

ORIGINAL ARTICLE

Mammal diversity during the Pleistocene–Holocene transition in Eastern Europe

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Abstract

Fossil record data on the mammal diversity and species richness are of importance for the reconstruction of the evolution of terrestrial ecosystems during the Late Pleistocene–Holocene transition. In Eastern Europe, the transformations during the Pleistocene–Holocene transition consisted mainly in changes in zonal structure and local fauna composition (Markova & Kolfschoten 2008). We investigated the species richness and the analogues of the α , β diversity indexes (in the sense of Whittaker 1972) of large and medium size mammals for 13 climate-stratigraphic units dating to the Late Pleistocene and the Holocene, from the Hasselo Stadial (44–39 kBP) to the Subatlantic period and the present day. The biological diversity of the Last Glacial Maximum (LGM) and the Holocene thermal optimum was investigated in more detail using information about all mammalian taxa (PALEOFAUNA database; Markova 1995). One of our results show that the α , β diversity values show only a negative correlation with the temperature conditions during the Late Pleistocene, the period that is characterized by the so-called ‘Mammoth Fauna’ complex. For the Holocene faunas the diversity indexes are nearly independent from physical conditions; the α diversity index decreased and the β diversity index increased. The relatively low α diversity and high β diversity indexes for the present-day faunas are referred to the decrease of the population number of some forest species in historical time and the increase of the dominance of unspecialized species or the species connected with intra-zonal ecosystems. The study shows furthermore the occurrence of several East European ‘centers’ with a high mammal diversity, which are relatively stable during the Pleistocene–Holocene transition. The orientation of the boundaries between the large geographical mammal assemblages depended, particularly in the northwestern part of Eastern Europe, on the expansion of the Scandinavian ice sheet.

Key words: Eastern Europe, Holocene climatic optimum, mammal diversity, Pleistocene–Holocene transition, Pleistocene Last Glacial Maximum

INTRODUCTION

Fossil data on the mammal diversity and species richness during the Late Pleistocene–Holocene transition are of extreme importance for the reconstruction of the evolution of terrestrial ecosystems as well as for the un-

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derstanding of the present-day species phylogeography. These data can provide useful information that is relevant for the debate on how to conserve mammal genetic resources in view of the effects of modern day climate change. The dramatic transformations of north Eurasian mammal assemblages during the Pleistocene–Holocene transition have already been documented; however, the focus of such studies is mainly on changes in the zonal distribution of local faunal assemblages of the ‘Mammoth Fauna’ complex and the extinction of key species (Vereshchagin & Baryshnikov 1992; Markova *et al.* 1995, 2002a,b, 2003, 2006; Markova & Puzachenko 2007; Puzachenko & Markova 2007; Markova & Kolfschoten 2008; Baryshnikov & Markova 2009).

So far, the biological diversity of fossil mammalian assemblages in a paleogeographical context has not been analyzed quantitatively. The study of ecological diversity (in the sense of Whittaker 1972) applied to paleontological data presented in this paper covers different aspects: (i) local diversity or ‘local species richness’ (i.e. the number of species recorded in a particular locality or, as in the present paper, in a ‘local faunal assemblage’) and its variation; (ii) diversity over a wider geographical area (i.e. variations of the species richness across the geographical space); and (iii) diversity at a larger scale (e.g. in biomes or other larger biogeographical units). In the study of the ecology and biogeography of modern faunas these α , β and γ diversity indexes are used in a similar way. Quantitative estimates of the diversity indexes are based on entropy data (Shannon entropy) and derived coefficients (Margalef 1957; Patten 1962; Pielou 1966; Whittaker 1972).

The database PALEOFAUNA, which was developed by a group of Russian scientists (Markova *et al.* 1995), offers the opportunity to investigate the mammalian biodiversity during different intervals of the Late Pleistocene and the Holocene. Most of the information registered in the database is from northern Eurasia and, in particular, from Eastern Europe.

First, we analyze the mammal diversity in Eastern Europe during 2 different time intervals. Both intervals are characterized by relatively extreme climatic conditions: the Last Glacial Maximum (LGM) and the Atlantic period of the Holocene (the Holocene thermal optimum). For the present study, we used data for all mammalian species recorded in the PALEOFAUNA database.

Second, we analyze the diversity indexes for the mammalian assemblages consisting of large-sized and medium-sized species (ranging from mammoth to bea-

ver) during the time interval from approximately 50 000 Before Present (BP) to the recent time. This group of mammals includes species with differences in ecological preferences/niches, and differences in distribution (widespread or with a restricted distribution) and in attitude to migration (i.e. migratory or non-migratory).

MATERIALS AND METHODS

The following climate-stratigraphic units cover the time interval of our study: the Hasselo Stadial (^{14}C uncalibrated conventional dates, 44–39 kBP, HAS); the Hengelo Interstadial (38 [39] to 36 kBP) (HEN); the Huneborg Stadial (36–33 kBP, HUN); the Denekamp (= Bryansk) Interstadial (33 to approximately 25 kBP) (DEN); the Valday (Weichselian) maximum cooling (24–17 kBP) (LGM), the Late Glacial (or Deglaciation) (17–12.4 kBP) (LGT); the Bølling and Allerød Interstadials separated by the Middle Dryas cooling (12.4–10.9 kBP) (BAIC); the Younger Dryas Stadial (10.9–10.2 kBP) (YD); the Preboreal warming (10.2–9.0 kBP) (PB); the Boreal period (9–8 kBP) (BO); the Atlantic period (8–5 kBP) (AT); the Subboreal period (5–2.5 kBP) (SB); and the Subatlantic period (2.5–0 kBP) (SA) (Mol 2008; Velichko & Faustova 2009).

The age of the species records is, in most cases, based on radiocarbon dating; the data are summarized in the PALEOFAUNA database (Markova *et al.* 1995). Conventional ^{14}C dates were calibrated using the calibration curve Intcal09 (Reimer *et al.* 2009) using OxCal 4.1. The climate (temperature) data were inferred from the Greenland Ice Core Chronology (GICC05) that is based on the ^{18}O isotope concentration in the ice core ($\delta^{18}\text{O}$, ‰). The point zero of this absolute chronometric scale corresponds to the year 2000 (presently designated as b2k) (Rasmussen *et al.* 2006; Vinther *et al.* 2006; Svenssen *et al.* 2008).

In the first part of our study, the biological diversity of Eastern European mammal communities was analyzed for the 2 climatically extreme intervals: for the coldest, and the warmest intervals of the Late Pleistocene–Holocene period, which are the Last Glacial Maximum (LGM) and the Atlantic period, respectively (Fig. 1). The aim was to quantitatively assess the spatial pattern of the species diversity within the chosen intervals. The study includes the following stages: (i) plotting the initial data (‘presence’ or ‘absence’ of the species) onto a regular grid with cell size 150×150 km (approximately $1.35^\circ \times 1.35^\circ$) using GIS MapInfo (Fig. 2); (ii) calculating the Jaccard distance, which measures

dissimilarity in species composition between every pair of grid cells; (iii) using the Jaccard dissimilarity matrix in the non-metric multidimensional scaling (Kruskal 1964) procedure (NMDS), which visualizes the proximity of relations of the grid cells by distances between points in a low dimensional Euclidean space; (iv) using the coordinate of this Euclidean space (NMDS axes)

for performing hierarchical UPMGA clustering (Euclidean distance) and identification of spatial clusters of the grid cells (for large faunal assemblages) (Fig. 3); and (v) estimating the α , β and γ diversity indexes based on the number of species in the grid clusters.

Figure 1 shows the $\delta^{18}\text{O}$ curve as the basis for the selection of the ‘coldest’ and ‘warmest’ periods during the Late Pleistocene and the Holocene. The coldest interval started approximately 28 kBP (32 000 b2k) and came to an end approximately 19 700 BP (23 500 b2k) ago. Within the Atlantic period of the Holocene the warmest interval falls between 7350 BP (8130 b2k) and 4850 BP (5580 b2k); the dates match well with presently accepted boundaries of the Atlantic climatic optimum of the Holocene in Europe (Janssen & Törnqvist 1991; Kul’kova *et al.* 2001; Schröder *et al.* 2004). Dated mammal localities (or individual horizons of some localities) are chosen for each of the considered time intervals. Altogether, we analyzed 193 localities with 78 mammal species from the coldest interval (LGM) and 130 localities with 87 mammal species from the warmest interval (Atlantic period). In the second part of the study the initial data (‘presence’ or ‘absence’ of the species) are plotted onto a regular grid with a cell size of 222×222 km ($2^\circ \times 2^\circ$), and the estimation of the α and β diversity indexes are presented for the selected assemblages of large-sized and medium-sized mammals. Adjustment of the scale was necessary because of the lower density of localities for many time slices compared to the Atlantic period and the LGM. The input data for the calculation of the diversity indices are presented in Table 1.

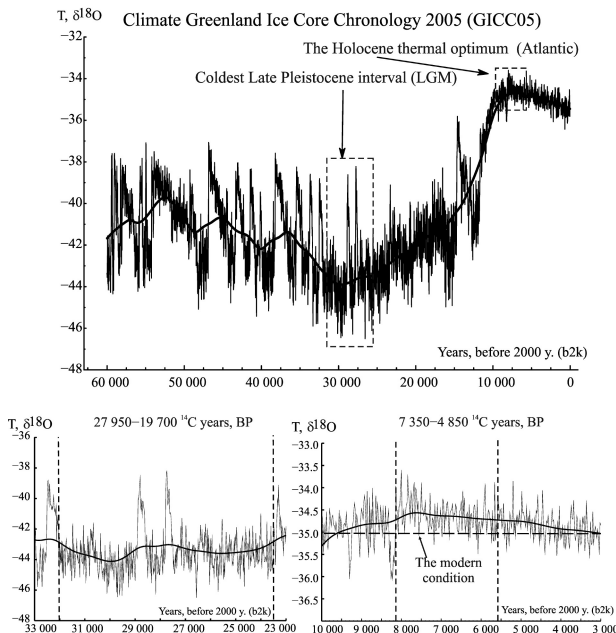


Figure 1 Climatic time series spanning the past 60 ka reconstructed from ^{18}O isotope values in the Greenland ice sheet. Highlighted are the coldest Late Pleistocene and warmest Holocene intervals.

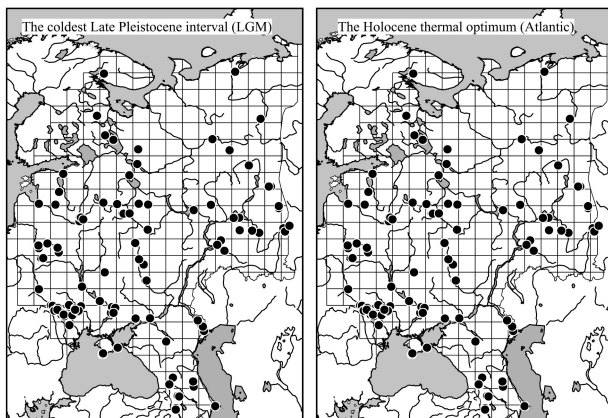


Figure 2 Position of mammal localities in Eastern Europe relative to cells of the regular grid shown for the coldest Late Pleistocene and warmest Holocene intervals.

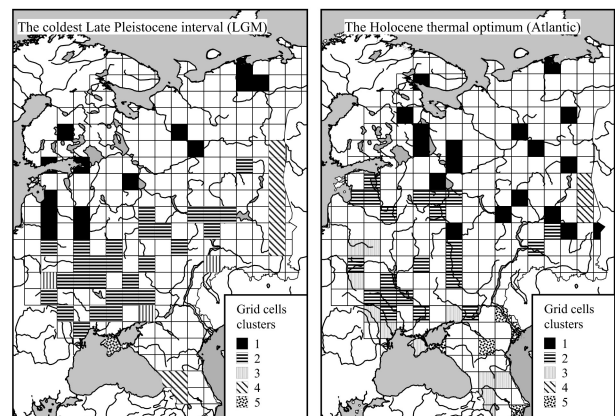


Figure 3 Position of five mammal assemblages (grid cells clusters) at the coldest Late Pleistocene and warmest Holocene intervals (1 to 5–mammal assemblages numbers).

Table 1 Data for diversity indexes calculating for the selected large and medium size mammals species

Climate-stratigraphic units	Number of grid cells ($2^\circ \times 2^\circ$) with at least one locality	Species number per climate-stratigraphic unit
Holocene		
The present time	139	28
Subatlantic (SA)	63	22
Subboreal (SB)	77	28
Atlantic (AT)	60	31
Boreal (BO)	32	25
Preboreal (PB)	12	29
Pleistocene		
Younger Dryas Stadial (YD)	12	11
Bølling and Allerød interstadials complex (BAIC)	17	17
Late Glacial (or Deglaciation) (LGT)	40	28
Valday (Weichselian) glacial epoch (LGM)	54	28
Denekamp (= Bryansk) Interstadial (DEN)	54	27
Huneborg Stadial (HUN)	24	25
Hengelo Interstadial (HEN)	22	18
Hasselo Stadial (HAS)	31	32

The analogue of the α diversity (Whittaker 1972) ($D\alpha$) is Shannon's entropy of frequency distribution of species abundance (p_i): $D\alpha = -\sum p_i \log_2 p_i$ (bit/species). In analogy, β diversity ($D\beta$) is calculated as the entropy of the distribution of the species number in grid cells (p_j): $D\beta = -\sum p_j \log_2 p_j$ (bit/grid cell). We calculated the γ diversity for both the LGM and the Atlantic period on the basis of the species distribution in 5 grid clusters (large geographical faunal assemblages), as shown in Figure 3.

RESULTS AND DISCUSSION

First, our study indicates that the boundaries of the geographical distribution of the mammal assemblages from the coldest and warmest intervals during the Late Pleistocene and the Holocene show different directions (Fig. 3). During the LGM the boundaries had a southwest to northeast orientation (except for the southernmost regions of Eastern Europe), whereas during the Holocene the boundaries ran in predominantly an west–east direction. Evidently, the Scandinavian ice sheet influenced the boundaries during the Late Pleistocene. The decay of the ice sheet caused an angular displacement (shift) of the boundaries towards a more latitudinal orientation. We obtained the same result previously, by superposing the main ecosystem boundaries within northern Europe at different time intervals during the Late Pleistocene and Holocene, the LGM, the Late Gla-

cial, the Bolling–Allerød complex, the Preboreal–Boreal and the Atlantic optimum (Markova *et al.* 1995, 2001, 2002a,b,c, 2003; Markova & Kolfshoten 2008). Based on the previous paleo-reconstructions, we assumed that the maximum deviation in the boundaries of the mammal assemblage in the Late Pleistocene–Early Holocene period was during the LGM when the boundaries were predominantly southwest–northeast oriented. During the Atlantic optimum, the boundaries of the analogous assemblages had a sub-latitudinal direction.

The spatial variability of the mammal species richness in Eastern Europe during the coldest interval of the Pleistocene and at the Holocene thermal optimum is illustrated in Figure 4. The maximum species richness during LGM time is recorded from the foot of the Carpathian Mountains and the in South Ural Mountains. The other Late Pleistocene centers rich in mammalian species have been recognized in the Crimea (Crimean Mountains) and in the area of the Central Russian Upland (the upper reaches of the Don River, Voronezh Region). The Holocene centers with a high species diversity include the Caucasus, the Urals, the Carpathians and the Central Russian Upland. A relatively high degree of mammal diversity during the Holocene thermal optimum is recorded in the western parts of Eastern Europe: in the Byelorussian Polesye and in the Zapadnaya Dvina drainage basins.

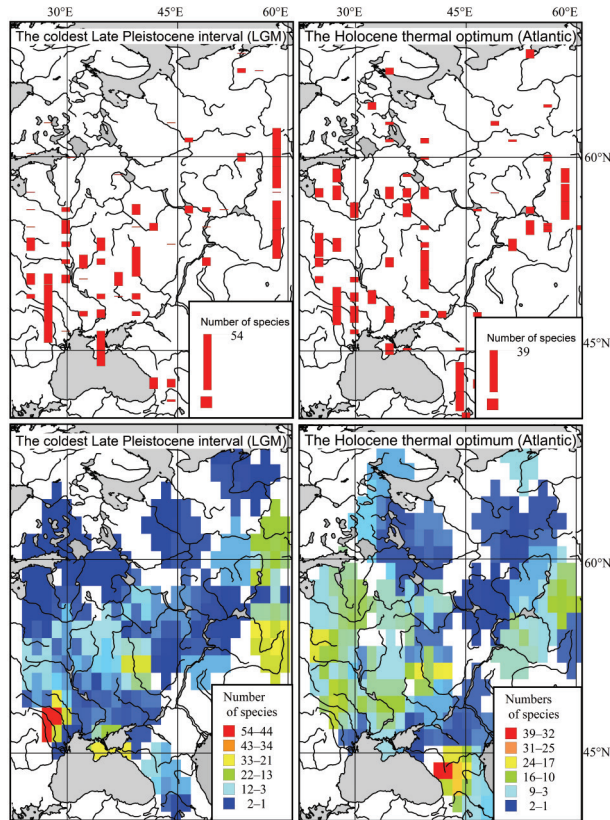


Figure 4 Mammal species (all taxa) richness (number of species/grid cell) in Eastern Europe at the coldest Late Pleistocene and warmest Holocene intervals: the upper series—initial data, the lower one—the reconstruction.

Thus, in Eastern Europe the main centers with a high mammal species diversity (including the Urals and Carpathian Mountains and the Central Russian Upland) are more or less the same during both the LGM and the Atlantic period. The higher species richness in mountains and highlands (comparing with lowlands) may be attributed to a higher degree of diversity in the local environment. The patterns in the spatial distribution of several indicator species have been studied before and presented in a number of publications (e.g. Markova *et al.* 1995; Markova & Puzachenko 2007; Markova & Kolfschoten 2008).

In the Holocene, the main center with the highest diversity in mammalian species is located in the Northern Caucasus. The relatively low species richness in the Caucasus during the Late Pleistocene may be, at least partly, attributed to the scarcity of the fossil record from that period. However, it should be taken into account

Table 2 The α , β and γ diversity indices of mammals (all taxa) in Eastern Europe during the Late Pleistocene maximum cooling and the Holocene thermal optimum

Sample number	Species number		Shannon entropy (H)	Evenness, E = H/Hmax	Index of diversity organization (redundancy), (1-E)
	Minimum	Maximum			
The Holocene thermal optimum (Atlantic) α diversity, bit/species					
87 species			5.51 \pm 0.044	0.86 \pm 0.007	0.14
β diversity, bit/grid cell ('local fauna')					
61 cells of grid	1	39	5.62 \pm 0.027	0.95 \pm 0.004	0.05
γ diversity, bit / 'geographical mammal assemblage'					
5 assemblages	13	66	2.08 \pm 0.046	0.89 \pm 0.02	0.11
The coldest interval of the Late Pleistocene (LGM) α diversity, bit/species					
78 species			5.59 \pm 0.044	0.89 \pm 0.007	0.11
β diversity, bit/grid cell ('local fauna')					
56 cells of grid	1	54	5.01 \pm 0.043	0.85 \pm 0.007	0.15
γ diversity, bit/ 'geographical mammal assemblage'					
5 assemblages	15	60	2.10 \pm 0.038	0.91 \pm 0.017	0.095

LGM, Last Glacial Maximum. MO (Measure of Organization) is equal to Index of diversity organization in Table 4.

that during the Late Pleistocene the suitable mammalian habitats were considerably reduced in areas affected by mountain glaciers. The Crimea, one of the centers with a high diversity during the Pleistocene, lost its significance during the Holocene; the same is true for the Urals, in particular the Southern Urals.

Quantitative data of species diversity based on species richness are presented in Table 2. The values of α diversity are nearly the same for both climatic intervals under consideration, except for a slightly higher diversity during the Atlantic. However, the β diversity value, showing variability of species richness in 'local' faunas, is statistically significantly ($P = 0.03$) lower in the Late Pleistocene than in the Holocene optimum. Accordingly, the degree of diversity during the coldest interval of the Late Pleistocene was higher. That is indicated by a high degree of correlation between the basic factor (NMDS axis 1) in the NMDS model and the species richness (Table 3). During the Atlantic, the species richness on the level of 'local faunas' increased and the ordering was reduced. The low value (0.05) of redundancy (Table 2), if taken formally, suggests practically stochastic variation of species numbers over the geographical area. It should be noted that in the Pleistocene the α diversity exceeds the β diversity, whereas the Holocene optimum indicates an inverse situation.

Gamma diversity characterizes the species richness variations between 5 large 'geographical mammal assemblages' (Fig. 3). This value appears somewhat higher during the Late Pleistocene maximum cooling in comparison to the Atlantic optimum. The identified variations in the γ diversity suggest that the mammal assem-

blages are less distinctly differentiated with respect to species richness during the Pleistocene in comparison to the Middle Holocene.

During the Late Pleistocene, the α diversity and β diversity values correlate negatively with the temperature values (Table 4, Fig. 5). Hence, it can be concluded that the climate conditions affected the fauna composition as well as the spatial distribution of the species. During the Holocene, a period of relatively slightly increasing temperatures, the α diversity index is steadily decreasing in time, while the β diversity index is increasing. Fluctuations in the α diversity index correspond to the changes in distribution of the frequency of species.

The low values indicate the dominance of several widespread species. For example, for the YD Stadial, bison (*Bison priscus* Bojanus, 1827) and horse (*Equus ferus* Linnaeus, 1758) cover overall nearly 26% of the observations; during the Hengelo Interstadial the mammoth frequency was 42%. A maximum of the α diversity index dates to the beginning of the Holocene (Preboreal) when the frequency of each of the most common species [e.g. *Equus ferus*, *Vulpes vulpes* (Linnaeus, 1758), *Canis lupus* Linnaeus, 1758 and *Cervus elaphus* Linnaeus, 1758)] was not more than 5%–9%. Accordingly, the local fauna was most diverse. In the Atlantic period, there was no clearly marked dominant species and approximately 7 forest mammals had frequencies from 5%–9% [*Alces alces* (Linnaeus, 1758), *Castor fiber* Linnaeus, 1758, *Sus scrofa* Linnaeus, 1758, *Bison bonasus* (Linnaeus, 1758), *Ursus arctos* Linnaeus, 1758, *C. elaphus*, *Capreolus capreolus* (Linnaeus, 1758), *V. vulpes*, *Ca. lupus* and *Meles meles* (Linnaeus, 1758)].

Table 3 The Spearman rank correlation coefficients for non-metric multidimensional scaling (NMDS) axes, the geographical coordinates of the grid cell centers and the species richness values (number of species per grid cell)

Coordinates of grid cell center	NMDS axis 1	NMDS axis 2	NMDS axis 3
Model for the Holocene thermal optimum			
Longitude	0.49	−0.04	0.07
Latitude	0.58	−0.55	0.33
Species richness	−0.38	0.55	0.45
Model for the coldest Late Pleistocene interval (LGM)			
Longitude	−0.27	−0.11	−0.05
Latitude	0.29	−0.38	−0.13
Species richness	−0.86	−0.15	−0.41

LGM, Last Glacial Maximum.

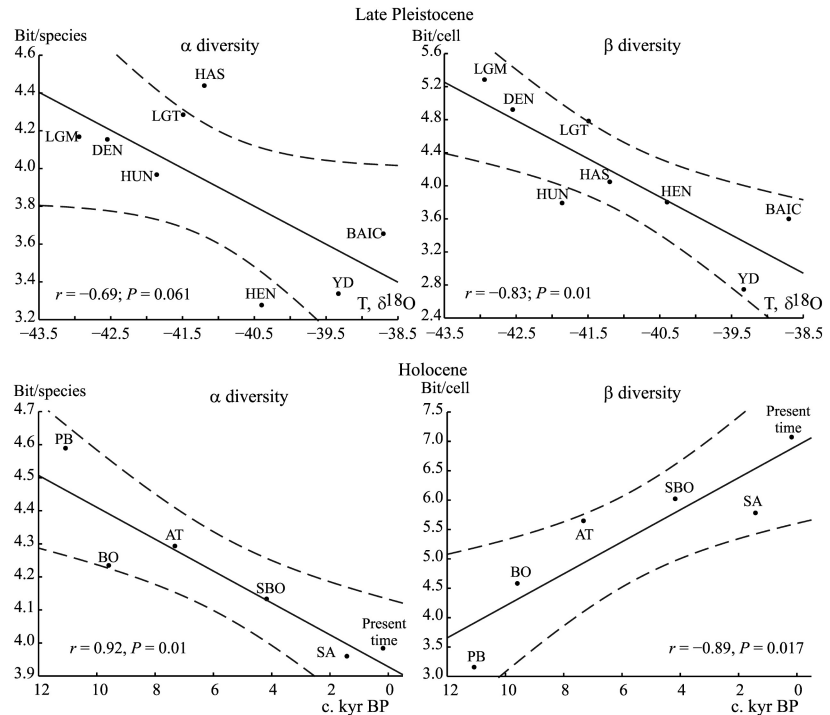


Figure 5 α , β diversity in different climate-stratigraphic units of Late Pleistocene and Holocene age in Eastern Europe. In the Late Pleistocene, both indexes are correlated negatively with temperature (T , $\delta^{18}O$). In the Holocene, α diversity decreased after a rapid increase in the Preboreal time, but β diversity increased. Both indexes changed independently from the climate changes during the Holocene.

The steady downfall of the α diversity index during the Holocene (Fig. 5) is caused predominantly by the wide distribution of the forest species, such as brown bear, elk, red deer, roe deer, beaver and others. A contemporary value of this index (3.98 bit/species) is low relative to the Holocene data and does not differ from the mean for the entire SA period. The frequencies of dominant species in the ‘local fauna’ varied from 10% to 12% in the SA (beaver, elk and brown bear) and from 10% to 11% at present time [red fox, wolf, otter [*Lutra lutra* (Linnaeus, 1758)], European badger].

In the Late Pleistocene, a relatively high level of α diversity occurred during the Hasselo Stadial when the frequency of each of 5 widespread species [*E. ferus*, *Ca. lupus*, *B. priscus*, *Coelodonta atiquitatis* (Blumenbach, 1807) and *C. elaphus*] varied from 5% to 8%. However, in this case there was a strongly pronounced dominant species, the mammoth (18%).

The β diversity index reflects the changes of species richness in geographical space. Low values reflect more heterogeneity in space (Table 4: HEN, HUN, BAIC, YD, SBO and SA). High values indicate more even distribution of species richness in Eastern Europe. The contemporary β diversity index is quite high (7.1 bit/grid

cell); it is caused by the absolute dominance of widespread species and the almost absence of ‘centers’ with a high species diversity in the mammalian group under study.

The index of diversity organization (Table 4) reflects in general the level of influence of factors that limit the diversity (e.g. climate, orography and biocoenotic). The index of diversity organization $MO \alpha$ (MO indicating the Measure of Organization, which is equal to the Index of diversity organization; see Table 4) in the Pleistocene and Holocene do not differ on average. At the same time, the $MO \beta$ was significantly higher during the Pleistocene than in the Holocene (Mann–Whitney $U = 3$, $Z = 2.7$, $P = 0.005$). These differences in parameters reflect a considerably less important role of the climate and the orography in the biological diversity of the mammal group under study.

CONCLUSION

For the first time various aspects of biological diversity of the East European mammal assemblages were quantitatively estimated for the maximum Valdai cooling (LGM), the Holocene climatic optimum and 13 oth-

Table 4 Diversity indexes calculated for the different climate-stratigraphic units of the Late Pleistocene–Holocene in Eastern Europe based on data of the distribution of large and medium sized mammals (mainly ungulates and carnivores)

Climate-stratigraphic units	α diversity ($D\alpha$)		β diversity ($D\beta$)		Index of diversity organization ($MO \beta = 1 - H/H_{max}$)
	Shannon entropy (H), bit/species	Index of diversity organization ($MO \alpha = 1 - H/H_{max}$)	Shannon entropy grid cell	Index of diversity organization ($MO \beta = 1 - H/H_{max}$)	
Holocene					
The present time	3.98 ± 0.02	0.17	7.80 ± 0.01	0.01	
Subatlantic (SA)	3.96 ± 0.03	0.11	5.79 ± 0.02	0.03	
Subboreal (SB)	4.13 ± 0.04	0.14	6.04 ± 0.02	0.04	
Atlantic (AT)	4.30 ± 0.04	0.13	5.66 ± 0.03	0.04	
Boreal (BO)	4.24 ± 0.06	0.09	4.60 ± 0.06	0.08	
Preboreal (PB)	4.59 ± 0.07	0.05	3.16 ± 0.08	0.12	
Pleistocene					
Younger Dryas Stadial (YD)	3.34 ± 0.12	0.07	2.75 ± 0.21	0.21	
Bölling and Allerød interstadials complex (BAIC)	3.66 ± 0.11	0.10	3.60 ± 0.11	0.12	
Late Glacial (or Deglaciation) (LGT)	4.29 ± 0.04	0.11	4.79 ± 0.04	0.10	
Valday (Weichselian) maximum cooling (LGM)	4.17 ± 0.05	0.13	5.29 ± 0.04	0.08	
Denekamp (= Bryansk) Interstadial (DEN)	4.16 ± 0.07	0.13	4.93 ± 0.08	0.14	
Hünegberg Stadial (HUN)	3.97 ± 0.11	0.15	3.80 ± 0.11	0.17	
Hengelo Interstadial (HEN)	3.28 ± 0.19	0.21	3.81 ± 0.15	0.15	
Hasselo Stadial (HAS)	4.44 ± 0.09	0.11	4.05 ± 0.01	0.18	

MO, Measure of Organization. MO is equal to index of diversity organization in Table 2.

er climate-stratigraphic units of Late Pleistocene and Holocene age. First, it has been indicated that the total number of species (species richness) remained practically the same for the extreme cold (the LGM) as well as the extreme warm time interval (the Atlantic), in spite of essential difference in the geographic distribution of the species richness in both periods. The variations in species richness and distribution were due to changes in climatic conditions as well as to the swift extinction of large herbivores and carnivores from the 'Mammoth Fauna' complex at the end of the Pleistocene. The species composition of the mammal fauna was subject to radical changes in every region of Eastern Europe. These aspects of changes in species diversity and the re-establishment of the mammal assemblages in Europe at the Pleistocene–Holocene transition are described and discussed in more details in an earlier work (Markova & Kolfschoten 2008).

The results of this studies allow the identification of several 'centers' with a high mammalian species richness: those established for the Late Pleistocene maximum cooling (Valday) are confined to the Carpathians, the Crimea Mountains, the South Urals and the Central Russian Upland; in the Atlantic, the centers of maximum species richness are found in every mountainous region, including the Caucasus. Therefore, it can be concluded that the geographical positions of the main diversity centers in the Eastern Europe are relatively stable.

The geographical boundaries of the mammal assemblages from the coldest and warmest intervals show different orientation during the Late Pleistocene and the Holocene. Their orientation is effected by the Scandinavian ice sheet, particular in the northwestern part of the region.

At the time of the LGM a limited number of species inhabited the zone fringing the ice sheet (north of approximately 55°N) (Fig. 4); further south, on the plains of Eastern Europe down to 45°N, the discovered species increased in number to approximately 12. The species richness still grew (up to 22 species) near the foot of the Carpathians, and probably also towards the coasts of the Black and Azov Seas (although the data for these 2 regions are extremely scarce). The central part of the Russian Plain shows rather stable values of species richness, probably due to widely spread periglacial open landscapes and the absence of a forest zone. At the Holocene optimum, the distribution of the mammal species richness from north to south appears to be quite different. According to our data, faunas with low species richness existed north of 60°N. Southwards, mam-

mal faunas gradually increased in species richness up to 15 species at 55°N. According to paleontological data, the number of species increased further south, up to 25 species, presumably due to the reoccurrence of a forest zone. The scarcity of data in some mountain regions (the Carpathians and the Crimean Mountains) precludes the reconstructing of real values of species richness in these areas; we assume that these values are high. The only identified region with a high species diversity for this interval is the Caucasus Mountains. A steadily high level of species richness (both in the Late Pleistocene and in the Holocene) was recorded in the high reaches of the Don River (Central Russian Upland). The same is true for the South Urals and partly for the Middle Urals. The Urals mammal species richness appeared to be higher during the Late Pleistocene cooling (LGM) than at the Holocene optimum or at present. That may be attributed to the penetration of tundra species from the north and steppe species from the south, along with some persisting forest dwellers. Remarkable is the relatively high level of species richness in western regions of Eastern Europe (Belarusian Paleśsie and the Western Dvina drainage basin); it was caused by the reoccurrence of a greater quantity of forest species.

It should be noted that in every case the data available were insufficient to reliably reconstruct the species richness for the all taxa. That is why we can only present relative estimates. Nevertheless, the data indicate the principal tendency in species richness that changes geographically from north to south.

The analogue values of the α and β diversity indexes were obtained for the first time using Eastern European paleontological data. These indexes are integral variables that reflect different aspects of the biodiversity structure. During the Late Pleistocene the values of both indexes correlate negatively with the temperature values. There is a link between the interstadial–stadial fluctuations and the dramatic collapse of the ‘Mammoth Fauna’ complex at the end of the Late Pleistocene. During the Holocene, Eastern Europe changed relatively quickly, with a widespread reestablishment of forest and the reoccurrence of forest species in the first place. The diversity indexes of large and medium sized mammals barely reacted to the changes in climatic conditions during the Holocene.

Nowadays, the α diversity index is relatively low and the β diversity index is relatively high, which we attribute to a decrease, in historical time, in the population number of some forest species (beaver, brown bear and red deer) and the increase of the dominance of species

that can occupy different habitats as well as an increase of species connected with intra-zonal ecosystems (i.e. red fox and European otter).

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REFERENCES

- Baryshnikov GF, Markova AK (2009). The main mammal assemblages during the Late Pleistocene cold epoch (map 23). In: Velichko AA, ed. *Paleoclimates and Paleoenvironments of Extra-Tropical Area of the Northern Hemisphere. Atlas-monograph*. GEOS Publishing, Moscow, pp. 79–87. (In Russian.)
- Janssen SR, Törnqvist TE (1991). The role of scale in the biostratigraphy and chronostratigraphy of the Holocene Series in the Netherlands. *The Holocene* **1**, 112–20.
- Kruskal B (1964). Multidimensional scaling by optimizing goodness of fit to nonmetric hypothesis. *Psychometrika* **29**, 1–27.
- Kul'kova MA, Mazurkevich AN, Dolukhanov PM (2001). Chronology and palaeoclimate of prehistoric sites in Western Dvina-Lovat' Area of northwestern Russia. *Geochronometria* **20**, 87–94.
- Margalef R (1957). Information theory in ecology. *Memorias de la Real Academia de Ciencias y Artes de Barcelona* **23**, 373–449.
- Markova AK, Kolfschoten T, eds (2008). *Evolution of European Ecosystems During Pleistocene–Holocene Transition (24–8 kyr BP)*. KMK Scientific Press, Moscow. (In Russian with English summaries.)
- Markova AK, Puzachenko AY (2007). Late Pleistocene mammals of Northern Asia and Eastern Europe. In: Elias SA, ed. *Vertebrate Records. Encyclopedia of Quaternary Science* **4**. Elsevier B.V., London, UK, pp. 3158–74.
- Markova AK, van Kolfschoten T, Simakova AN, Puzachenko AY, Belonovskaya EA (2006). Ecosystems of Europe during the Late Glacial Bølling–Allerød warming based on pollen data and mammal fauna. *Izvestiya Russian Academy of Sciences, Seria Geographicheskaya* **1**, 15–25. (In Russian.)

- Markova AK, Simakova AN, Puzachenko AY (2003). Ecosystems of Eastern Europe at the Atlantic optimum of the Holocene based on floristic and theriological data. *Russian Academy of Sciences, Doklady* **391**, 545–9.
- Markova AK, Simakova AN, Puzachenko AY (2002a). Ecosystems of Eastern Europe at the time of maximum cooling of the Valday glacial epoch based on floristic and theriological data. *Russian Academy of Sciences, Doklady* **389**, 681–5.
- Markova AK, Simakova AN, Puzachenko AY, Kitayev LM (2002b). Reconstruction of the natural zonality on the Russian Plain during the Bryansk warm interval (33–24 ka BP). *Izvestiya of Russian Academy of Sciences. Seriya Geograficheskaya* **4**, 45–57.
- Markova AK, Smirnov NG, Kozincev PA *et al.* (2001). Zoogeography of Holocene mammals in northern Eurasia. *Lynx* **32**, 233–45.
- Markova AK, Smirnov NG, Kozharinov AV, Kazantseva NE, Simakova AN, Kitaev LM (1995). Late Pleistocene distribution and diversity of mammals in Northern Eurasia (PALEOFAUNA database). *Paleontologia i Evolucio* **28–29**, 5–143.
- Mol J (2008). Definition of the time slices. Landscape and climate change during the Last Glaciation in Europe; a review. In: Markova AK, van Kolfschoten T, eds. *Evolution of European Ecosystems during Pleistocene–Holocene Transition (24–8 kyr BP)*. KMK Scientific Press, Moscow, pp. 73–87.
- Patten BC (1962). Species diversity in net phytoplankton of Raritan Bay. *Journal of Marine Research* **20**, 57–75.
- Pielou EC (1966). The measurement of diversity in different types of biological collections. *Journal of Theoretical Biology* **13**, 131–44.
- Puzachenko AY, Markova AK (2007). Spatial and temporal dynamics of mammal species diversity in Europe within a geologically short time interval (Late Pleistocene–Holocene). In: Pavlov DS, Zakharov VM, eds. *Climatic Changes and Biodiversity in Russia: Statement of the Problem*. Acropolis Publishing House, Moscow, pp. 73–94.
- Rasmussen SO, Andersen KK, Svensson AM *et al.* (2006). A new Greenland ice core chronology for the last glacial termination. *Journal Geophysical Research* **111**, D06102.
- Reimer PJ, Bailli, MGL, Bard E *et al.* (2009). Intcal09 and Marine09 radiocarbon calibration curves, 0–50 cal kBP. *Radiocarbon* **51**, 1111–50. OxCal 4.1. [Cited 25 Feb 2011.] Available from URL: <http://c14.arch.ox.ac.uk/embed.php?File=oxcal.html>
- Schröder N, Højlund PL, Juel BR (2004). 10,000 years of climate change and human impact on the environment in the area surrounding Lejre. *The Journal of Transdisciplinary Environmental Study* **3/1**, 1–27.
- Svensson A, Andersen KK, Bigler M *et al.* (2008). A 60 000 year Greenland stratigraphic ice core chronology. *Climate of the Past* **4**, 47–57.
- Velichko AA, Faustova MA (2009). The ice sheet development during Late Pleistocene. In: Velichko AA, ed. *Paleoclimates and Paleoenvironments of Extra-Tropical Area of the Northern Hemisphere. Atlas-mono-graph*. GEOS Publishing, Moscow, pp. 32–41. (In Russian.)
- Vereshchagin NK, Baryshnikov GF (1992). The ecological structure of the ‘Mammoth Fauna’ in Eurasia. *Annales Zoologici Fennici* **28**, 253–9.
- Vinther BM, Clausen HB, Johnsen SJ *et al.* (2006). A synchronized dating of three Greenland ice cores throughout the Holocene. *Journal of Geophysical Research* **111**, D13102.
- Whittaker RH (1972). Evolution and measurement of species diversity. *Taxon* **21**, 213–51.