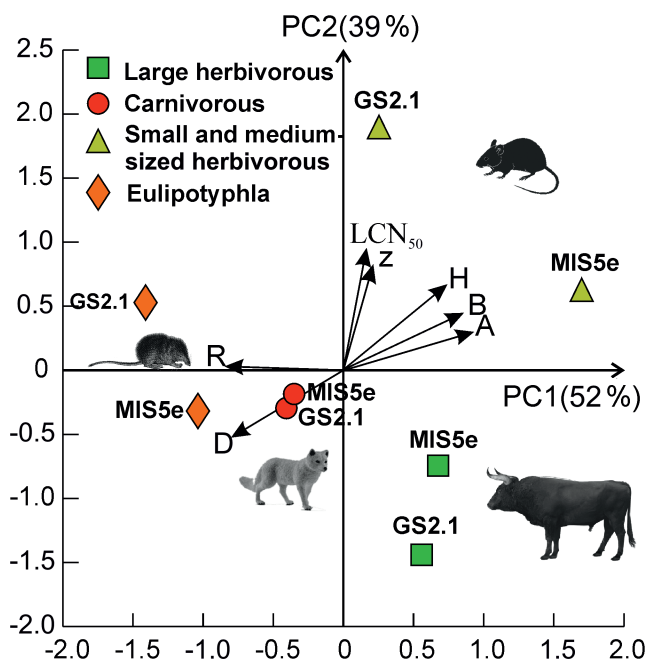
Synthesis

Diversity parameters in the mammal groups considered here were obtained by two independent methods: (1) based on rank distributions of occurrences of sites/localities with remains of different species (entropy, dominance index, self-organization index), and (2) as a result of parameter estimation of a non-linear model approximating SLR. The parameters obtained in different ways, which are highly correlated with each other, generally contain the same information about diversity. This information is therefore invariant with respect to the way it is obtained from the same initial data. These parameters characterize the diversity of the whole complex of mammals inhabiting the territory of Europe in the Late Pleistocene during the periods of maximum contrasting climatic conditions – MIS 5e and GS 2.1. They characterize the state of spatial diversity of species ranges and species richness in the mammal groups for Europe as a whole for each time interval separately.

Taking into account the correlations between parameters, I constructed a general model of their variability using



Text-fig. 6. Species – localities number relationship in Eem interglacial (MIS 5e: a, c, e, g) and Last Glacial Maximum (GS 2.1: b, d, f, h). a, b – large herbivorous, c, d – carnivorous, e, f – small and medium-sized herbivorous, g, h – Eulipotyphla.



Text-fig. 7. Principal components (PC) biplot (varimax normalized rotation) of mammal groups in Eem interglacial (MIS 5e), GS 2.1 and diversity parameters. A, B, z – constants of equation $A + B [\ln(LCN)]^z$; H – entropy, D – dominance index, R – self-organization index.

the standard principal component method with varimax normalized rotation of the first two PCs (Text-fig. 7). PC1 of this model reproduces the variability of the parameters H, D, R and the constants A and B in the SLR. PC2 describes the variability of the LCN_{50} parameter and z constant in SLR, which are independent from the first group of parameters. Each of the mammal groups occupies a distinct position in the PC space, showing a specific response to the contrasting environmental conditions of the Late Pleistocene interglacial and Glacial Maximum.

Consistent with the original data, the diversity of range sizes in all groups is greater to varying degrees in MIS 5e, as was the average number of species found per site. At the same time, the self-organization index, reflecting the contrast between large and small ranges, is higher in GS 2.1, as was the dominance index. Changes in the proportion of ranges of different sizes and their degree of overlap in geographical space are more pronounced in groups of herbivorous mammals, but the direction of this variability (along PC2) is opposite for large and small animals. The LCN_{50} for large herbivores is lower in GS 2.1, i.e., range overlap increases on average, but the opposite is true for small herbivores.

Overall, the range pattern of carnivorous mammals in GS 2.1 is not very different from that in MIS 5e, despite a moderate loss of total species richness (Tab. 3) and a slight increase in the proportion of species with medium and large ranges.

Conclusion

In this study, I used only the simplest information on the presence of mammal remains in the 665 European sites.

Two ecologically contrasting Late Pleistocene intervals (the Eem interglacial, stadial GS 2.1 at the end of the LGM), and four ecologically distinct mammal groups were selected for the estimation of diversity parameters. Both the traditional review of faunal composition and the comparison of rank distributions of the occurrence of species remains across sites allowed describing the compositions of groups of typical and indicator species for each of the time intervals.

Diversity parameters – entropy, dominance index and self-organization index – were estimated from the rank distributions of the species occurrence. These traditional parameters reflect the variability of species ranges, i.e., the variability of species distribution in geographical space.

The next parameters are constants of the non-linear function describing the SLR and LCN_{50} . I proposed a biogeographical interpretation to these parameters. The fact that a statistically valid function with the expected properties was obtained testifies to the suitability of the original data for solving the problem of this study. An additional argument for this conclusion was the high correlation between some diversity parameters obtained by different methods.

The diversity of range sizes in all mammal groups appeared to be higher in MIS 5e, as was the average number of species in local faunas. The contrast between wide and small ranges was on average higher in GS 2.1, as was the dominance index. For large herbivores, the average range overlap was higher in GS 2.1 than in the Eem interglacial, while the opposite relationship found in the small herbivorous group. The range patterns of carnivorous mammals in GS 2.1 and MIS 5e were not significantly different.

Among the most informative parameters are entropy (depends on species richness and the number of species with small ranges), self-organization index (contains information about the shape of rank distribution independent of entropy), constant z in the function describing SLR (related in our case to species richness and LCN_{50} value). All the parameters characterize the structure of species assemblages as a whole over a fixed area (Europe) and a fixed time scale (MIS 5e or GS 2.1). In this context, they are “macroscopic” parameters, by analogy with thermodynamic parameters in physics, such as mass, pressure, volume, temperature, entropy, etc. Their peculiarity is that they do not reveal the details of evolution and its specific mechanisms, but they allow us to detect changes, determine their directions and formulate hypotheses. The detail of changes in the spatial pattern of species distribution is possible by analyzing the structure of the rank distributions themselves together with the reconstruction of palaeoranges of individual species.

A change in geographical scale should almost certainly lead to a change in the values of the diversity parameters. Whether there is any regularity in this will be the subject of future research. A similar statement of the problem applies to changes in time scale.

Acknowledgments

The study was supported in part by the grant of the Institute of Geography, RAS.FMWS-2024-0007 (1021051703468-8).

References

- Abrams, G., Bello, S. M., Di Modica, K., Pirson, S., Bonjean, D. (2014): When Neanderthals used cave bear (*Ursus spelaeus*) remains: Bone retouchers from unit 5 of Scladina cave (Belgium). – *Quaternary International*, 326–327: 274–287.
<https://doi.org/10.1016/j.quaint.2013.10.022>
- Agadzhanian, A. K. (2009): Melkie mlekopitayushchie plio-tsen-pleistotsena Russkoy ravniny [Small mammals of the Pliocene-Pleistocene of the Russian Plain]. – *Proceedings of the Paleontological Institute RAS*, 289: 1–676. (in Russian)
- Akhmetgaleeva, N. B., Burova, N. D. (2021): The originality of the Byki sites among known LGM industries on the Russian Plain. – *Quaternary International*, 581–582: 296–314.
<https://doi.org/10.1016/j.quaint.2020.08.035>
- Almuzara, A. C., Maestu, I. B. (2001): El Paleolítico superior de la cueva de Zatoya (Navarra): actualización de los datos en 1997 [The Upper Palaeolithic of the Zatoya Cave (Navarra): update of data in 1977]. – *Trabajos de arqueología Navarra*, 15: 5–100. (in Spanish)
- Alonso, A. D., Gómez-Olivencia, A., San Pedro-Calleja, Z. (2013): La fauna de macromamíferos de los niveles pleistocenos de la Cueva de Arlanpe (Lemoa, Bizkaia) [The fauna of macromammals from the Pleistocene levels of the Arlanpe Cave (Lemoa, Bizkaia)]. – In: Rios-Garaizar, J., Garate Maidagan, D., Gómez-Olivencia, A. (eds), *La Cueva de Arlanpe (Lemoa): Ocupaciones humanas desde el Paleolítico Medio Antiguo hasta la Prehistoria Reciente*. Kobie, Ser. BAI, 3: 123–160. (in Spanish)
- Altuna, J. (1972): Fauna de Mamíferos de los Yacimientos prehistoricos de Guipuzcoa [Mammalian Fauna of the Prehistoric Sites of Guipuzcoa]. – *Munibe*, 24: 1–464. (in Spanish)
- Altuna, J. (1986): The mammalian faunas from the prehistoric site of La Riera. – In: Straus L., Clark G. (eds), *La Riera Cave: Stone age hunter-gatherer adaptations in northern Spain*. *Anthropological Research Papers*, 36: pp. 237–284.
- Altuna, J., Mariezkurrena, C. (2011): Estudio de los macromamíferos del yacimiento de Aitzbitarte III (excavación de la entrada) [Study of the macromammals of the Aitzbitarte III site (excavation of the entrance)]. – In: Altuna, J., Mariezkurrena, K., Ríos, J. (eds), *Aitzbitarte III (Euskal Herria) Giza aztarnak 33.600–18.400 BP (sarrerako eremua)*. Centro de Patrimonio Cultural Vasco, Vitoria-Gasteiz, pp. 395–480. (in Spanish)
- Archibald, E. E. A. (1949): The Specific Character of Plant Communities: II. A Quantitative Approach. – *The Journal of Ecology*, 37(2): 274–288.
<https://doi.org/10.2307/2256609>
- Arrhenius, O. (1921): Species and Area. – *The Journal of Ecology*, 9(1): 95–99.
<https://doi.org/10.2307/2255763>
- Arribas, A. (1994a): El yacimiento mesopleistoceno de Villacastin (Segovia, España): geología y paleontología de micromamíferos [The Middle Pleistocene site of Villacastin (Segovia, Spain): geology and palaeontology of micromammals]. – *Boletín Geológico y Minero*, 105(2): 146–166. (in Spanish)
- Arribas, A. (1994b): Paleontología de macromamíferos del yacimiento mesopleistoceno de Villacastin (Segovia, España) [Paleontology of macromammals from the Middle Pleistocene site of Villacastin (Segovia, Spain)]. – *Boletín Geológico y Minero*, 105(4): 344–361. (in Spanish)
- Arsuaga, J. L., Gómez-Olivencia, A., Sala, N., Martínez-Pillado, V., Pablos, A., Bonmatí, A., Pantoja-Pérez, A., Lira-Garrido, J., Alcázar De Velasco, A., Ortega, A. I., Cuenca-Bescós, G., García, N., Aranburu, A., Ruiz-Zapata, B., José Gil-García, M., Rodríguez-Álvarez, X. P., Ollé, A., Mosquera, M. (2017): Evidence of paleoecological changes and Mousterian occupations at the Galería de las Estatuas site, Sierra de Atapuerca, northern Iberian plateau, Spain. – *Quaternary Research*, 88(2): 345–367.
<https://doi.org/10.1017/qua.2017.46>
- Bachura, O., Kosintsev, P. (2007): Late Pleistocene and Holocene small- and large-mammal faunas from the Northern Urals. – *Quaternary International*, 160(1): 121–128.
<https://doi.org/10.1016/j.quaint.2006.09.013>
- Baigusheva, V. S., Titov, V. V. (2007): Prirodnaya sreda i usloviya zhizni okhotnikov na zubrov v Priazov'e [Natural environment and living conditions of bison hunters in the Azov region]. – *Anthropology Bulletin*, 15: 113–151. (in Russian)
- Bañuls-Cardona, S., López-García, J. M., Blain, H. A., Lozano-Fernández, I., Cuenca-Bescós, G. (2014): The end of the Last Glacial Maximum in the Iberian Peninsula characterized by the small-mammal assemblages. – *Journal of Iberian Geology*, 40(1): 19–27.
https://doi.org/10.5209/rev_JIGE.2014.v40.n1.44085
- Barnosky, A. D., Hadly, E. A., Bascompte, J., Berlow, E. L., Brown, J. H., Fortelius, M., Getz, W. M., Harte, J., Hastings, A., Marquet, P. A., Martinez, N. D., Mooers, A., Roopnarine, P., Vermeij, G., Williams, J. W., Gillespie, R., Kitzes, J., Marshall, C., Matzke, N., Mindell, D. P., Revilla, E., Smith, A. B. (2012): Approaching a state shift in Earth's biosphere. – *Nature*, 486(7401): 52–58.
<https://doi.org/10.1038/nature11018>
- Baryshnikov, G., Hoffecker, J. F., Burgess, R. L. (1996): Palaeontology and zooarchaeology of Mezmaiskaya Cave (Northwestern Caucasus, Russia). – *Journal of Archaeological Science*, 23(3): 313–335.
<https://doi.org/10.1006/jasc.1996.0030>
- Batchelor, C. L., Margold, M., Krapp, M., Murton, D. K., Dalton, A. S., Gibbard, P. L., Stokes, C. R., Murton, J. B., Manica, A. (2019): The configuration of Northern Hemisphere ice sheets through the Quaternary. – *Nature Communications*, 10(1): 3713.
<https://doi.org/10.1038/s41467-019-11601-2>
- Berto, C., Rubinato, G. (2013): The upper Pleistocene mammal record from Caverna degli Orsi (San Dorligo della Valle e Dolina, Trieste, Italy): A faunal complex between eastern and western Europe. – *Quaternary International*, 284: 7–14.
<https://doi.org/10.1016/j.quaint.2011.07.025>
- Blain, H.-A., López-García, J. M., Cordy, J.-M., Pirson, S., Abrams, G., Di Modica, K., Bonjean, D. (2014): New

- contribution to the study of the small-vertebrate assemblages of Scladina cave (Late Pleistocene, Province of Namur, Belgium). – In: Book of Abstracts. Middle Palaeolithic in North-West Europe: Multidisciplinary approaches. Namur, Moulins de Beez Conference, 2014 March the 20th–21st, p. 50.
- Bouchud, J. (1952): Les oiseaux d'Isturitz. – *Bulletin de la Société préhistorique de France*, 49(8): 450–459.
<https://doi.org/10.3406/bspf.1952.5087>
- Boulton, G. S., Dongelmans, P., Punkari, M., Broadgate, M. (2001): Palaeoglaciology of an ice sheet through a glacial cycle: The European ice sheet through the Weichselian. – *Quaternary Science Reviews*, 20(4): 591–625.
[https://doi.org/10.1016/S0277-3791\(00\)00160-8](https://doi.org/10.1016/S0277-3791(00)00160-8)
- Boylan, P. J. (1981): A new revision of the Pleistocene mammalian fauna of Kirkdale Cave. – *Proceedings of Yorkshire Geological Society*, 43(3): 253–280.
<https://doi.org/10.1144/pygs.43.3.253>
- Bratlund, B. (1999): Taubach Revisited. – *Jahrbuch des Römisch-Germanischen Zentralmuseums Mainz*, 46: 61–74.
- Brugal, J.-P., Jaubert, J. (1991): Les gisements paléontologiques pléistocènes à indices de fréquentation humaine : un nouveau type de comportement de prédation? – *Paléo*, 3(1): 15–41.
<https://doi.org/10.3406/pal.1991.1034>
- Brugal, J.-P., Cochard, D., Ellwood, B., Girard, M., Jaubert, J., Jeannet, M., Kervazo, B., Louchart, A., Quinif, Y., Thery-Parisot, I. (2001): Tour-de-Faure: Grotte de Couduous II. – In: *Bilan Scientifique de La Région Midi Pyrénées 2000*. Ministère de la Culture et des Communications, Directions régionales des affaires culturelles, Service régional de l'archéologie, Sous-direction de l'archéologie, pp. 126–128.
- Bush, A. B. G., Philander, S. G. H. (1999): The climate of the Last Glacial Maximum: Results from a coupled atmosphere-ocean general circulation model. – *Journal of Geophysical Research Atmospheres*, 104(D20): 24509–24525.
<https://doi.org/10.1029/1999JD900447>
- Butchart, S. H. M., Walpole, M., Collen, B., van Strien, A., Scharlemann, J. P. W., Almond, R. E. A., Baillie, J. E. M., Bomhard, B., Brown, C., Bruno, J., Carpenter, K. E., Carr, G. M., Chanson, J., Chenery, A. M., Csirke, J., Davidson, N. C., Dentener, F., Foster, M., Galli, A., Galloway, J. N., Genovesi, P., Gregory, R. D., Hockings, M., Kapos, V., Lamarque, J., Francois, L. F., Loh, J., McGeoch, M. A., McRae, L., Minasyan, A., Morcillo, M. H., Idfield, Th. E. E., Pauly, D., Quader, S., Revenga, C., Sauer, J. R., Skolnik, B., Spear, D., Stanwell-Smith, D., Stuart, S. N., Symes, A., Tierney, M., Tyrrell, T. D., Vié, J. Ch., Watson, R. (2010): Global Biodiversity: Indicators of Recent Declines. – *Science*, 328(5982): 1164–1168.
<https://doi.org/10.1126/science.1187512>
- Castaños, P. (1984): Estudio de los Macromamíferos de la Cueva de Santimamiñe (Vizcaya) [Study of the Macromammals of the Cueva de Santimamiñe (Vizcaya)]. – *Kobie, Serie Paleontología y Ciencias Naturales*, 14: 235–318. (in Spanish)
- Castel, J., Liolios, D., Laroulandie, V., Chauvière, X., Chadelle, J., Pike-tay, A., Geneste, J. (2006): Solutrean Animal Resource Exploitation at Combe Saunière (Dordogne, France). – In: Maltby M. (ed.), *Integrating Zooarchaeology, Proceedings of the 9th Conference of the International Council of Archaeozoology, Durham, August 2002*. Oxbow Books Oxford, pp. 138–152.
- Ceregatti, L., Berto, C., Fewlass, H., Baca, M., Luzi, E., Brancaloni, G., Pereswiet-Soltan, A., Peresani, M. (2023): Integration of direct radiocarbon dating, genetic studies and taxonomy of small mammals to investigate the chronology of past climatic oscillations: The Last Glacial Maximum sequence of Grotta della Ferrovia (Fabriano, Italy). – *Quaternary Science Reviews*, 309: 108095 (16 pp.).
<https://doi.org/10.1016/j.quascirev.2023.108095>
- Chubur, A. A. (2001): Byki. Novyy paleoliticheskiy mikroregion i ego mesto v verkhnem paleolite Russkoy ravniny [The Byki. The new Paleolithic microregion and its place in the Upper Paleolithic of the Center Russian plain]. – *Briansk segodnya, Briansk*, 132 pp. (in Russian)
- Clark, P. U., Dyke, A. S., Shakun, J. D., Carlson, A. E., Clark, J., Wohlfarth, B., Mitrovica, J. X., Hostetler, S. W., McCabe, A. M. (2009): The Last Glacial Maximum. – *Science*, 325(5941): 710–714.
<https://doi.org/10.1126/science.1172873>
- Cooper, J. (1996): Quaternary micromammals from Gorcham's cave Gibraltar and their paleoenvironmental significance. – *Almoraima: revista de estudios campogibraltareños*, 15: 69–86.
- Cordy, J.-M. (1992): Bio- et chronostratigraphie des dépôts quaternaires de la grotte Scladina (province de Namur, Belgique) à partir des micro-mammifères. – In: Otte, M. (ed.), *Recherches aux grottes de Sclayn, 1: Le Contexte*. ERAUL, 27: 79–125.
- Costamagno, S., Barshay-Szmidt, C., Kuntz, D., Laroulandie, V., Pétillon, J. M., Boudadi-Maligne, M., Langlais, M., Mallye, J. B., Chevallier, A. (2016): Reexamining the timing of reindeer disappearance in southwestern France in the larger context of late glacial faunal turnover. – *Quaternary International*, 414: 34–61.
<https://doi.org/10.1016/j.quaint.2015.11.103>
- Crégut-Bonnoure, E., Boulbes, N., Daujeard, C., Fernandez, P., Valensi, P. (2010): Nouvelles données sur la grande faune de l'Éemien dans le Sud-Est de la France. – *Quaternaire*, 21(3): 227–248.
<https://doi.org/10.4000/quaternaire.5592>
- Currant, A., Jacobi, R. (2001): A formal mammalian biostratigraphy for the Late Pleistocene of Britain. – *Quaternary Science Reviews*, 20(16-17): 1707–1716.
[https://doi.org/10.1016/S0277-3791\(01\)00035-X](https://doi.org/10.1016/S0277-3791(01)00035-X)
- Cyrek, K., Socha, P., Stefaniak, K., Madeyska, T., Mirosław-Grabowska, J., Sudoł, M., Czyzewski, Ł. (2010). Palaeolithic of Biśnik cave (Southern Poland) within the environmental background. – *Quaternary International*, 220(1-2), 5–30.
<https://doi.org/10.1016/j.quaint.2009.09.014>
- Dabkowski, J., Limondin-Lozouet, N. (2022): Comparison of temperature and humidity during MIS 11 and MIS 5e interglacials with the Holocene using stable isotopes in tufa deposits from northern France. – *Quaternary Research*, 107: 147–158.
<https://doi.org/10.1017/qua.2021.66>

- Dahl-Jensen, D., Albert, M. R., Aldahan, A., Azuma, N., Balslev-Clausen, D., Baumgartner, M., Berggren, A. M., Bigler, M., Binder, T., Blunier, T., Bourgeois, J. C., Brook, E. J., Buchardt, S. L., Buizert, C., Capron, E., Chappellaz, J., Chung, J., Clausen, H. B., Cvijanovic, I., Davies, S. M., Ditlevsen, P., Eicher, O., Fischer, H., Fisher, D. A., Fleet, L. G., Gfeller, G., Gkinis, V., Gogineni, S., Goto-Azuma, K., Grinsted, A., Gudlaugsdottir, H., Guillevic, M., Hansen, S. B., Hansson, M., Hirabayashi, M., Hong, S., Hur, S. D., Huybrechts, P., Hvidberg, C. S., Iizuka, Y., Jenk, T., Johnsen, S. J., Jones, T. R., Jouzel, J., Karlsson, N. B., Kawamura, K., Keegan, K., Kettner, E., Kipfstuhl, S., Kjær, H. A., Koutnik, M., Kuramoto, T., Köhler, P., Laepple, T., Landais, A., Langen, P. L., Larsen, L. B., Leuenberger, D., Leuenberger, M., Leuschner, C., Li, J., Lipenkov, V., Martinerie, P., Maselli, O. J., Masson-Delmotte, V., McConnell, J. R., Miller, H., Mini, O., Miyamoto, A., Montagnat-Rentier, M., Mulvaney, R., Muscheler, R., Orsi, A. J., Paden, J., Panton, C., Pattyn, F., Petit, J. R., Pol, K., Popp, T., Possnert, G., Prié, F., Prokopiou, M., Quiquet, A., Rasmussen, S. O., Raynaud, D., Ren, J., Reutenauer, C., Ritz, C., Röckmann, T., Rosen, J. L., Rubino, M., Rybak, O., Samyn, D., Sapart, C. J., Schilt, A., Schmidt, A. M. Z., Schwander, J., Schüpbach, S., Seierstad, I., Severinghaus, J. P., Sheldon, S., Simonsen, S. B., Sjolte, J., Solgaard, A. M., Sowers, T., Sperlich, P., Steen-Larsen, H. C., Steffen, K., Steffensen, J. P., Steinhage, D., Stocker, T. F., Stowasser, C., Sturevik, A. S., Sturges, W. T., Sveinbjörnsdottir, A., Svensson, A., Tison, J. L., Uetake, J., Vallelonga, P., Wal, R. S. W. van de, Wel, G. van der, Vaughn, B. H., Vinther, B., Waddington, E., Wegner, A., Weikusat, I., White, J. W. C., Wilhelms, F., Winstrup, M., Witrant, E., Wolff, E. W., Xiao, C., Zheng, J. (2013): Eemian interglacial reconstructed from a Greenland folded ice core. – *Nature*, 493: 489–494.
<https://doi.org/10.1038/nature11789>
- Danukalova, G., Kosintsev, P., Yakovlev, A., Yakovleva, T., Osipova, E., Kurmanov, R., van Kolfshoten, T., Izvarin, E. (2020): Quaternary deposits and biostratigraphy in caves and grottoes located in the Southern Urals (Russia). – *Quaternary International*, 546: 84–124.
<https://doi.org/10.1016/j.quaint.2020.02.007>
- Danukalova, G., Yakovlev, A. (2006): A review of biostratigraphical investigations of palaeolithic localities in the Southern Urals region. – *Quaternary International*, 149: 37–43.
<https://doi.org/10.1016/j.quaint.2005.11.016>
- Danukalova, G., Yakovlev, A., Osipova, E., Alimbekova, L., Yakovleva, T., Kosintsev, P., Morozova, E., Ereemeev, A., Kosintsev, P. (2011): Biostratigraphy of the Late Upper Pleistocene (Upper Neopleistocene) to Holocene deposits of the Belaya River valley (Southern Urals, Russia). – *Quaternary International*, 190(1-2): 28–43.
<https://doi.org/10.1016/j.quaint.2010.06.034>
- Daujeard, C., Moncel, M. H., Rivals, F., Fernandez, P., Aureli, D., Auguste, P., Bocherens, H., Crégut-Bonnoure, É., Debard, É., Liouville, M. (2011): What Occupation type in the Unit F at Payre (Ardèche, France)? A Specialised Hunting Stop or a Short-term Camp? An example of a Multi-disciplinary Approach. – In: Bon, F., Costamagno, S., Valdeyron, N. (eds), *Hunting Camps in Prehistory: Current Archaeological Approaches*. *Paletnologie*, 3: 77–101.
<https://doi.org/10.4000/paletnologie.6966>
- David, A., Pascariu, V. (2012): Teriofauna i ekologicheskaya obstanovka periglyacial'noy zony pozdnevaldayskogo oledeneniya severo-zapada i severa Respubliki Moldova [The theriofauna and environmental conditions of the periglacial zone of the Late Valdai Glaciation in the north-west and north of the Republic of Moldova]. – *Buletin Ştiinţific. Revistă de Etnografie, Ştiinţele Naturii şi Muzeologie*, 18: 152–158. (in Russian)
- Davis, S. (2002): The mammals and birds from the Gruta do Caldeirão, Portugal. – *Revista portuguesa de arqueologia*, 5(2): 29–98.
- Defleur, A., Crégut-Bonnoure, E., Radulescu, C., Villette, P. (1990): La grotte des Cèdres, commune du Plan d'Aups (Var). – *Bulletin de la Société préhistorique française*, 87(9): 270–274.
<https://doi.org/10.3406/bspf.1990.9447>
- Delpech, F. (1983): Les Faunes du Paleolithique Superieur dans le Sud-Ouest de la France. – *Cahiers du Quaternaire*, Université de Bordeaux I, 6: 1–456.
- Delpech, F. (2012): Biostratigraphy of the Solutrean layers of Laugerie-Haute (Les Eyzies, Dordogne). *Archaeological implications*. – *Paléo*, 23: 105–116.
<https://doi.org/10.4000/paleo.2458>
- Demidenko, Y. E., Noiret, P. (2012): The Siuren I Aurignacian of Krems-Dufour type industries in the context of the European Aurignacian. – In: Demidenko, Y. E., Otte, M., Noiret, P. (eds), *Siuren I Rock-Shelter. From Late Middle Paleolithic and Early Upper Paleolithic to Epi-Paleolithic in Crimea*. ERAUL 129: 343–357.
- Demidov, I., Houmark-Nielsen, M., Kjær, K., Larsen, E. (2006): The last Scandinavian Ice Sheet in northwestern Russia: Ice flow patterns and decay dynamics. – *Boreas*, 35(3): 425–443.
<https://doi.org/10.1080/03009480600781883>
- Demuro, M., Arnold, L. J., Aranburu, A., Gómez-Olivencia, A., Arsuaga, J. L. (2019): Single-grain OSL dating of the Middle Palaeolithic site of Galería de las Estatuas, Atapuerca (Burgos, Spain). – *Quaternary Geochronology*, 49: 254–261.
<https://doi.org/10.1016/j.quageo.2018.02.006>
- Dietrich, A. K., Berckhemer, F. (1983): Der Urmensch und seine Umwelt im Eiszeitalter auf Untertürkheimer Markung – Ein Beitrag zur Urgeschichte des Neckarlandes. – *Bürgerverein Untertürkheim*, Stuttgart, 88 pp.
- Dodonov, A. E., Tchepalyga, A. L., Mihailescu, C. D., Zhou, L. P., Markova, A. K., Trubikhin, V. M., Simakova, A. N., Konikov, E. G. (2000): Last-interglacial records from central Asia to the northern Black Sea shoreline: Stratigraphy and correlation. – *Geologie en Mijnbouw/Netherlands Journal of Geosciences*, 79: 303–311.
<https://doi.org/10.1017/S0016774600021788>
- Döppes, D., Kempe, S., Rosendahl, W. (2008): Dated Paleontological cave sites of Central Europe from Late Middle Pleistocene to early Upper Pleistocene (OIS 5 to OIS 8). – *Quaternary International*, 187(1): 97–104.
<https://doi.org/10.1016/j.quaint.2007.03.023>

- Ehlers, J., Astakhov, V., Gibbard, P. L., Mangerud, J., Svendsen, J. I. (2013): Glaciation. Late Pleistocene in Eurasia. – In: *Encyclopedia of Quaternary Science*. Elsevier, pp. 224–235.
<https://doi.org/10.1016/B978-0-444-53643-3.00117-5>
- Ehlers, J., Gibbard, P. (2008): Extent and chronology of Quaternary glaciation. – *Episodes*, 31: 211–218.
<https://doi.org/10.18814/epiiugs/2008/v31i2/004>
- Fabre, M. (2010): Environnement et subsistance au Pléistocène supérieur dans l'est de la France et au Luxembourg: Étude ostéologique des gisements de la Baume de Gigny (Jura), Vergisson II (Saône et Loire) et Oetrange (Luxembourg); Thèse de doctorat. – MS, Faculté des lettres et sciences humaines, Université de Provence Aix-Marseille I, Aix-en-Provence, France, 1–391 (text), 1–131 (annex) (available online)
<https://theses.hal.science/tel-00617613v1>
- Fadeeva, T. V., Gimranov, D. O., Kosintsev, P. A., Yakovlev, A. G. (2023): Fossil Fauna of Small Mammals from Imanay Cave, Southern Urals, Russia. – *Biology Bulletin*, 50(8): 2067–2080.
<https://doi.org/10.1134/S106235902308006X>
- Falguerès, C., Yokoyama, Y., Arrizabalaga, A. (2005): La Geocronología del yacimiento pleistocénico de Lezetxiki (Arrasate, País Vasco). Crítica de las dataciones existentes y algunas nuevas aportaciones [Geochronology of the Pleistocene site of Lezetxiki (Arrasate, Basque Country). A critique of available dating and some new contributions.]. – *Munibe (Antropologia-Arkeologia)*, 57: 93–106. (in Spanish)
- Ferrant, V., Friant, M. (1937): La faune pleistocene d'Oetrange (G. D. de Luxembourg). – *Bulletins Mensuels, Societe des Naturalistes Luxembourgeois*, 6(2): 45–80.
- Foerster, H. von (1960): On Self-Organizing Systems and Their Environments. – In: Yovits M. C., Cameron, S. (eds), *Self-Organizing Systems*. Pergamon Press, London, pp. 31–50.
- Foury, Y., Desclaux, E., Daujeard, C., Defleur, A., Moncel, M.-H., Raynal, J.-P. (2016): Evolution des faunes de rongeurs en moyenne vallée du Rhône (rive droite, Ardèche, France) au cours du pléistocène moyen final et du pléistocène supérieur ancien, du mis 6 au mis 4. – *Quaternaire*, 27(1): 55–79.
<https://doi.org/10.4000/quaternaire.7527>
- García-Ibaibarriaga, N., Murelaga, X., Bailón, S., Rofes, J., Ordiales, A. (2013): Estudio de los microvertebrados de la cueva de Arlanpe (Lemoa, Bizkaia) [Study of the microvertebrates of the Arlanpe cave (Lemoa, Bizkaia)]. – In: Rios-Garaizar, J., Garate Maidagan, D., Gómez-Olivencia, A. (eds), *La Cueva de Arlanpe (Lemoa): Ocupaciones humanas desde el Paleolítico Medio Antiguo hasta la Prehistoria Reciente*. Kobie, Ser. BAI, 3: 81–210. (in Spanish)
- García-Ibaibarriaga, N., Suárez-Bilbao, A., Bailón, S., Arrizabalaga, A., Iriarte-Chiapusso, M. J., Arnold, L., Demuro, M., Murelaga, X. (2018): Paleoenvironmental and paleoclimatic interpretation of the stratigraphic sequence of Lezetxiki II Cave (Basque Country, Iberian Peninsula) inferred from small vertebrate assemblages. – *Quaternary Research*, 90(1): 164–179.
<https://doi.org/10.1017/qua.2018.17>
- Germonpré, M. (2003): Mammoth taphonomy of two fluvial sites from the Flemish Valley, Belgium. – *Deinsea*, 9: 171–183.
- Germonpré, M., Sablin, M., Khlopachev, G. A., Grigorieva, G. V. (2008): Possible evidence of mammoth hunting during the Epigravettian at Yudinovo, Russian Plain. – *Journal of Anthropological Archaeology*, 27(4): 475–492.
<https://doi.org/10.1016/j.jaa.2008.07.003>
- Gleason, H. A. (1925): Species and Area. – *Ecology*, 6(1): 66–74.
<https://doi.org/10.2307/1929241>
- Golovachev, M. V., Titov, V. V. (2019): Novye dannye o taksonomii i raznoobrazii krupnykh mlekopitayushchikh srednego i pozdnego neopleystotsena po rezul'tatam analiza kostnykh ostatkov iz otlozheniy geologicheskikh razrezov v okrestnostyakh s. Chyornyy yar (Astrakhan-skaya oblast', Rossiya) [New data on the large mammals fauna taxonomic diversity of the Middle and Late Neopleistocene by analysis of bone remains from geological sections near Cherny yar village (Astrakhan region, Russia)]. – *Bulletin of the Commission for Study of the Quaternary*, 77: 160–166. (in Russian)
- Grayson, D. K., Guthrie, R. D., Harington, C. R., Jefferson, G. T., Martin, L. D., McDonald, H. G., Morlan, R. E., Semken, H. A. Jr., Webb, S. D., Werdelin, L., Graham, R. W., Wilson, M. C., Lundelius, E. L. Jr., Graham, M. A., Schroeder, E. K., Toomey, R. S. III, Anderson, E., Barnosky, A. D., Burns, J. A., Churcher, C. S. (1996): Spatial Response of Mammals to Late Quaternary Environmental Fluctuations. – *Science*, 272: 1601–1606.
<https://doi.org/10.1126/science.272.5268.1601>
- Guadelli, J.-L., Sirakov, N., Ivanova, S., Sirakova, S., Anastassova, E., Courtaud, P., Dimitrova, I., Djabarska, N., Fernandez, P., Ferrier, C., Fontugne, M., Gambier, D., Guadelli, A., Jordanova, D. D., Jordanova, D. D., Kovacheva, M., Krumov, I., Leblanc, J.-C., Mallye, J.-B., Marinska, M., Miteva, V., Popov, V. V., Spassov, R., Taneva, S., Tisnerat-Laborde, N., Tsanova, T. (2005): Une séquence du paléolithique inférieur au paléolithique récent dans les Balkans: la grotte Kozarnikà Orechets (Nord-Ouest de la Bulgarie). – In: Molines, N., Moncel, M.-H., Monnier, J.-L. (eds), *Les premiers peuplements en Europe*. BAR International Series, 1364: 87–103.
- Hammer, Ø., Harper, D. A. T., Ryan, P. D. (2001): Past: Paleontological statistics software package for education and data analysis. – *Palaeontologia Electronica*, 4(1): 1–9.
- Hanquet, C. (2011): Évolution des paléoenvironnements et des paléoclimats au Pléistocène moyen, en Europe méridionale, d'après l'étude des faunes de micromammifères. – Université Paul Valéry-Montpellier III, Français, 446 pp.
<https://theses.hal.science/tel-00698690>
- Harting, P. (1875): Le système Émien. – *Archives Néerlandaises des Sciences Exactes et Naturelles*, 10: 443–454.
- Harvati, K., Darlas, A., Bailey, S. E., Rein, T. R., El Zaatri, S., Fiorenza, L., Kullmer, O., Psathi, E. (2013): New Neanderthal remains from Mani Peninsula, Southern Greece: The Kalamakia Middle Paleolithic cave site. – *Journal of Human Evolution*, 64(6): 486–499.
<https://doi.org/10.1016/j.jhevol.2013.02.002>

- Heinrich, W.-D., Jánossy, D. (1977): Insektivoren und Rodentier aus dem Travertin von Taubach bei Weimar. – Quartärpaläontologie, 2: 401–411.
- Hernández Fernández, M. (2006): Rodent paleofaunas as indicators of climatic change in Europe during the last 125,000 years. – Quaternary Research, 65: 308–323. <https://doi.org/10.1016/j.yqres.2005.08.022>
- Hernandez, M., Mercier, N., Rigaud, J. P., Texier, J. P., Delpech, F. (2014): A revised chronology for the Grotte Vaufray (Dordogne, France) based on TT-OSL dating of sedimentary quartz. – Journal of Human Evolution, 75: 53–63. <https://doi.org/10.1016/j.juageo.2015.06.003>
- Horáček, I. (2005): Nejmladší minulost přírody, Vojen Ložek a něco z glaciálu [Nature's youngest past, Vojen Ložek and something from the glacial]. – Ochrana přírody, 60(7): 203–208. (in Czech)
- Horáček, I., Lebedová, K. (2022): Cricetinae in the Quaternary fossil record of the Czech Republic and Slovakia (Rodentia: Cricetidae). – Lynx, n. s., 53: 365–415. <https://doi.org/10.37520/lynx.2022.024>
- Jánossy, D. (1964): Letztinterglaziale Vertebratenfauna aus der Kalman Lambrecht Höhle (Bükk-Gebirge, Nordost Ungarn) I. – Acta Zoologica Hungarica, 9–10: 139–197.
- Jánossy, D. (1986): Pleistocene vertebrate faunas of Hungary (Developments in Palaeontology and Stratigraphy, no. 8). – Elsevier Science, Amsterdam, 205 pp.
- Jánossy, D., Kretzoi-Varrók, S., Herrmann, M., Vértes, L. (1957): Forschungen in der Bivakhöhle, Ungarn. – Quaternary Science Journal, 8(1): 18–36. <https://doi.org/10.3285/eg.08.1.02>
- Jones, J. R., Marín-Arroyo, A. B., Corchón Rodríguez, M. S., Richards, M. P. (2021): After the Last Glacial Maximum in the refugium of northern Iberia: Environmental shifts, demographic pressure and changing economic strategies at Las Caldas Cave (Asturias, Spain). – Quaternary Science Reviews, 262: 106931 (18 pp.). <https://doi.org/10.1016/j.quascirev.2021.106931>
- Jones, J. R., Marín-Arroyo, A. B., Straus, L. G., Richards, M. P. (2020): Adaptability, resilience and environmental buffering in European Refugia during the Late Pleistocene: Insights from La Riera Cave (Asturias, Cantabria, Spain). – Scientific Reports, 10(1): 1217 (17 pp.). <https://doi.org/10.1038/s41598-020-57715-2>
- Jürgensen, J., Drucker, D. G., Stuart, A. J., Schneider, M., Buuveibaatar, B., Bocherens, H. (2017): Diet and habitat of the saiga antelope during the late Quaternary using stable carbon and nitrogen isotope ratios. – Quaternary Science Reviews, 160: 150–161. <https://doi.org/10.1016/j.quascirev.2017.01.022>
- Kahlke, H.-D. (1958): Die jungpleistozänen Säugetierfaunen aus dem Travertingebiet von Taubach-Weimar-Ehringsdorf. Vorbericht. – Alt-Thüringen, 3: 97–130.
- Kahlke, H.-D. (1961): Revision der Säugetierfaunen der klassischen deutschen Pleistozän-Fundstellen von Süßenborn, Mosbach und Taubach. – Geologie, 10: 493–532.
- Kahlke, R.-D. (1995): Die Abfolge plio-/pleistozäner Säugetierfaunen in Thüringen (Mitteldeutschland). – Cranium, 12(1): 5–18.
- Kahlke, R.-D. (2014): The origin of Eurasian Mammoth Faunas (*Mammuthus-Coelodonta* Faunal Complex). – Quaternary Science Reviews, 96: 32–49. <https://doi.org/10.1016/j.quascirev.2013.01.012>
- Kindler, L., Smith, G. M., García Moreno, A., Gaudzinski-Windeheuser, S., Pop, E., Roebroeks, W. (2020): The last interglacial (Eemian) lakeland of Neumark-Nord (Saxony-Anhalt, Germany). Sequencing Neanderthal occupations, assessing subsistence opportunities and prey selection based on estimations of ungulate carrying capacities, biomass production and energy. – In: García-Moreno, A., Hutson, J. M., Smith, G. M., Kindler, L., Turner, E., Villaluenga, A., Gaudzinski-Windeheuser, S. (eds), Human behavioural adaptations to interglacial lakeshore environments. Propylaeum, Heidelberg, pp. 67–104.
- Kirillova, I. V., Svitoch, A. A. (1994): Novye nakhodki srednepleystotsenovykh mlekopitayushchikh v razreze Chnernyy Yar (nizhnee “Povolzh’e”) i ikh stratigraficheskoe znachenie [New finds of Middle Pleistocene mammals in the Chnernyi Yar section (lower “Volga”) and their stratigraphic significance]. – Doklady Rossiyskoy akademii nauk, 334(6): 731–734. (in Russian)
- Kolfschoten, T. van (2002): The Eemian mammal fauna of the Northwestern and central European continent. – Le Dernier Interglaciaire et les occupations humaines du Paléolithique moyen. Publications du CERP, 8: 21–30.
- Kolfschoten, T. van (2000): The Eemian mammal fauna of central Europe. – Geologie En Mijnbouw/Netherlands Journal of Geosciences, 79(2-3), 269–281. <https://doi.org/10.1017/S0016774600021752>
- Koenigswald, W. von (1983): Kleine Säugetiere und ihre biostratigraphische Einstufung. – In: Stampfli, H. R. (ed.), Rislisberghöhle. Archäologie und Ökologie einer Fundstelle aus dem Spätmagdalénien bei Önsingen im Solothurner Jura (Academia Helvetica, 4, 1). Paul Haupt, Bern, pp. 69–81.
- Kosintsev, P. A., Yakovlev, A. G., Plasteeva, N. A., Gimranov, D. O. (2022): Mammalian fauna of the Late Pleistocene from the Barsuchiy Dol Cave (Southern Urals). – Russian Journal of Theriology, 21(2): 180–191. <https://doi.org/10.15298/rusjtheriol.21.2.09>
- Kotsakis, A., Abbazzi, L., Angelone, C., Argenti, P., Barisone, G., Fanfani, F., Marcolini, F., Masini, F. (2003): Plio-Pleistocene biogeography of Italian mainland micro-mammals. – Deinsea, 10: 313–342.
- Kotsakis, T., Pandolfi, L., Maiorino, L., Petronio, C., Sansalone, G., Salari, L. (2020): Small vertebrates from the Late Pleistocene of Avetrana (Apulia, southern Italy) karst filling. – Estudios Geológicos, 76(1): e122 (23 pp.). <https://doi.org/10.3989/egol.43378.508>
- Kukla, G. J., Bender, M. L., Beaulieu, J.-L. de, Bond, G., Broecker, W. S., Cleveringa, P., Gavin, J. E., Herbert, T. D., Imbrie, J., Jouzel, J., Keigwin, L. D., Knudsen, K.-L., McManus, J. F., Merkt, J., Muhs, D. R., Müller, H., Poore, R. Z., Porter, S. C., Seret, G., Shackleton, N. J., Turner, C., Tzedakis, P. C., Winograd, I. J. (2002): Last Interglacial Climates. – Quaternary Research 58(1): 2–13. <https://doi.org/10.1006/qres.2001.2316>
- Kuzmin, Y. V., Kosintsev, P. A., Vasiliev, S. K., Fadeeva, T. V., Hodgins, G. W. L. (2017): The northernmost and lat-

- est occurrence of the fossil porcupine (*Hystrix brachyura vinogradovi* Argyropulo, 1941) in the Altai Mountains in the Late Pleistocene (ca. 32,000–41,000 cal BP). – *Quaternary Science Reviews*, 161: 117–122.
<https://doi.org/10.1016/j.quascirev.2017.02.010>
- Kuzmina, E. A. (2009): Late Pleistocene and Holocene small mammal faunas from the South Trans-Urals. – *Quaternary International*, 201(1-2): 25–30.
<https://doi.org/10.1016/j.quaint.2008.06.013>
- Laplana, C., Sevilla, P., Martínez, N. L., Corchón, M. S. (2018): Micromamíferos (Soricomorpha, Erinaceomorpha, Chiroptera, Rodentia y Lagomorpha) del Solutrense y Magdalenense (Pleistoceno Superior Final) de la cueva de Las Caldas (Oviedo, Asturias) [Small mammals (Soricomorpha, Erinaceomorpha, Chiroptera, Rodentia and Lagomorpha) from the Solutrian and Magdalenian (late Upper Pleistocene) of Las Caldas Cave (Oviedo, Asturias)]. – In: Soledad Corchón Rodríguez, M. (ed.), *La cueva de Caldas (Priorio, Oviedo)*. Universidad de Salamanca, Salamanca, pp. 181–208. (in Spanish)
<https://doi.org/10.2307/j.ctvqht8p.12>
- Lecervoisier, B. (2003): Étude stratigraphique, sédimentologique, micromorphologique et paléoclimatique de remplissages de grottes du Pléistocène supérieur ancien de l'Europe méditerranéenne: Sites moustériens du Boquete de Zafarraya (Andalousie), de Madonna dell'Arma (Ligurie) et de Kalamakia (Laconie, Péloponnèse); Thèse. – Muséum national d'Histoire naturelle, Paris, France, 251 pp. (available online)
<https://theses.hal.science/tel-00702639>
- Lisiecki, L. E., Raymo, M. E. (2005): A Pliocene-Pleistocene stack of 57 globally distributed benthic $\delta^{18}\text{O}$ records. – *Paleoceanography*, 20(1): A1003 (17 pp.).
<https://doi.org/10.1029/2004PA001071>
- Lisiecki, L. E., Stern, J. V. (2016): Regional and global benthic $\delta^{18}\text{O}$ stacks for the last glacial cycle. – *Paleoceanography*, 31: 1368–1394.
<https://doi.org/10.1002/2016PA003002>
- Lofverstrom, M. (2020): A dynamic link between high-intensity precipitation events in southwestern North America and Europe at the Last Glacial Maximum. – *Earth and Planetary Science Letters*, 534: 116081 (9 pp.).
<https://doi.org/10.1016/j.epsl.2020.116081>
- Lomolino, M. V. (2001): The species-area relationship: new challenges for an old pattern. – *Progress in Physical Geography: Earth and Environment*, 25(1): 1–21.
<https://doi.org/10.1177/030913330102500101>
- López-García, J. M., Blain, H. A., Morales, J. I., Lorenzo, C., Bañuls-Cardona, S., Cuenca-Bescós, G. (2013): Small-mammal diversity in Spain during the late Pleistocene to early Holocene: Climate, landscape, and human impact. – *Geology*, 41(2): 267–270.
<https://doi.org/10.1130/G33744.1>
- López-García, J. M., Fernández-García, M., Blain, H. A., Sanz, M., Daura, J. (2016): MIS 5 environmental and climatic reconstruction in northeastern Iberia using the small-vertebrate assemblage from the terrestrial sequence of Cova del Rinoceront (Castelldefels, Barcelona). – *Palaeogeography, Palaeoclimatology, Palaeoecology*, 451: 13–22.
<https://doi.org/10.1016/j.palaeo.2016.03.015>
- López-García, J. M., Soler, N., Maroto, J., Soler, J., Alcalde, G., Galobart, À., Bennàsar, M., Burjachs, F. (2015): Palaeoenvironmental and palaeoclimatic reconstruction of the Latest Pleistocene of L'Arbreda Cave (Serinyà, Girona, northeastern Iberia) inferred from the small-mammal (insectivore and rodent) assemblages. – *Palaeogeography, Palaeoclimatology, Palaeoecology*, 435: 244–253.
<https://doi.org/10.1016/j.palaeo.2015.06.022>
- Lorenc, M. (2013): Radiocarbon ages of bones from Vistulian (Weichselian) cave deposits in Poland and their stratigraphy. – *Acta Geologica Polonica*, 63(3): 399–424.
<https://doi.org/10.2478/agp-2013-0017>
- Ludwig, P., Schaffernicht, E. J., Shao, Y., Pinto, J. G. (2016): Regional atmospheric circulation over Europe during the last Glacial maximum and its links to precipitation. – *Journal of Geophysical Research*, 121(5): 2130–2145.
<https://doi.org/10.1002/2015JD024444>
- Luzi, E., Pazonyi, P., López-García, J. M. (2019): The influence of climate on morphometric traits of fossil populations of *Microtus arvalis* and *M. agrestis* from the Carpathian Basin, northern Hungary. – *Lethaia*, 52(1): 123–132.
<https://doi.org/10.1111/let.12294>
- Magurran, A. E. (2004): *Measuring Biological Diversity*. – Blackwell Science, Oxford, 256 pp.
- Makkaveyev, A. N., Faustova, M. A., Karpukhina, N. V. (2020): Maksimal'naya granitsa skandinavskogo lednikovogo pokrova v valdaykuyu (vislinskuyu) epokhu i osobennosti rel'efa ego perefericheskoy zony [Maximum extent of the Valdaian (Weichselian) glaciation and relief in the peripheral area of the ice sheet]. – *Geomorfologiya*, 3: 3–19. (in Russian)
<https://doi.org/10.31857/S0435428120030098>
- Markova, A. K. (1995): Ostatki gryzunov iz pozdnepaleoliticheskoy stoyanki Yudinovo (Bassejn r. Desny) [The small mammal remains from the Late Palaeolithic site Yudinovo (Desna river basin)]. – *Citology*, 7: 625–627. (in Russian)
- Markova, A. K. (2000): The Mikulino (= Eemian) mammal faunas of the Russian Plain and Crimea. – *Geologie en Mijnbouw/Netherlands Journal of Geosciences*, 79(2/3): 293–301.
<https://doi.org/10.1017/S0016774600021776>
- Markova, A. K., van Kolfschoten, T., Bohncke, S. J. P., Kossintsev, P. A., Mol, J., Puzachenko, A. Yu., Simakova, A. N., Smirnov, N. G., Verporte, A., Golovachev, I. B. (2019): Evolution of European Ecosystems during Pleistocene-Holocene transition (24–8 kyr BP). – *GEOS, Moscow*, 277 pp.
- Markova, A. K., Puzachenko, A. Yu. (2018): Preliminary analysis of European small mammal faunas of the Eemian Interglacial: Species composition and species diversity at a regional scale. – *Quaternary*, 1(2): 9 (21 pp.).
<https://doi.org/10.3390/quat1020009>
- Markova, A. K., Puzachenko, A. Yu. (2021): The Palaeoenvironment of the Central Russian Plain during the end of the Valdai Glaciation based on Small Mammal data from the Late Palaeolithic site Byki 7 (Seim R. Basin). – *Geography, Environment, Sustainability*, 15(1): 102–111.
<https://doi.org/10.24057/2071-9388-2021-124>
- McFarlane, D. A., Ford, D. C. (1998): The age of the Kirkdale Cave palaeofauna. – *Cave and Karst Science, Transactions of the British Cave Research Association*, 25(1): 3–6.

- McGill, B. J., Etienne, R. S., Gray, J. S., Alonso, D., Anderson, M. J., Benecha, H. K., Dornelas, M., Enquist, B. J., Green, J. L., He, F., Hurlbert, A. H., Magurran, A. E., Marquet, P. A., Maurer, B. A., Ostling, A., Soykan, C. U., Ugland, K. I., White, E. P. (2007): Species abundance distributions: Moving beyond single prediction theories to integration within an ecological framework. – *Ecology Letters*, 10(10): 995–1015.
<https://doi.org/10.1111/j.1461-0248.2007.01094.x>
- Michel, V., Shen, G., Valensi, P., Lumley, H. de (2009): ESR dating of dental enamel from Middle Palaeolithic levels at Lazaret Cave, France. – *Quaternary Geochronology* 4(3), 233–240.
<https://doi.org/10.1016/j.quageo.2008.07.003>
- Miracle, P. T., Mauch Lenardić, J., Brajković, D. (2010): Last glacial climates, “Refugia”, and faunal change in Southeastern Europe: Mammalian assemblages from Veternica, Velika pećina, and Vindija caves (Croatia). – *Quaternary International*, 212(2): 137–148.
<https://doi.org/10.1016/j.quaint.2009.06.003>
- Mix, A. C., Bard, E., Schneider, R. (2001): Environmental processes of the ice age: Land, oceans, glaciers (EPILOG). – *Quaternary Science Reviews*, 20(4): 627–657.
[https://doi.org/10.1016/S0277-3791\(00\)00145-1](https://doi.org/10.1016/S0277-3791(00)00145-1)
- Moncel, M. H. (2005): Baume Flandin et Abri du Maras: Deux exemples de débitage laminaire du début du Pléistocène supérieur dans la Vallée du Rhône (sud-est, France). – *Anthropologie*, 109(3): 451–480.
<https://doi.org/10.1016/j.anthro.2005.06.002>
- Moncel, M. H. (2010): L’abri des Pêcheurs (Ardèche, sud-est France). Des occupations néandertaliennes dans une “grotte en forme de fissure”. – *Annales d’Université “Valahia” Targoviste, Section d’Archeologie et d’Histoire*, 12(2): 7–21.
<https://doi.org/10.3406/valah.2010.1059>
- Moncel, M. H., Allué, E., Bailon, S., Barshay-Szmidt, C., Béarez, P., Crégut, É., Daujeard, C., Desclaux, E., Debard, É., Lartigot-Campin, A.-S., Puaud, S., Roger, T. (2015): Evaluating the integrity of palaeoenvironmental and archaeological records in MIS 5 to 3 karst sequences from southeastern France. – *Quaternary International*, 378: 22–39.
<https://doi.org/10.1016/j.quaint.2013.12.009>
- Moncel, M. H., Crégut-Bonnoure, É., Daujeard, C., Lartigot, A. S., Lebon, M., Puaud, S., Boulbes, N., Croizet, S. (2008): Le site de la baume Flandin (commune d’Orgnac-l’Aven): Nouvelles données sur ce gisement du Paléolithique moyen. – *Comptes Rendus Palevol*, 7(5): 315–325.
<https://doi.org/10.1016/j.crpv.2008.03.005>
- Monnier, J.-L., Lefort, J.-P., Cliquet, D., Hinguant, S., Huet, B., Pigeaud, R., Ravon, A.-L. (2016): Des mammoths et des hommes en Armorique. Occupations humaines et variations de l’environnement au Pléistocène dans l’Ouest de la France. – *Bulletin du Musée d’Anthropologie et de Préhistoire de Monaco, suppl. 6*: 91–121.
- Musil, R. (2010a): The environment of the middle Palaeolithic sites in Central and Eastern Europe. – *Acta Universitatis Wratislaviensis, Studia Archaeologica*, 41: 121–179.
- Musil, R. (2010b): Palaeoenvironment at Gravettian sites in central Europe with emphasis on Moravia (Czech Republic). – *Quartär*, 57: 95–123.
- Nadachowski, A., Valde-Nowak, P. (2016): New Late Pleistocene faunal assemblages from Podhale Basin, Western Carpathians, Poland: Preliminary results. – *Acta Zoologica Cracoviensia*, 58(2): 181–194.
https://doi.org/10.3409/azc.58_2.181
- Nekhoroshev, P. E., Giryra, E. Yu. (2004): Nekotorye itogi issledovaniy verkhnepleoliticheskoy stoyanki v peshchere Kul’yurt-Tamak (Yuzhnyy Ural) [Some results of studies of the Upper Palaeolithic site in the Kul’yurt-Tamak cave (Southern Urals)]. – *Ufa Archaeological Bulletin*, 5: 12–36. (in Russian)
- Pandolfi, L., Petronio, C., Salari, L. (2013): Catastrophic death assemblages from the Late Pleistocene of Italy: The case of Avetrana karst filling (Taranto, Southern Italy). – *Rivista Italiana di Paleontologia e Stratigrafia*, 119(1): 109–124.
- Pazonyi, P., Kordos, L. (2004): Late Eemian (Late Pleistocene) vertebrate fauna from the Horváti-lik (Uppony, NE Hungary). – *Fragmenta palaeontologica hungarica*, 22(2): 107–117.
- Pearce, E. A., Mazier, F., Normand, S., Fyfe, R., Andrieu, V., Bakels, C., Balwierz, Z., Bińka, K., Boreham, S., Borisova, O. K., Brostrom, A., Beaulieu, J.-L. de, Gao, C., González-Sampériz, P., Granoszewski, W., Hryniewicz, A., Kołaczek, P., Kuneš, P., Magri, D., Malkiewicz, M., Mighall, T., Milner, A. M., Möller, P., Nita, M., Noryśkiewicz, B., Pidek, I. A., Reille, M., Robertsson, A.-M., Salonen, J. S., Schläfli, P., Schokker, J., Scussolini, P., Šeirienė, V., Strahl, J., Urban, B., Winter, H., Svenning, J.-C. (2023): Substantial light woodland and open vegetation characterized the temperate forest biome before *Homo sapiens*. – *Science Advances*, 9: eadi913 (14 pp.).
<https://doi.org/10.1126/sciadv.adi9135>
- Pemán, E. (2011): Los micromamíferos del yacimiento de Aitzbitarte III (Rentería, Gipuzkoa) (zona de entrada) [The small mammals of the Aitzbitarte III site (Rentería, Gipuzkoa) (entrance area)]. – In: Altuna, J., Mariezkurrena, K., Ríos, J. (eds), Aitzbitarte III (Euskal Herria) Giza aztarnak 33.600–18.400 BP (sarrerako eremua). Centro de Patrimonio Cultural Vasco, Vitoria-Gasteiz, pp. 481–492. (in Spanish)
- Popov, V. V., Marinska, M. (2007): An almost one million year long (Early to Late Pleistocene) small mammal succession from the archaeological layers of Kozarnika Cave in Northern Bulgaria. – *Courier Forschungsinstitut Senckenberg*, 259: 79–92.
- Povoas, L., Zilhao, J., Chaline, J., Brunet-Lecomte, P. (1992): La faune de rongeurs du Pléistocène supérieur de la grotte de Caldeirao (Tomar, Portugal). – *Quaternaire*, 3(1): 40–47.
<https://doi.org/10.3406/quate.1992.1971>
- Puzachenko, A. Yu., Markova, A. K. (2019): Evolution of mammal species composition and species richness during the Late Pleistocene-Holocene transition in Europe: A general view at the regional scale. – *Quaternary International*, 530-531: 88–106.
<https://doi.org/10.1016/j.quaint.2018.12.025>

- Puzachenko, A. Yu., Markova, A. K. (2020): Evolution of Mammalian Diversity in the Late Pleistocene–Middle Holocene of the Mountainous Regions of Northern Eurasia: Between Two Interglacials. – *Biology Bulletin*, 47: 153–171.
<https://doi.org/10.1134/S1062359020020077>
- Puzachenko, A. Yu., Markova, A. K. (2023): The Scandinavian ice sheet against the Atlantic ocean: How the Scandinavian ice sheet affected European small mammal assemblage during the Greenland stadial GS-2.1. – *Quaternary Science Reviews*, 305: 108013 (18 pp.).
<https://doi.org/10.1016/j.quascirev.2023.108013>
- Puzachenko, A. Yu., Markova, A. K., Pawłowska, K. (2022): Evolution of Central European regional mammal assemblages between the late Middle Pleistocene and the Holocene (MIS7–MIS1). – *Quaternary International*, 633: 80–102.
<https://doi.org/10.1016/j.quaint.2021.11.009>
- Puzachenko, A. Yu., Titov, V. V., Kosintsev, P. A. (2021): Evolution of the European regional large mammal assemblages in the end of the Middle Pleistocene – The first half of the Late Pleistocene (MIS 6–MIS 4). – *Quaternary International*, 605–606: 155–191.
<https://doi.org/10.1016/j.quaint.2020.08.038>
- Rasmussen, S. O., Bigler, M., Blockley, S. P., Blunier, T., Buchardt, S. L., Clausen, H. B., Cvijanovic, I., Dahl-Jensen, D., Johnsen, S. J., Fischer, H., Gkinis, V., Guillevic, M., Hoek, W. Z., Lowe, J. J., Pedro, J. B., Popp, T., Seierstad, I. K., Steffensen, J. P., Svensson, A. M., Vallelonga, P., Vinther, B. M., Walker, M. J. C., Wheatley, J. J., Winstrup, M. (2014): 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. – *Quaternary Science Reviews*, 106: 14–28.
<https://doi.org/10.1016/j.quascirev.2014.09.007>
- Razhev, D. I., Kosintsev, P. A., Ulitko, A. I. (2005): Fauna krupnikh mlekopitayushchikh pozdnego pleystotsena i golotsena iz grota Bobylek (Sredniy Ural) [Late Pleistocene and Holocene large mammal fauna from the Bobylek grotto (Middle Urals)]. – In: Razhev, D. I., Kosintsev, P. A., Ulitko, A. I. (eds), *Ural and Sibiria faunas at Pleistocene and Holocene times*. Rossiyskaya Akademiya nauk, Chelyabinsk, pp. 190–211. (in Russian)
- Reimer, P. J., Austin, W. E. N., Bard, E., Bayliss, A., Blackwell, P. G., Bronk Ramsey, C., Butzin, M., Cheng, H., Edwards, R. L., Friedrich, M., Grootes, P. M., Guilderson, T. P., Hajdas, I., Heaton, T. J., Hogg, A. G., Hughen, K. A., Kromer, B., Manning, S. W., Muscheler, R., Palmer, J. G., Pearson, C., Plicht, J. van der, Reimer, R. W., Richards, D. A., Scott, E. M., Southon, J. R., Turney, C. S. M., Wacker, L., Adolphi, F., Büntgen, U., Capano, M., Fahrni, S. M., Fogtmann-Schulz, A., Friedrich, R., Köhler, P., Kudsk, S., Miyake, F., Olsen, J., Reinig, F., Sakamoto, M., Sookdeo, A., Talamo, S. (2020): The IntCal20 Northern Hemisphere Radiocarbon Age Calibration Curve (0–55 cal kBP). – *Radiocarbon*, 62(4): 725–757.
<https://doi.org/10.1017/RDC.2020.41>
- Rekovets, L. I. (1985): Mikroteriofauna desnyansko-pozdnepepovskogo pozdnego paleolita [Small mammal fauna of Desna-Dnieper Late Palaeolithic]. – *Naukova Dumka*, Kiev, 166 pp. (in Russian)
- Rofes, J., Murelaga, X., Martínez-García, B., Bailon, S., López-Quintana, J. C., Guenaga-Lizasu, A., Ortega, L. Á., Cruz Zuluaga, M., Alonso-Olazabal, A., Castaños, J., Castaños, P. (2014): The long paleoenvironmental sequence of Santimamiñe (Bizkaia, Spain): 20,000 years of small mammal record from the latest Late Pleistocene to the middle Holocene. – *Quaternary International*, 339–340: 62–75.
<https://doi.org/10.1016/j.quaint.2013.05.048>
- Royer, A., Montuire, S., Legendre, S., Discamps, E., Jeannet, M., Lécuyer, C. (2016): Investigating the influence of climate changes on rodent communities at a regional-scale (MIS 1–3, Southwestern France). – *PLoS ONE*, 11(1): e0145600 (25 pp.).
<https://doi.org/10.1371/journal.pone.0145600>
- Rusakov, A., Nikonov, A., Savelieva, L., Simakova, A., Sedov, S., Maksimov, F., Kuznetsov, V., Savenko, V., Starikova, A., Korkka, M., Titova, D. (2015): Landscape evolution in the periglacial zone of Eastern Europe since MIS5: Proxies from paleosols and sediments of the Chermoshnik key site (Upper Volga, Russia). – *Quaternary International*, 365: 26–41.
<https://doi.org/10.1016/j.quaint.2014.09.029>
- Rustioni, M., Mazza, P., Balestri, M. (1999): The Middle-Late Pleistocene mammal fauna from Montignoso (Lepignano, central Italy). – *Alpine and Mediterranean Quaternary*, 12(1): 105–111.
- Sadykova, N. O. (2002): Melkie mlekopitayushchie pozdnelednikov'ya iz mestonakhozhdeniya Dyrovatyy Kamen' na r. Serge [Small mammals of the Late Glacial period from the Dyrovaty Kamen locality on the Serge River]. – *Biota of mountain territories: History and current state*. Ekaterinburg, pp. 183–185. (in Russian)
- Salari, L., Petronio, C., Kotsakis, T., Di Stefano, G., Grossi, F., Maiorino, L., Pandolfi, L., Rolfo, M. F., Ruiu, F. D., Sansalone, G., Tagliacozzo, A. (2019): Reassessing the faunal assemblages of the late pleistocene stratified karst filling from Avetrana (Apulia, Southern Italy): The BED 8, palaeoenvironment and biochronology. – *Alpine and Mediterranean Quaternary*, 32(2): 101–115.
- San'ko, A. F., Motuzko, A. N. (1991): Mollyuski i mlekopitayushchie iz izvestkovykh tufov Bopisovoy gopy na Zapadnoy Dvine [The mollusks and mammals from the limestone tufa of Borisova Gora on Zapadnaya Dvina River]. – *Doklady Belorusskoy AN SSR*, 35(11): 1004–1008. (in Russian)
- Schäfer, D., Heinrich, W.-D., Böhme, G., Steiner, W. (2007): Aspects of the geology, palaeontology and archaeology of the travertine site of Weimar-Ehringsdorf (Thuringia, Central Germany). – *Courier Forschungsinstitut Senckenberg*, 259, 141–147.
- Scheiner, S. M. (2003): Six Types of Species-Area Curves. – *Global Ecology and Biogeography*, 12(6): 441–447.
<https://doi.org/10.1046/j.1466-822X.2003.00061.x>
- Semken, H. A., Graham, R. W., Stafford, T. W. (2010): AMS ¹⁴C analysis of Late Pleistocene non-analog faunal components from 21 cave deposits in southeastern North America. – *Quaternary International*, 217: 240–255.
<https://doi.org/10.1016/j.quaint.2009.11.031>

- Shannon, C. E. (1948): A Mathematical Theory of Communication. – *Bell System Technical Journal*, 27: 379–423. <https://doi.org/10.1002/j.1538-7305.1948.tb01338.x>
- Simonet, P., Monnier, J. L. (1991): Approche paléo-écologique et taphonomique de la grande faune du gisement moustérien du Mont-Dol (Ille-et-Vilaine, France). – *Quaternaire*, 2(1): 5–15. <https://doi.org/10.3406/quate.1991.1948>
- Simpson, E. H. (1949): Measurement of diversity. – *Nature*, 163: 688. <https://doi.org/10.1038/163688a0>
- Slimak, L., Lewis, J. E., Crégut-Bonnaure, E., Metz, L., Ollivier, V., André, P., Chrząwcz, J., Giraud, Y., Jeannet, M., Magnin, F. (2010): Le Grand Abri aux Puces, a Mousterian site from the Last Interglacial: Paleogeography, paleoenvironment, and new excavation results. – *Journal of Archaeological Science*, 37(11): 2747–2761. <https://doi.org/10.1016/j.jas.2010.06.010>
- Smirnov, N. G., Bolshakov, V. N., Kosintsev, P. A., Panova, N. K., Korobeinikov, Y. I., Olshvang, V. N., Erokhin, N. G., Bykova, G. V. (1990): Istoricheskaya ekologiya zhivotnykh gor Yuzhnogo Urala [Historical ecology of animals of the mountains of the Southern Urals]. – *Ural Branch of the Academy of Sciences of the USSR, Sverdlovsk*, 244 pp. (in Russian)
- Socha, P. (2014): Rodent palaeofaunas from Biśnik cave (Kraków-czestochowa upland, Poland): Palaeoecological, palaeoclimatic and biostratigraphic reconstruction. – *Quaternary International*, 326-327: 64–81. <https://doi.org/10.1016/j.quaint.2013.12.027>
- Soler, L., Schmiti, A., Rambaud, D., Mistrot, V., Liolios, D., Liard, M., Brun-Ricalens, F. le, Laroulandie, V., Houmard, C., Henry-Gambier, D., Guérin, S., Griggo, C., Berthet, A.-L., Langlais, M., Gabelleau, J., Brou, L., Primault, J., Taborin, Y., Vissac, C. (2007): La grotte du Taillis des Coteaux à Antigny (Vienne): Intérêts d'une séquence originale à la structuration des premiers temps du Magdalénien. – *Bulletin de la Société préhistorique française*, 104(4): 743–758. <https://doi.org/10.3406/bspf.2007.13620>
- Stampfli, H. R. (1983): Die großen Säugetiere und das Schneehuhn als mögliche Jagdfauna. – In: Stampfli, H. R. (ed.), *Risliisberghöhle. Archäologie und Ökologie einer Fundstelle aus dem Spätmagdalénien bei Önsingen im Solothurner Jura* (Academia Helvetica, 4, 1). Paul Haupt, Bern, pp. 37–67.
- Stefaniak, K., Nadachowski, A., Tomek, T., Socha, P. (2009): Palaeontological studies in the Czestochowa Upland. – In: Stefaniak, K., Tyc, A., Socha, P. (eds), *Karst of the Czestochowa Upland and of the Eastern Sudetes: Palaeoenvironments and protection* (Studies of the Faculty of Earth Sciences, University of Silesia, No. 56). Faculty of Earth Sciences, University of Silesia, Zoological Institute, University of Wrocław, Sosnowiec, Wrocław, pp. 85–144.
- Straus, L. G., Straus, L. G. (1990): Human occupation of Euskalerria during the Last Glacial Maximum: The Basque Solutrean. – *Munibe*, 42: 33–40.
- Stringer, C. B., Finlayson, J. C., Barton, R. N. E., Fernández-Jalvo, Y., Cáceres, I., Sabin, R. C., Rhodes, E. J., Currant, A. P., Rodríguez-Vidal, J., Giles-Pacheco, F., Riquelme-Cantal, J. A. (2008): Neanderthal exploitation of marine mammals in Gibraltar. – *Proceedings of the National Academy of Sciences of the United States of America*, 105(38): 14319–14324. <https://doi.org/10.1073/pnas.0805474105>
- Stuart, A. J. (1986): Pleistocene Occurrence of *Hippopotamus* in Britain. – *Quartärpaläontologie*, 6: 209–218. <https://doi.org/10.1515/9783112652565-023>
- Sutcliffe, A. J. (1960): Joint Mitnor cave, Buckfastleigh. – *Transactions of the Torquay Natural History Society*, 13(1): 1–26.
- Svendsen, J. I., Alexanderson, H., Astakhov, V. I., Demidov, I., Dowdeswell, J. A., Funder, S., Gataullin, V., Henriksen, M., Hjort, C., Houmark-Nielsen, M., Hubberten, H. W., Ingólfsson, Ó., Jakobsson, M., Kjær, K. H., Larsen, E., Lokrantz, H., Lunkka, J. P., Lyså, A., Mangerud, J., Matiouchkov, A., Murray, A., Möller, P., Niessen, F., Nikolskaya, O., Polyak, L., Saarnisto, M., Siegert, C., Siegert, M. J., Spielhagen, R. F., Stein, R. (2004): Late Quaternary ice sheet history of northern Eurasia. – *Quaternary Science Reviews*, 23(11-13): 1229–1271. <https://doi.org/10.1016/j.quascirev.2003.12.008>
- Thery-Parisot, I., Renault-Miskovsky, J., Girard, M., Brugal, J.-P., Kervazo, B. (2008): Étude paléobotanique des dépôts du Pléistocène supérieur de la grotte de Coudoulous II (Tour-de-Faure, Lot, France). – *Quaternaire*, (19)3: 205–216.
- Tillier, A.-m., Sirakov, N., Guadelli, A., Fernandez, P., Sirakova, S., Dimitrova, I., Ferrier, C., Guérin, G., Heidari, M., Krumov, I., Leblanc, J. C., Miteva, V., Popov, V., Taneva, S., Guadelli, J. L. (2017): Evidence of Neanderthals in the Balkans: The infant radius from Kozarnika Cave (Bulgaria). – *Journal of Human Evolution*, 111: 54–62. <https://doi.org/10.1016/j.jhevol.2017.06.002>
- Titov, V. V., Golovachev, M. V. (2017): The skeleton of mammoth *Mammuthus trogontherii* cf. *chosaricus* Dubrovo, 1966 from terminal Middle Pleistocene of the Lower Volga region (Russia). – *Russian Journal of Theriology*, 16(1): 15–29. <https://doi.org/10.15298/rusjtheriol.16.1.02>
- Ulitko, A. I. (2006): Golotsenovye mlekopitayushchie iz karstovykh polostey Srednego Urala [Holocene mammals from karst cavities of the Middle Ural]. – In: Savinetskiy, A. B. (ed.), *Dinamika sovremnykh ekosistem v golotsene: Materialy Rossiyskoy nauchnoy konferencii, 2–3 fevralya 2006 g* [Dynamics of the Recent Ecosystems over the Holocene. Proceedings of the Russian scientific conference, February 2–3, 2006]. *Tovaryshchestvo nauchnykh izdaniy KMK* [KMK Scientific Press], Moskva [Moscow], pp. 243–247. (in Russian)
- Valensi, P., Abbassi, M. (1998): The reconstitution of a quaternary palaeoenvironment using different methods on a mammalian fauna – application to the Lazaret cave. – *Quaternaire*, 9(4): 291–302. <https://doi.org/10.3406/quate.1998.1611>
- Valensi, P., Crégut-Bonnaure, E., Defleur, A. (2012): Archaeozoological data from the Mousterian level from Moul-la-Guercy (Ardèche, France) bearing cannibalised Nean-

- derthal remains. – *Quaternary International*, 252: 48–55.
<https://doi.org/10.1016/j.quaint.2011.07.028>
- Valensi, P., Psathi, E. (2004): Faunal exploitation during the Middle Palaeolithic in South-Eastern France and North-Western Italy. – *International Journal of Osteoarchaeology* 14(3-4): 256–272.
<https://doi.org/10.1002/oa.760>
- Valladas, H., Mercier, N., Falguères, C., Bahain, J. (1999): Contribution des méthodes nucléaires à la chronologie des cultures paléolithiques entre 300 000 et 35 000 ans BP. – *Gallia préhistoire*, 41(1): 153–166.
<https://doi.org/10.3406/galip.1999.2163>
- Vaquero, M., Made, J. van der, Blain, H. A., Ibáñez, N., López-García, J. M., Rivals, F., Alonso, S., Ameijenda, A., Bennàsar, M., Fernández-García, M., Lombra-Hermida, A. de, Valverde, I. (2018): Fauna, environment and human presence during MIS5 in the North of Spain: The new site of Valdavara 3. – *Comptes Rendus Palevol*, 17(8): 557–593.
<https://doi.org/10.1016/j.crpv.2018.03.004>
- Velichko, A. A., Faustova, M. A., Pisareva, V. V., Gribchenko, Y. U. N., Sudakova, N. G., Lavrentiev, N. V. (2011): Glaciations of the east European plain. Distribution and chronology. – *Developments in Quaternary Science*, 15: 337–359.
<https://doi.org/10.1016/B978-0-444-53447-7.00026-X>
- Vinther, B. M., Clausen, H. B., Johnsen, S. J., Rasmussen, S. O., Andersen, K. K., Buchardt, S. L., Dahl-Jensen, D., Seierstad, I. K., Siggaard-Andersen, M. L., Steffensen, J. P., Svensson, A., Olsen, J., Heinemeier, J. (2006): A synchronized dating of three Greenland ice cores throughout the Holocene. – *Journal of Geophysical Research, Atmospheres*, 111: D13102 (11 pp.).
<https://doi.org/10.1029/2005JD006921>
- Višnjević, V., Herman, F., Prasicek, G. (2020): Climatic patterns over the European Alps during the LGM derived from inversion of the paleo-ice extent. – *Earth and Planetary Science Letters*, 538: 116185 (10 pp.).
<https://doi.org/10.1016/j.epsl.2020.116185>
- Waechter, J. d’A. (1951): Excavations at Gorham’s Cave, Gibraltar. Preliminary report for the seasons 1948 and 1950. – *Proceedings, Prehistorical Society*, 17: 83–92.
<https://doi.org/10.1017/S0079497X00018806>
- Wenzel, S. (1998): Die Funde aus dem Travertin von Stuttgart-Untertürkheim und die Archäologie der letzten Warmzeit in Mitteleuropa. – *Universitätsforschungen zur Prähistorischen Archäologie* 52: 1–272.
- Wood, R. E., Barroso-Ruiz, C., Caparrós, M., Jordá Pardo, J. F., Santos, B. G., Higham, T. F. G. (2013): Radiocarbon dating casts doubt on the late chronology of the Middle to Upper Palaeolithic transition in southern Iberia. – *Proceedings of the National Academy of Sciences of the United States of America*, 110(8): 2781–2786.
<https://doi.org/10.1073/pnas.1207656110>
- Yakovlev, A. G. (2014): Pozdneneopleystocenovaya fauna melkikh mlekopitayushchikh iz mestonakhozhdeniya v peshchere Kul’yurt-Tamak (Yuzhnyy Ural) [Late Pleistocene fauna of small mammals from the locality in the Kullyurt-Tamak cave (Southern Urals)]. – *Institute of Geology, Ufa Scientific Centre of the Russian Academy of Sciences, Ufa*, pp. 84–85. (in Russian)
- Zilhão, J. (2006): Chronostratigraphy of the Middle-to-Upper Paleolithic Transition in the Iberian Peninsula. – *Pyrenae*, 37(1): 7–84.
- Zilhão, J., Angelucci, D. E., Arnold, L. J., D’Errico, F., Dayet, L., Demuro, M., Deschamps, M., Fewlass, H., Gomes, L., Linscott, B., Matias, H., Pike, A. W. G., Steier, P., Talamo, S., Wild, E. V. (2021): Revisiting the Middle and Upper Palaeolithic archaeology of Gruta do Caldeirão (Tomar, Portugal). – *PLoS ONE*, 16(10): e0259089 (65 pp.).
<https://doi.org/10.1371/journal.pone.0259089>