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Diversity dynamics of large- and medium-sized mammals in the Late Pleistocene and the Holocene on the East European Plain: Systems approach

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ABSTRACT

In this study, we analyze the large-sized and medium-sized mammalian species (ranging from mammoth to beaver and fox) which were distributed on the East European Plain from 50 ka BP to the recent, organized into four faunal Complexes. We would like to answer a general and basic question: which category of natural processes (linear – nonlinear, equilibrium – nonequilibrium, steady – unsteady and reversible – irreversible) characterizes evolution of fauna composition and dynamics of species richness. Several hypotheses about the influence of "geographical factor" on the parameters (entropy, measure of order, beta diversity analog) of mammals' diversity evolutionary dynamics were tested. For all Complexes, individual multivariate models (with 2–3 dimensions) of the faunal assemblage dynamics were developed to describe the Late Pleistocene–Holocene transition. The beginning of radical fauna transformation on the East European Plain is dated, approximately, by the end of Greenland Stadial 2.1a (14,650 BP). The main drivers of changes in the fauna composition were radical climate changes during the Late Pleistocene. Unlike the composition of faunal assemblages, variability of the species richness did not correlate with climate, except for the transition time. On the East European Plain, the replacement of the "lost species" from the "Mammutus – Coelodonta" faunal Complex with the "new ones" from the forest and more thermophilic species groups proceeded without considerable decrease of general species richness of large mammals. Different faunal Complexes have some specific features that reflect the geographical latitudinal gradient in both the composition of faunal assemblages and species richness. Two relatively independent processes influenced the content of evolution of mammal assemblages: 1) species compositions changes classified as nonlinear, non-equilibrium, irreversible and stationary in the Pleistocene, but not in the Holocene; 2) dynamics of species richness is characterized as linear, reversible and stationary throughout, except for the transition time. In the Holocene, species richness was restored very quickly, but it did not exceed the level which was typical for the Late Pleistocene. It is likely that the Late Pleistocene ecological capacity of ecosystems was probably higher in comparison with modern Holocene ecosystems.

1. Introduction

Fossil record data on the mammal diversity and species richness are of importance for the reconstruction of 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. The sharp transformations of Eastern European mammal assemblages on the Pleistocene–Holocene boundary have already been documented (Markova et al., 2001, 2002a,b, 2003, 2006; Baryshnikov and Markova, 2002, 2009; Markova and Puzachenko, 2007; Puzachenko and Markova, 2007; Markova and Kolfschoten, 2008; Ponomarev et al., 2013). Nonetheless, dynamics of the biological diversity of fossil mammalian assemblages in a paleo-geographical context on the East European Plain have not been analyzed in detail (Puzachenko and Markova, 2014).

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Common research programs for reconstruction of local fauna spatial distribution involve comparison of “even-aged” faunal assemblages. This multivariate analysis includes the estimation of the “distance” between local faunas according to differences of their species compositions. The results of classification/clustering of the localities have been mapped and this “picture” is the basis for further geographical reconstructions. These reconstructions reflect the situation “on average” for the chosen time interval, which corresponds to selected stages of global climate dynamics. The traditional approach usually does not directly involve study of temporal dynamics of faunal assemblages. In this case, the raw material is divided according to time slices, which defined a priori relation to paleontological data. In such studies for the Late Pleistocene and the Early-Middle Holocene, there were more or less reasonable assumptions that observed fauna changes are the effects of global climate changes, in the first instance. Analysis of the dynamics compares the results obtained for different time intervals. The main problem, which significantly causes difficulty, is the incompleteness of the initial paleontological data and uneven distribution of localities within the geographic space.

The database PALEOFAUNA, developed by a group of Russian scientists (Markova et al., 1995) during last 20 years, offers an opportunity to investigate the mammalian biodiversity in the Late Pleistocene and the Holocene in Northern Eurasia. A considerable part of information registered in the database is from Eastern Europe.

In previous studies (Puzachenko and Markova, 2011; Markova and Puzachenko, 2012; Puzachenko and Markova, 2014), we examined the variables of biological diversity (species richness) throughout the East European Plain as a “unified system” in the Late Pleistocene and the Holocene. It shows a negative relationship between biodiversity with the temperature conditions during the Late Pleistocene, but a lack of this correlation in the Holocene. In addition, the species richness of mammals in the Late Glacial Maximum and the Holocene climatic optimum were about equal.

In this study, we tested a hypothesis about ‘system nature’ of the changes in fauna observed on the East European Plain during the Late Pleistocene and the Holocene. We would like to answer the general and basic question: which category of natural processes (linear – nonlinear, equilibrium – nonequilibrium, steady – unsteady and reversible – irreversible) characterize the evolution of fauna composition and dynamics of species richness. In addition, we have tested several hypotheses on the influence of “geographical factor” on mammal diversity dynamics, and compared species diversity on the East European Plain during the Late Pleistocene–Holocene transition.

2. Regional setting

The East European Plain (or Russian Plain) is a part of Europe extending eastward approximately from 25° to 60° longitude, from the Polish Plain to the Ural Mountains. The average height of the plain is 170 m a.s.l., maximum height – 479 m a.s.l. It is divided into two unequal parts: the ground-denudation plain on the Baltic shield and the Russian plain proper, with the erosion-denudation and accumulation relief on the Russian and Scythian plates.

The greater part of the East European Plain belongs to the region of temperate zone that has a west–east transition from marine to continental climate. The modern natural zonality of the East European Plain includes, from north to south: tundra, forest belt (dark coniferous taiga, coniferous-broadleaf forests, and broadleaf forest), forest-steppe and steppe zones. Rainfall decreases from 600 to 900 mm per year in the west to 300–200 mm in the south and the southeast. The southern East European plain has dry (true) steppes, and in the extreme southeast and the Caspian lowland, semi-deserts and deserts (Mil'kov and Gvozdezki, 1986).

3. Material and methods

The age of the species records is, in most cases, based on radiocarbon dating. Data are summarized in the PALEOFAUNA database (Markova et al., 1995). Conventional ^{14}C dates were calibrated using the calibration curve Intcal13 using OxCal 4.2 (Ramsey, 2009; Ramsey, Lee, 2013; Reimer et al., 2013). The climate (temperature) data were inferred from the Greenland Ice Core Chronology (GICC05) based on the ^{18}O isotope concentration in the Greenland Ice Core ($\delta^{18}O$, ‰) (Andersen et al., 2006; Rasmussen et al., 2014; Vinther et al., 2006; Svensson et al., 2008).

The “landscape-zonal” approach in biogeography based on the study of species, linked with each other with in the shared natural community or having ecological relationships both with each other and with components of plant communities (Abdurakhmanov et al., 2001). The zoogeographical contours can coincide with the natural zonality. Within the framework of the “faunal-genetical” approach, the zoogeographical zonation is based on detailed study of the species ranges (especially endemics and relicts) and faunal complexes, as well as on finding historical differences between faunas. In the framework, which we are developing in this study, both methods are combined in one procedure.

In the first step, the data (spatial contours) of ranges of extant Eastern Europe mammals (95 taxa; bats excluded) were aggregated by the regular spatial grid cells in GIS MapInfo Professional (Pitney Bowes Software Inc.). Each grid cell was represented by the tetragonal polygon with the sides equal to 2°. Using grids for aggregation of spatially distributed data is a conventional technique in different research fields (Davis et al., 2003; Malkhazova et al., 2012; Šímová et al., 2014). All preliminary calculations were carried out in the GIS. For species range conversions into the grid table, each grid cell that overlaps with the contour of the range was assigned value “1”, and all other cells were assigned value of “0”. The summary table contains the data of all species.

In the second step, quantitative differences (distances) between any pairs of grid cells by their species composition were measured. The Jaccard index has been calculated to estimate the cell–cell distances. The matrix of Jaccard distances was used in the multivariate statistical analysis in the next step of data processing. In our case, the goals of multivariate analysis were as follows: 1) developing the model that visualizes the proximity of relations of the grid cells by distances in a low dimensional Euclidean space, 2) clustering of grid cells on the coordinates of this modeling space. The first goal was reached using the non-metric multidimensional scaling method (Shepard, 1962; Kruskal, 1964; Davison and Jones, 1983).

The coordinates of modeling space contain independent information from data. The cluster analysis (UPGMA method) based on these coordinates was used for clustering of grid cells. The result of clustering for the selected level was mapped in GIS (several small clusters were combined) (Fig. 1a) (see also Markova and Kolfschoten, 2008: p. 280). Overall, the result of zoning reflects both the latitudinal extent of the extant species range boundaries and the close link between mammal distributions and types of the plant communities.

There are four present-day “faunal complexes”: Complex I – the tundra/forest-tundra-northern taiga, Complex II – the middle and southern taiga, mixed forests, Complex III – the broadleaf deciduous forests and wooded steppe and Complex IV – the true steppe. We used these spatial units for the further study of time evolution of mammalian paleontological complexes.

The data of the remains of 43 large-sized and medium-sized mammals from 497 paleontological sites were selected from the PALEOFAUNA database. This information was aggregated in GIS using the four spatial units – “Complexes” (Fig 1b).

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