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Evolution of the European regional large mammals assemblages in the end of the Middle Pleistocene – The first half of the Late Pleistocene (MIS 6–MIS 4)

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ABSTRACT

The Middle Pleistocene – Late Pleistocene transition of European large mammal's fauna (Proboscidea, Artiodactyla, Perissodactyla, Carnivora, *Hystrix* and *Castor*) assemblages has been studied in 18 European regional faunal assemblages. This study is based on the data yielded from 423 palaeontological sites (758 localities) dated within interval of MIS 6–MIS 4. All the data was aggregated by 9 time intervals (time scale). For ten bioregions, we have been able to obtain descriptive models of evolution of their faunal assemblages. It allowed detecting common rules of changes in large mammals' fauna composition in Europe on the whole as well as changes in the distribution of individual species and their groups within the regions. We have studied the changes in biodiversity parameters (Shannon index, index of self-organization) and Mourelle–Ezcurra species turnover index within MIS 6–MIS 4 time interval. The evolution of European fauna was compared for MIS 6–MIS 5 transition and MIS 2–MIS 1 transition as well as influence of change in global temperature on these transitions was described. In addition, we have showed the correlation between modern species richness with the species richness in MIS 6, MIS 5 and MIS 4 and proposed the hypothesis of historical succession of European bioregions.

1. Introduction

A large volume of data on the large mammals – inhabitants of Europe at the end of Middle and the first half of the Late Pleistocene – have been accumulated by the European palaeontologists over the recent decades. The information should be generalized and interpreted so as to get a notion of the general pattern and regional characteristics of the ecosystem evolution in the western Eurasia on the background of wide fluctuations of the global climate at the end of Middle and Late Pleistocene: Dnieper (= Saale, Wolston, Riss, Pechora) Glaciation – Mikulino (= Eem, Ipswich) Interglacial – Valdai (= Vistula, Weichsel, Würm, Devens) Glaciation (Glückert, 1974; Rose, 1987; Velichko et al., 2005, 2011; 2012; Litt et al., 2007; Fiebig and Preusser, 2008; Gibbard et al., 2009; Ehlers et al., 2013; Astakhov et al., 2016).

There are many published papers dealing with the mammal fauna at the time of the Last Glacial Maximum (MIS 2) and the transition to the Holocene Interglacial (MIS 1), the period most important also for understanding the evolution of human populations (Markova et al., 2019; Pavelková Řičánková et al., 2015; ; Álvarez-Lao and Méndez, 2016; Crees et al., 2016; Fernández-García et al., 2016; Danukalova et al., 2018; Puzachenko, 2019; Kovalchuk et al., 2020). At the same time, we have not yet a comprehensive knowledge of the general regularities, nor regional specific features of the large mammal fauna evolution at the boundary of MIS 6 (~200/191–140/130 ka BP) MIS 5e (~130–115/111 ka BP) (Shackleton et al., 2003; Lisiecki and Raymo, 2005; Molodkov and Bolikhovskaya, 2006; Otvos, 2015). The same is true, even to a greater extent, of the fauna evolution from Eemian interglacial to the Weishel (= Valdai) Glaciation (MIS 5d–MIS 4). The evolutionary changes in the fauna composition and the ranges of individual species at the Middle/Late Pleistocene boundary might have a pronounced effect on the range and quantity of hominids (and first of all, Neanderthals), which used many species of that group (including members of megafauna) as an important source of food (Defleur and Desclaux, 2019).

In this work we included species of Proboscidea, Artiodactyla (= Cetartiodactyla), Perissodactyla, Carnivora (including small-sized mustelids) and Rodentia (*Hystrix*, *Castor*) orders into the "large mammal"

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group. The environmental and feeding preferences of that species group are highly variable. Most of them are herbivorous, and the proportion of carnivorous is much smaller. Many herbivores are known for gregarious habits, some of them make seasonal migrations. Several species (mammoths, woolly rhino, reindeer, cave lion, and some others) form the main body of the "*Mammuthus–Coelodonta*" fauna that developed at the end of Middle – the early stage of the Late Pleistocene and reached its maximum at the second part of the Late Pleistocene in Northern Eurasia (Kahlke, 2014).

Unlike small mammals (Markova and Puzachenko, this volume), a great number of megafauna species became extinct, in particular at the end of the Late Pleistocene – beginning of the Holocene. Changes in the spatial distribution of certain species (straight-tusked elephant, mammoths, rhinoceros, reindeer, fallow deer, roe deer, elk, saiga, beaver, and porcupines) are reliable indicators of environmental changes. The large mammal fauna response to the sharp rise of the global temperature in MIS 6–MIS 5, and in MIS 5e phase especially, is of particular interest.

Large mammals are known for a high diversity of their morphology, various environmental preferences and ethological diversity; all those characteristics determine their leading position in the Pleistocene ecosystem functioning. It was the extinction of megafauna that resulted in a radical transformation of the terrestrial ecosystems not only in Europe, but also all over Northern Eurasia. Similar, though probably not quite identical, processes took place also in the South-East of Asia and in North America at the end of the Pleistocene (Grayson, 2007; Wan and Zhang, 2017).

Numerous and diversified findings of large mammals make it possible to trace the changes in the species assemblages both in time (at a scale of the oxygen isotope stages – MIS) and in space – over large areas and individual regions of Europe. The abundance of data permits to use statistical analysis of the data for describing regularities of evolution, including its regional characteristics. In the present paper the statistical methods were applied to estimating changes in some parameters of the biological diversity of the large mammals at the end of Middle Pleistocene – the first half of the Late Pleistocene, the models of faunal assemblage evolution being developed for some regions. In this work we leaned on our previous experience in statistics application to the analysis of large massifs of palaeontological data available on the second half of the Late Pleistocene and the Holocene in Europe (Puzachenko and Markova, 2014, 2016; 2020; Puzachenko, 2019).

Our investigations were primarily aimed at estimating of general regularities in temporal changes in the large mammal fauna in Europe beginning from individual species and up to regional faunal assemblage. Multivariate analysis of a large array of palaeontological data was used to obtain descriptive models of evolution of regional mammal assemblages. We also studied changes of species richness and spatial (within regions) diversity of species distribution for the time intervals corresponding to MIS 6, MIS 5e, MIS 5d–MIS 5a, and MIS 4. We discussed the problem of the stability/instability of mammalian faunal complexes at the Middle Pleistocene – Early Late Pleistocene and at the end of the Late Pleistocene – Holocene, and, in conclusion, we gave the evidence of the hypothesis about relative temporal stability of European zoogeographic units (bioregions).

2. Materials and methods

2.1. European bioregions

The European biogeographical zones used in this studies as in the previous ones (Markova and Puzachenko, 2018; Puzachenko and Markova, 2019; Puzachenko, 2019) are based on modern terrestrial mammal ranges (Spatial Data, IUCN Red List of Threatened Species: https://www.iucnredlist.org/resources/spatial-data-download). We used regular spatial grid cells (150 × 150 km) with lists of species and classified them that have been described in literature (Heikinheimo et al., 2007; Kreft and Jetz, 2010). The matrix of pairwise dissimilarities of grid cells was calculated using the Jaccard coefficient as the distance metric. Then, we used nonmetric multidimensional scaling in order to estimate multidimensional Euclidian space for grid' cells ordination. Four first axes of this modelled space were used for cell clustering using the dichotomy k-means clustering algorithms in order to form clusters with the most similar cells. The names and abbreviations of 18 regions are given in Table 1 and Fig. 1.

Here we consider the European territory within its conventional geographical boundaries. In the east the boundaries are drawn rather arbitrarily, as the European subcontinent is actually a part of Eurasia and is not separated from Asia proper by substantial geographical barriers. Nevertheless, various variants of the biogeographical zonation (Mekaev, 1987; Krivokhatsky and Emeljanov, 2000), including those based on generalized data of the remote sensing of the Earth (Condé et al., 2002), provide corroborative evidence for the validity of the south-eastern boundary of Europe being drawn between the edge of the East European Platform (Russian Platform) and the Caspian Depression. The formal boundary between Europe and Asia (West Siberia) is the Ural Mountains running from north to south. The present-day fauna of the Urals is of mixed composition and includes many species with the major part of the range lying in Siberia. According to our classification, the range of the modern mammal assemblage of the Urals (the Middle and Southern Urals and adjoining territory) belongs to North Eurasian "East European – Asian West-Siberian Central" region (Table 1). Palaeontological data do not contradict that conclusion, as will be shown below. So we included into our investigations localities in the Ob' River drainage basin and Western Altai region (Fig. 1).

2.2. Database

The study was carried out using the palaeontological bibliographic database PALEOFAUNA (Markova et al., 1995, 2019), which was collected and maintained by the authors over the past 25 years at the Institute of Geography, Russian Academy of Sciences (registration number 2011620493). Full list of the 441 geographical sites with 708 palaeontological localities (layers, units, etc.), used in our meta-analysis, are placed in the Supporting materials (Table S1). We used presence – absence data of species ("incidence" data) in order to include in the study as many as possible information sources.

The list of 36 localities datable to MIS 6 – MIS 4 and presenting a great interest in the context of the performed work includes (Fig. 1B): (1) Ambrona (MIS 6–5b, but the "Lower member AS1" dated by ESR in a wide range of 286–83 ka BP) (Soto et al., 2001; Falguères et al., 2006); (2) Barsuchii Dol (MIS 5e) (Kuzmin et al., 2017); (3) Bobylek (strata 5–6, MIS 5e) (Kosintsev et al., 2016; Danukalova et al., 2020), (4) Bolomor (layer XII, 152 ± 18 ka BP (MIS 6), layer IV, MIS 6–MIS 5e) (Blasco and Fernández Peris, 2012), (5) Burgtonna I, II, III (104–111 ka BP, MIS 5) (Kahlke, 1995; Kolfschoten, 2000); (6) Caverna degli Orsi (sondage B, units 120–122, MIS 5e) (Berto and Rubinato, 2013); (7) Chernyi Yar (sands above Singil clay, MIS 5e–d) (Titov and Golovachev, 2017; Golovachev and Titov, 2018, 2019); (8) Ciota Ciara (S.U. 13 and 14, MIS 5) (Berto et al., 2016; Buccheri et al., 2016); (9) Crayford (MIS 6) (Schreve, 1998); (10) Crumstadt 1 (MIS 5) (Koenigswald, 1991); (11) Cueva del Angel (I-XIII, 121 + 11/-10 ka BP, MIS 5) (Barroso Ruíz et al., 2011; Falguères et al., 2019); (12) Denisova Cave (188–60 ka BP, MIS 6–MIS 4) (Druzhkova et al., 2017; Jacobs et al., 2019); (13) Divje babe I (layers 8–10, 124–61 ka BP, MIS 5–MIS 4) (Toškan, 2006, 2007; Pacher and Stuart, 2009); (14) Gatzarria Cave (layer Cj, 100 ka BP, MIS 5) (Ready, 2013); (15) Hijenska pećina (MIS 5) (Pičuljan, 2012); (16) Ignatievskaya Cave (layers 8, 10, "excavation V″, MIS 6–MIS 4) (Gimranov and Kosintsev, 2015; Kosintsev et al., 2016; Fadeeva et al., 2018); (17) Il'skaya 2 (lower level of the layer 1, 135 ± 25 ka BP, MIS 6–MIS 5b) (Hoffecker et al., 1991; Baryshnikov and Hoffecker, 1994); (18) Joint Mitnor Cave (MIS 5) (Stuart, 1986; Currant and Jacobi, 2001); (19) Kalman Lambrecht (layers 5, 4, MIS 5) (Jánossy, 2001; Musil, 2010); (20) Kirkdale Cave (121 ± 48 ka BP MIS 5) (Boylan, 1981; McFarlane

Table 1
European biogeographic regions that were characterized in this study, number of sites, localities (layers, pits, etc.) related to MIS 6–MIS 4 and number of species (*SPN*).

Number on the Fig. 1	Region code	Name	Number of sites	Number of localities	*SPN*
I, II	MEAWSMIS, MEAWSMIN	South European Mediterranean Iberian Southern and Northern	26, 16	39, 22	40, 36
III	MEAWNCS	Middle European Western	92	237	55
IV	MEAWNCN	Middle European Atlantic	59	90	46
V	MEAWNWEN	West European Atlantic Southern: Wales and England except part of the Middle European Atlantic region	29	33	29
VI	MEAWNWSC	West European Atlantic Northern (Scotland)	2	2	3
VII	MEAWSMA	South European Mediterranean Apennine	29	33	33
VIII	MEAWSMBA	South European Mediterranean Balkan	3	7	~24
IX	MEAWNCES	Middle European Central – Southern	59	101	47
X	MEAWNCEN	Middle European Central –Northern	31	46	39
XI	NEAWNWSS	Middle European Boreal	1	1	1
XII	NEAWNWNK	North European Polar	1	1	1
XIII	NEAECNENNW	Asian North-Siberian Western	1	1	2
XIV	NEAWCE	East European – Asian West-Siberian Central sub-regions: (1) Northern part, (2) Middle part, (3) Southern part. The region includes the Middle and Southern Ural	28	39	40
XV	NEAWCESE	Asian West-Siberian South-Eastern	19	60	44
XVI	MEAWNEP	East European-Asian Ponto-Caspian	24	28	34
XVII	MEAWSECBSCA	Western Asian Caucasian (excluding Eastern Transcaucasia)	11	17	26
XVIII	NEAWNWNM	North European Scandinavian	1	1	1

and Ford, 1998); (21) Kiik-Koba (MIS 5) (Kolosov et al., 1993); (22) Kozarnika (layer Xb, 183–128 ka BP, MIS 6–MIS 5) (Tillier et al., 2017); (23) Kudaro 1 (lenses X, 172 ± 35 ka BP, MIS 6) (Crégut-Bonnoure and Baryshnikov, 2005); (24) Lazaret (layers CIII8-7, CII, 28–15, upper layer, 187–72 ka BP, MIS 6 – MIS 5) (Valensi, 2000; Valensi and Psathi, 2004; Valensi et al., 2007, 2013; Channarayapatna et al., 2016); (25) Makhnevskaya Ice (Ledyanaya) Cave (layers 10-11, MIS 5) (Kosintsev et al., 2016; Kuzmin et al., 2017; Fadeeva et al., 2020); (26) Melpignano-Cursi and San Sidero area (MIS 5) (Bologna et al., 1994; Petronio et al., 2008); (27) Molodovo 1 (layer 4, MIS 4–MIS 3) (Ivanova, 1982; Demay et al., 2012); (28) Montignoso (MIS 6) (Mann and Vandermeersch, 1997; Rustioni et al., 1999); (29) la Baume Moula-Guercy (layers IV-XI, XIX-XVII, XV, 160–65 ka BP, MIS 6–MIS 4) (Crégut-Bonnoure et al., 2010; Foury et al., 2016); (30) Nietoperzowa Cave (MIS 5) (Musil, 2010; Krajcarz and Madeyska, 2010); (31) Rozhok 1 (Mousterian layers V, VI, MIS 5) (Baigusheva and Titov, 2007); (32) Scladina (layers 3–5, 130–83 ka BP, MIS 5) (Bocherens et al., 1997; Döppes et al., 2008; Abrams et al., 2014); (33) Shkurlat (MIS 5) (Markova, 1985; Shevyrev et al., 1985); (34) Taubach (layers 11, 7, 116–111 ka BP, MIS 5) (Gerrit, 2009; Crégut-Bonnoure et al., 2010; Bratlund, 2015); (35) Veshenskaya (lower and upper bone beds, MIS 6–MIS 5) (Litvinenko and Titov, 2005; Baigusheva et al., 2014); (36) Vindija Cave (layers H, K, L M, J, 18–65 ka BP, MIS 6–MIS 5) (Musil, 2010; Miracle et al., 2010).

2.3. Time scale

In the bioregions provided with starting data in sufficient amount, the information on the species occurrence was aggregated in 9 (s09–s01) time intervals in accordance with the scheme given in Fig. 2.

In Western Europe the Saalian ice sheet covered great areas reaching 50° N at its maximum (Svendsen et al., 2004). In Eastern Europe the Middle Pleistocene – Dnieper – glaciation developed in two stages: Dnieper and Moscow ones (Fig. 1A). The southern limit of the ice sheet at the Dnieper stage the ice reached almost as far south as 48° N, and its boundary turned abruptly northwards east of the Dnieper drainage basin, while at the Moscow stage the ice ran slightly south of Moscow (~55° N) (Gerasimov and Markov, 1939; Markov et al., 1965). The temperature regime at MIS 6 was relatively stable, with global temperature minimum falling on the last third of the interval (Fig. 2). When constructing the scale for MIS 6–MIS 4 time interval, we were guided by the relative content of the heavy oxygen isotope yielded from LR04 stack of marine sediments (Lisiecki and Raymo, 2005).

The intervals of the scale for MIS 6 correspond to nomenclature suggested by (Railsback et al., 2015): s09 – MIS 6e + MIS 6d, s08 – MIS 6c + MIS 6b, s07 – MIS 6b + MIS 6a, and s06 – MIS 6a. When dealing with MIS 5, the subdivision of that isotope stage into 5 substages was taken into consideration (Shackleton et al., 2003; Otvos, 2015): s05 – MIS 5e, s04 – MIS 5d + MIS 5c, s03 – MIS 5c + MIS 5b + MIS 5a, s02 – MIS 5a. Marine Isotope Stage 4 as a whole falls within one interval (s01) of the scale.

There is a noticeable uncertainty resulting from different dating techniques applied and occasionally from the absence of direct dates. The uncertainty would certainly affect reconstructions of dynamics of the regional fauna composition. That is particularly true of the non-instrumental methods for estimating the fauna age based on indirect indicators and on the composition of the faunal assemblages themselves. We proceeded from the assumption that in case of a large massif of starting data the deviations of dates had mostly a random distribution and might be corrected to a certain extent when constructing the model of evolution.

2.4. Multivariate model

The method of constructing a multidimensional model of the evolutionary dynamics of faunal assemblages was described in detail earlier (Puzachenko and Markova, 2014, 2016; Puzachenko, 2019). For

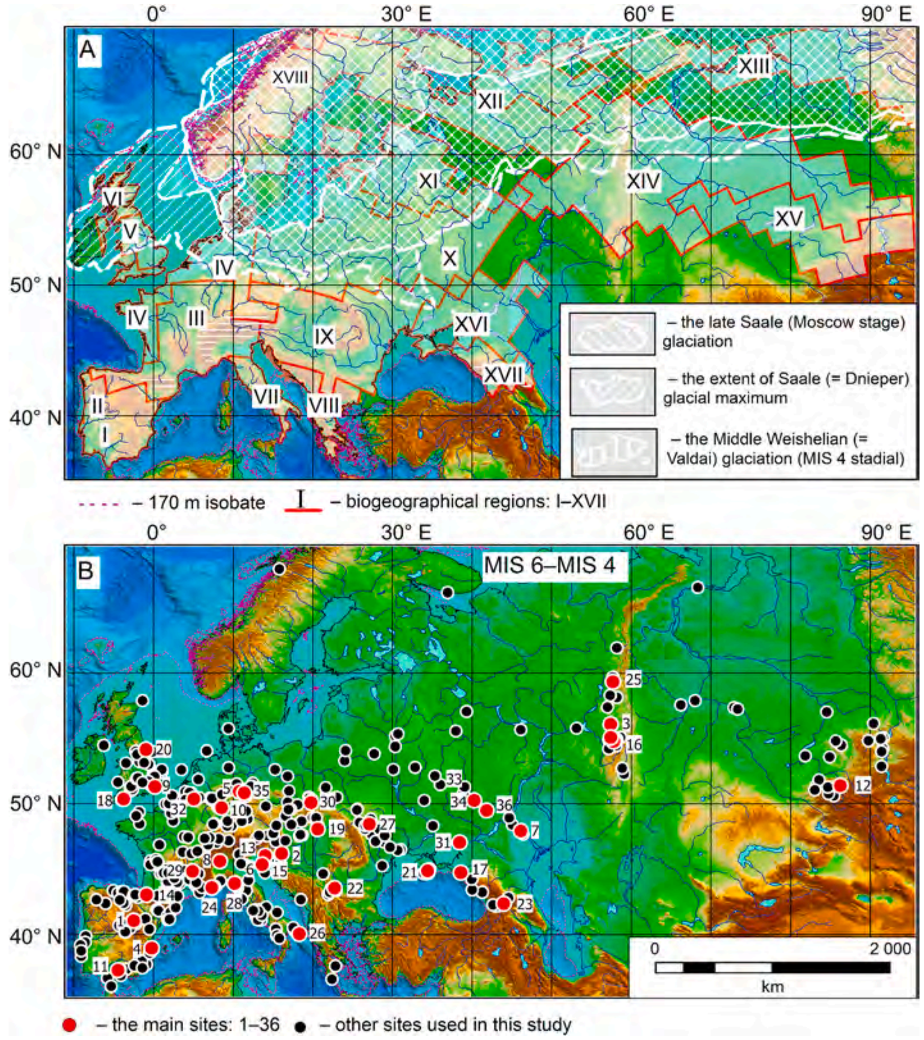

Fig. 1. Maps of the European bioregions and palaeontological sites related to MIS 6–MIS 4. A – the map of the bioregions (I–XVIII; Table 1) used in this study. The extents of the ice sheets are shown schematically after (Velichko et al., 2012; Ehlers et al., 2013). B – the palaeontological sites related to MIS 6–MIS 4; the names and short description of the main sites (1–36) see in the text. This figure is available in colour online.

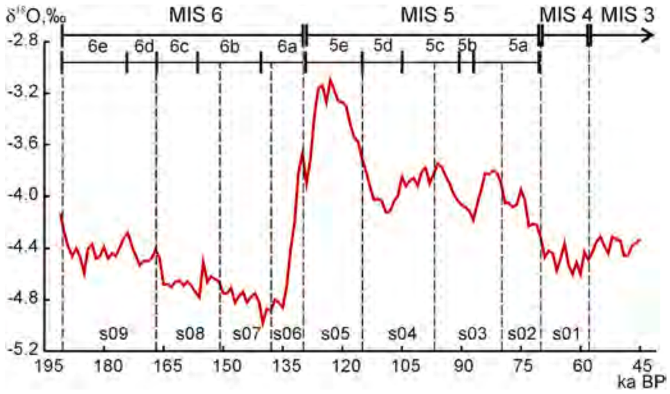

Fig. 2. Time scale (s09–s01) used in this study. This figure is available in colour online.

each timescale interval, we determined the total number of species and for each species - the frequency of occurrence of the localities, in which it was discovered. Arcsine transformation (Sokal and Rohlf, 1995) of the frequencies was used to "normalize" their distribution. The Bray–Curtis index (Bray and Curtis, 1957; Ricotta and Podani, 2017) was used to pairwise comparison of the time intervals, s09–s01. Then, square matrix of the Bray–Curtis indexes was processed by nonmetric multidimensional scaling (NMDS; Davison, 1983; Hout et al., 2013) in order to ordinate time intervals within Euclidian space with small dimensions.

The "best-minimum" dimension (i.e., how many coordinates ("axes") in a NMDS model) of the particular data set was estimated based on the "stress formula 1'' (Kruskal Stress) – the Goodness-of-Fit assessment of the NMDS model (for more details see (Abramov and Puzachenko, 2005; Abramov et al., 2009)).

A dimensionality of models varied from two to four for different bioregions, and the NMDS coordinates labelled as BC1–BC4 in the text.

To interpret coordinates of NMDS model Spearman's rank correlation was calculated between axes and δ^{18}O (‰, median value for each interval of the time scale) and the number of species (*SPN*, species richness for each time interval). In addition, to interpret some coordinates, Pearson correlation between axes and frequencies of localities with different species was counted because frequencies were normalized previously.

2.5. *Biological diversity*

The volume of the data available on certain bioregions makes it possible to estimate some parameters of the biological diversity. To calculate the biodiversity characteristics the data were aggregated by time intervals corresponding to: (1) MIS 6 stage, (2) MIS 5e, (3) MIS 5d-a substage, and (4) MIS 4. Such a subdivision is justified as we are most interested in the fauna changes at the boundary between: (1) MIS 6 and MIS 5e (between the Moscow stage of the Dnieper (Saale) Glaciation and the Eem (Mikulino) Interglacial, MIS 5e), (2) MIS 5e and MIS 5d-a) (the beginning of the Last Glaciation) and (3) MIS 5d-a and MIS 4 (the earlier stadial of the Last Glaciation).

The following diversity parameters were calculated: the number of taxa identified to a species level (SPN) – species richness. Chao-1 (bias corrected) (Chao et al., 2009), which is estimation of potential total species richness (Gotelli and Colwell, 2011).

The species diversity was estimated using Shannon diversity index (H): $\Sigma_i(n_i/N)\ln(n_i/N)$, where number of localities with species i and N is the total number of localities within a region.

The next parameter of diversity was index of “order/self-organization” (Foerster, 1960) or redundancy (Shannon, 1948) which known better as equitability/evenness index (Patten, 1962): $R = 1\text{-}\ H/\ln(SPN)$, where $\ln(SPN) = H_{\max}$.

To compare the taxonomic composition between isotope stages or substages, we used the Mourelle–Ezcurra species turnover index (β_t): $(g + l)/2\alpha(n\text{-}1)$, where g is the changes in the number of observed species between successive isotopic stages (total “gain” of species), l is the number of undetected species (total “loss” of species), α is the average number of species observed in both successive isotopic stages, and n is the number of isotopic stages (min = 2) compared (Mourelle and Ezcurra, 1997). In cases of the pairwise comparisons, it is equal to Whittaker's β – diversity index.

It should be specially stressed that we use here frequencies of species occurrence in the localities, and not estimates of abundance of their remains; so the diversity parameters calculated using standard procedures should be interpreted differently than that is usually done in the species ecology or paleo-ecology. In the case under consideration the diversity parameters depict adequately the relationship between species in terms of their frequency of occurrence in space. Ideally, if the localities were distributed evenly, these parameters would be directly related to the size of species ranges within the region. In actual practice we can only assume such a relationship, and the greater the number of locations is and the more evenly distributed they are, the more valid this hypothesis will be.

2.6. Comments on taxonomy and nomenclature

The present work is aimed at a maximum (insofar as that is possible) preservation of continuity in the species names; that is particularly important, as the database PALEOFAUNA we used contains data published mostly since the second half of the XX century. However, for a number of taxa there is a diversity of opinions regarding species composition within genera. That results in discrepancy in taxonomy. So we consider it necessary to explain our views on the species diversity in a number of genera, which is necessary for the analysis.

Mammoths *Mammuthus*. There is a difference of views on the systematic position of the post-Cromerian elephants of Mammoth lineage (Labe and Guérin, 2005; Lister et al., 2005; Palombo and Ferretti, 2005; Foronova, 2007, 2014; Lister and Stuart, 2010; Paupe et al., 2010; Filoux et al., 2014). In the opinion of a number of specialists, the early Middle Pleistocene *M. trogontherii* Pohlig, 1885 was replaced by *M. primigenius* (Blumenbach, 1799) in the late Middle Pleistocene. Instead of “intermediate” form of mammoth from the Middle Pleistocene, there was described *M. intermedius* Jourdan, 1861, with more archaic teeth characteristics (a lamellar frequency ranging per 10 cm between 6 and 7.5 (8.5) on the m3) that appeared in Europe in the late Middle Pleistocene. In our opinion, *M. intermedius* inhabited Europe in the late Middle – early Late Pleistocene (MIS 8-MIS 5e, and at least up to MIS 4), but *M. primigenius* appeared in the continental part of Europe approximately in MIS 4. Another form of elephant – *M. t. chosaricus* Dubrovo, 1966 – presumably coexisted with *M. intermedius* in Eastern Europe (Titov and Golovachev, 2017).

Elephants *Palaeoloxodon*. The opinions of specialists on the taxonomic position of straight-tusked elephants varied considerably (Maglio, 1973; Shoshani et al., 2007; Todd, 2010; Lister, 2016; Meyer et al., 2017). Those elephants were widely spread over Eurasia in the Middle and Late Pleistocene. Some researchers attributed them to a separate genus *Palaeoloxodon* Matsumoto, 1924, or included into genus *Elephas* L., 1758, or suggested to consider them an individual subgenus within the *Elephas* genus. In our opinion, the *Palaeoloxodon* should be regarded as a separate genus. The taxonomy at a species level was also the subject of much controversy – some specialists suggested distinguishing several species/subspecies, while others insisted on integrating all the taxa into one species *P. antiquus*. Recently it became a common practice to distinguish two continental species – the European *P. antiquus* (Falconer et Cautley, 1847) and Asian *P. namadicus* (Falconer et Cautley, 1846). We don't consider here the dwarf forms from the Mediterranean islands.

Caballoid horses. The taxonomy of the caballoid horses of the Middle – Late Pleistocene in Europe calls for an essential revision. Up to the present days many taxa have been identified by certain distinctive features: *Equus caballus* L., 1758, *E. ferus* (Boddaert, 1785), *E. germanicus* Nehring, 1804, *E. mosbachensis* Reichenau 1903, *E. taubachensis* Freudenberg, 1911, *E. gmelini* Antonius, 1912, *E. caballus chosaricus* Gromova, 1949, *E. caballus latipes* Gromova, 1949, *E. uralensis* Kuzmina, 2000. Up to now there is no agreement among the specialists regarding the quantity of the horse taxa, so we restrict our consideration to *E. ferus*.

According to the opinion of various specialists, there existed two or three hippopotamus (*Hippopotamus* L., 1758) taxa in Western Europe in the Middle – Late Pleistocene. Aside from the generally recognized *H. antiquus* Desmarest, 1822 (= *H. major* Cuvier, 1824), *H. amphibius* L., 1758 (= *H. incognitus*), there was mentioned *H. tiberinus* Mazza, 1991. The species, in all probability, were somewhat different in their environmental preferences and inhabited different regions in different climatic cycles (Mazza, 1995; Petronio, 1995). All the hippopotamus species came into being at the Early Pleistocene and could appear in Europe episodically and repeatedly in the Middle-Late Pleistocene at the intervals of warming. The hippopotamus taxa have not been properly studied, so the identification to a level of species may be occasionally very approximate or mutually exclusive. For that reason we use *Hippopotamus* spp. in the text.

Chamois and Ibex. There are recognised two species of the chamois – *Rupicapra pyrenaica* Bonaparte, 1845, and *R. rupicapra* (L., 1758) (Valdez, 2011). The present range of Pyrenean chamoios, *R. pyrenaica* (including the subspecies *parva*, *pyrenaica* and *ornate*) covers south-western Europe (mostly the Iberian Peninsula). The species range of chamois, *R. rupicapra* (with the numerous local subspecies), includes different mountains regions of Europe and Caucasus mountain system. The chamois' range has repeatedly changed during the Pleistocene due to climatic and environmental fluctuations in the Europe. Phylogenetic studies based on mtDNA suggest of complicated chamois evolution, a wider range for *R. pyrenaica* in the Pleistocene and its hybridization with *R. rupicapra* (Rodríguez et al., 2010; Pérez et al., 2014, 2017). A significant part of fossil remains are not divided by two species for objective reasons. Therefore, in this study the material from the Iberian Peninsula is attributed to *R. pyrenaica, w*hile the finds outside the peninsula – to *R. rupicapra*.

Two mountainous goats – Alpine ibex *Capra ibex* L., 1758 and Pyrenean ibex *Capra pyrenaica* Schinz, 1838 populate the mountains of the European Alps and the Iberian Peninsula, respectively (Manceau et al., 1999). Recent molecular phylogenetic study (Ureña et al., 2018) show monophyly of both species, one-wave migration of wild goats into Western Europe followed by possible allopatric speciation during ~92–57 ka BP (MIS 5–MIS 4). Here we use the species names *C. pyrenaica* for fossil mountain goats from the Iberian Peninsula and *C. ibex* for all other mountain goats in Europe. Moreover, it is possible that during MIS 6 and in the Last Interglacial (MIS 5e) it was a single species. We also discussed the West Caucasian tur (*C. caucasica*

Güldenstädt and Pallas, 1783, the Greater Caucasus Mountains) and the Siberian goat (*Capra sibirica* Pallas 1776, Altai Mountain).

Antelope *Saiga*. Several species and subspecies were suggested to distinguish in the steppe antelope *Saiga* taxon at different times (i.e. *S. borealis* Tschersky, 1876; *S. prisca* Nehring, 1891; *S. ricei* Frick, 1937; *S. tatarica binagadensis* Alekperova, 1953; *S. t. tatarica* L., 1766, and *S. t. mongolica* Bannikov, 1946). Taking into consideration the latest integrative works on the genus morphology and genetics, we assume the existence of two subspecies on the European territory, namely the Middle-Late Pleistocene *S. t. borealis* and the modern *S. t. tatarica* (Kahlke, 1999; Ratajczak et al., 2016).

The spelaeoid (cave) bears lineage. There were two groups of cave bears in Europe at the end of Middle and in Late Pleistocene – a big cave bear and a small cave bear (Baryshnikov, 2007). The studies of the ancient mitochondrial DNA revealed several independent evolutionary lineages, which made it possible to distinguish a complex of species (Valdiosera et al., 2006; Rabeder et al., 2011; Stiller et al., 2014; Baca et al., 2014, 2016). The big cave bear group is presented by two species – *Ursus spelaeus* Rosenmüller, 1794 (including subspecies *U. s. spelaeus* Rosenmüller, 1794, *U. s. eremus* Rabeder et al., 2004, *U. s. ladinicus* Rabeder et al., 2004) and *U. kanivetz* Vereshchagin, 1973 (= *U. ingressus* Rabeder et al., 2004). *U. ingressus* haplogroup was identified in Medvezhiya Cave (= Medvezh'ya Cave) in Northern Ural (Knapp et al., 2009; Baca et al., 2012; Stiller et al., 2014) and this cave represents *terra typica* for *U. spelaeus kanivetz* (Vereshchagin, 1973). This name has priority, and therefore the species should be denominated *U. kanivetz* Vereshchagin, 1973 (= *ingressus*) (Baryshnikov and Puzachenko, 2017). A specific position is occupied by the Kudaro Cave bear, which inhabited the Caucasus – *U. kudarensis* Baryshnikov and Hoffecker, 1994 (Dabney et al., 2013; Baryshnikov and Puzachenko, 2019; Barlow et al., 2020). The only species in the small cave bear group is *U. savini* Andrews, 1922 (= *U. rossicus* Borissiak, 1930) (Baryshnikov, 2007; Sher et al., 2011). However, the validity of the identification of *U. savini* from the Middle Pleistocene of England with small cave bear (*U. rossicus*) is questionable (Rabeder et al., 2010; Wagner and Čermák, 2012; Baryshnikov and Puzachenko, 2017, 2020).

Despite significant progress in our knowledge, the cave bears taxonomy is still under discussion. A recent study of ancient nuclear DNA leads to the hypothesis of early divergence between the European group of large cave bears and *U. rossicus* (~0.94 Ma). Also, the phylogenetic tree based on nuclear DNA variability suggests a higher taxonomic status (up to a species level) of European *U. s. eremus* and Uralian *U. kanivetz* and closer relations between the Western European *U. spelaeus* (s.s.) and the Eastern European *U. ingressus* (s.s.) (Barlow et al., 2020).

Here we use the species names *U. spelaeus* (s.l.; Europe), *U. kanivetz* (s.s; Ural)*, U. rossicus* and *U. kudarensis* (Caucasus).

The cave lions (*Panthera fossilis* (von Reichenau, 1906), *P. spelaea* Goldfuss, 1810). A large-size cave lions that lived in Europe in the Middle Pleistocene was described as *P. fossilis* (von Reichenau, 1906) (Sotnikova and Foronova, 2014; Sotnikova and Kirillova, 2017); the species from the Late Pleistocene is known as *P. spelaea* Goldfuss, 1810 (Marciszak and Stefaniak, 2010; Barnett et al., 2016; Marciszak et al., 2019a). In this paper we apply the name *P. spelaea* to all the remains of cave lions.

The badgers (*Meles meles* L., 1758, *M. leucurus* Hodgson, 1847). At present the badger genus is represented by 2 species – *M. meles* and *M. leucurus*, the boundary between the ranges of two species goes through the drainage basins of the Volga and Pechora rivers (Devjashin et al., 2017). The species show considerable differences in the skull morphology, skin colour, and genetic markers (Abramov and Puzachenko, 2013). During the interglacials the badgers inhabited eastern regions of Europe, the Urals, and West Siberia. Remains of European badger – *M. meles* were recovered from the localities in the Urals dated to MIS 5 (Bachura, 2008; Fadeeva et al., 2020). West Siberia and the Altai mountains were inhabited by Asian badger – *M. leucurus* (Vasiliev et al., 2019).

The porcupines (*Hystrix brachyura* L., 1758, *H. brachyura vinogradovi* Argyropulo, 1941, *H. indica* Kerr, 1792, *H. refossa* Gervais, 1852). In Europe there were two species of large porcupines (*H. indica* and *H. refossa*) and one small-size species (*H. brachyura*) in the Middle and Late Pleistocene (Weers, 1994, 2006). At the same time the Caucasus was inhabited by *H. indica* and *H. brachyura* (Baryshnikov, 2003). Only *H. brachyura* (Kuzmin et al., 2017) occurred in the Urals and Altai Mts. in the Late Pleistocene. As the ancient DNA of *H. brachyura* has not been analysed as yet, Lopatin (2019) suggests retaining the species name *H. vinogradovi* Argyropulo, 1941 for a small-size fossil porcupine. Here we use for it the name *H. brachyura.*

3. Results

3.1. Large mammal faunas of MIS 6 – MIS 4 and their evolution at the regional setting

3.1.1. South European Mediterranean Iberian region

Two bioregions have been identified on the Iberian Peninsula, divided by a boundary running from east to west (Fig. 1A (I, II); Table 1). Here we combine the data on both regions for the purpose of constructing a better substantiated model of the faunal assemblage evolution over the entire MIS 6–MIS 4 interval. With this in mind, we have chosen 32 localities (Table S1). A general idea on the regional fauna diversity may be obtained from local faunas recovered from localities Ambrona, Bolomor, and Buena Pinta (Baquedano et al., 2012), for MIS 5 – Cueva del Angel, Cueva Negra (V) (Richard et al., 2019), Preresa (Yravedra et al., 2012; Panera et al., 2014; Moreno et al., 2019), Pinarillo-1 (Arribas et al., 2008), Cueva del Camino (Arsuaga et al., 2012; Álvarez-Lao et al., 2013), and for MIS 4 – Cueva del Boquete de Zafarraya (Lecervoisier, 2003), Casares (Alcaraz-Castaño et al., 2017). The complete list of mammal species and the frequency of their occurrence in localities are given in Tables S2A and S2B.

The list of mammal remains obtained from the Bolomor site, layer XII (MIS 6) (Blasco and Fernández Peris, 2012) includes *P. antiquus*, *Stephanorhinus hemitoechus, E. ferus*, *Bos primigenius*, *Hemitragus bonali*, *Cervus elaphus*, *Dama* spp., *Megaloceros giganteus*, *Lynx pardinus*, *Castor fiber*, and *Macaca sylvana.* In the layer IV (MIS 6–MIS 5e) found remains of *P. antiquus*, *Hippopotamus* spp., *E. hydruntinus*, *E. ferus*, *B. primigenius*, *Hemitragus cedrensis*, *C. elaphus*, *Dama* spp., *Sus scrofa*, *Canis lupus*, *Vulpes vulpes*, *Panthera spelaea*, *L. pardinus*, *Ursus arctos,* and *M. sylvana*. The species list of Cueva del Angel (MIS 5) includes: *P. antiquus*, *M. intermedius*, *S. hemitoechus*, *E. ferus*, *E. hydruntinus*, *Bison priscus*, *B. primigenius*, *Capra pyrenaica*, *C. elaphus*, *Dama* sp., *S. scrofa*, *C. lupus*, *Felis silvestris*, *Ursus spelaeus*, and *U. arctos*. Faunal assemblage of MIS 4 characterizes the remains from Cueva del Boquete de Zafarraya and Casares: *M. intermedius*, *S. hemitoechus*, *E. ferus*, *E. hydruntinus*, *B. primigenius*, *C. pyrenaica*, *Rupicapra pyrenaica*, *C. elaphus*, *Capreolus capreolus*, *S. scrofa*, *Cuon alpinus*, *C. lupus*, *V. vulpes*, *F. silvestris*, *Lynx lynx*, *L. pardinus*, *Panthera pardus*, *P. spelaea*, *Lutra* sp., *Mustela erminea*, *U. spelaeus*, and *U. arctos*.

30 mammal taxa dated to MIS 6 have been recorded in the region. The following taxa have been found in a greater number (in order of decreasing abundance): *C. elaphus*, *E. ferus*, *B. primigenius*, *P. antiquus*, *C. capreolus*, *and S. hemitoechus*. Of carnivorous animals, *V. vulpes* and *F. silvestris* are most common. *B. priscus*, *H. mediterraneus*, *C. alpinus*, *Hystrix refossa*, *P. pardus*, *U. spelaeus*, and *M. sylvan* occur occasionally. Among rare species, noteworthy are: *Hippopotamus* spp., *Haploidoceros mediterraneus*, *B. priscus*, *R. pyrenaica*, *H. cedrensis,* and *M. sylvana*. In the region the species richness did not remain constant during MIS 6. The maximum richness was recorded in the first half of MIS 6, during substages 6e–6c, according to (Railsback et al., 2015), while its minimum (12–13 species) fell at its end, in MIS 6a (Fig. 3A).

In MIS 5e the species richness was noticeably greater (22 species) than at the end of MIS 6a, though lower than during the entire stage MIS 6. In our sample the amount of localities dated to the interglacial is

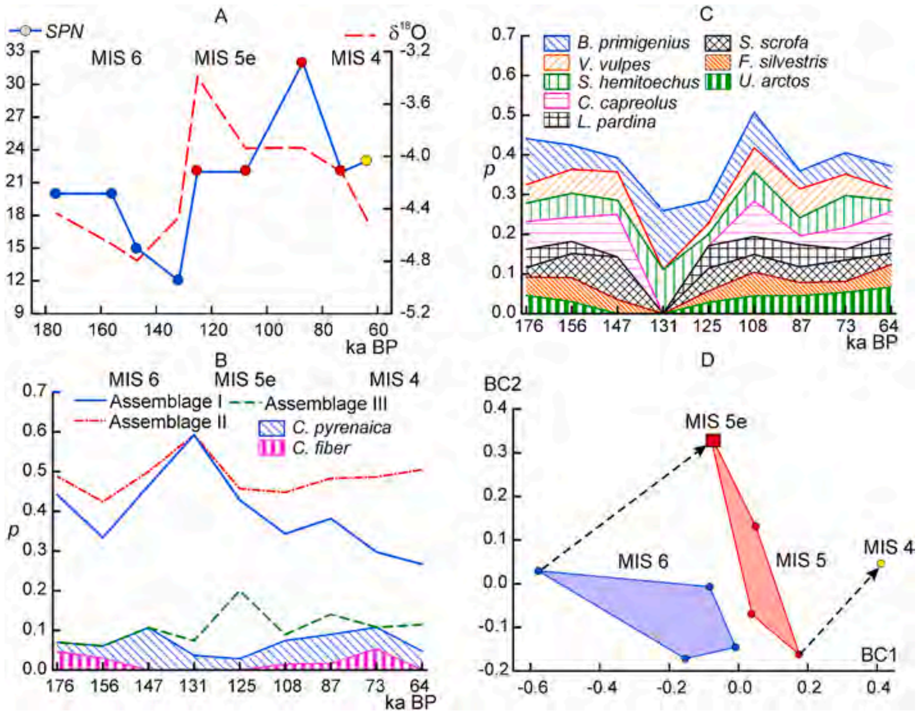

Fig. 3. Evolution of the South European Mediterranean Iberian large mammalian assemblage in MIS 6 – MIS 4 stages. A – changes in species richness (*SPN*) against the background of global temperature changes (δ^{18}O); B – "abundance" (relative frequencies of localities, *p*) of indicator species from the different ecological groups (assemblages I–III); C - "abundance" (relative frequencies of localities, p) of most common species; D – the "portrait" of regional mammalian assemblage evolution in projection on two first coordinates of the model (BC1, BC2). This figure is available in colour online.

relatively small: Villacastin (Arribas, 1994a, 1994b), Arenero del arroyo Culebro 1 (Panera et al., 2014), Cueva del Angel, Fuente Nueva-3 (upper archaeological level) (Martínez Navarro et al., 1997), and Cova del Rinoceront (layers IIIa, IIId, and IIIe) (Sanz et al., 2014; Daura et al., 2015; Sanz and Daura, 2018; López-García et al., 2016). The faunal assemblage of MIS 5e includes the following mammal species: *P. antiquus*, *M. intermedius*, *S. hundsheimensis* (Cova del Rinoceront, layer III (Daura et al., 2015)), *S. hemitoechus*, *E. ferus*, *E. hydruntinus*, *C. elaphus*, *D. dama*, *B. priscus*, *B. primigenius*, *H. albus*, *H. bonali*, *C. pyrenaica*, *S. scrofa*, *C. lupus*, *V. vulpes*, *L. pardinus*, *F. silvestris*, *U. arctos*, *U. spelaeus*, *M. eversmanii*, and *M. meles*.

The maximum species richness (34 species) is recorded in MIS 5c – MIS 5a. The following taxa may be considered as "dominant" (listed in order of a decreasing number of localities): *C. elaphus*, *E. ferus*, *C. pyrenaica*, *V. vulpes*, *S. hemitoechus,* and *B. primigenius*. Commonly present taxa are *L. pardinus, U. arctos, S. scrofa*, *C. capreolus, D. dama*, and *F. silvestris*. Besides, *M. intermedius, E. hydruntinus*, *Hemitragus* sp., *H. refossa* are still present. Of the rare species *M. sylvana*, *Lutra* sp., and *H. brachyura* should be noted.

The species diversity in the assemblage dropped sharply as early as MIS 5a, then stays at a relatively low level (22 species) during MIS 4 (Fig. 3A). Local faunas of that age are found at the following localities: Sopeña (XV, XIII, XII), (XV, XIII, XII), Gorham's Cave (R, K), Zafarraya, La Cova del Salt (XII–IX), Gruta Nova da Columbeira (8 (20)), Cueva de la Buena Pinta (2–5), Cova del Muscle, Arenero del arroyo Culebro 1, Buraca Escura (GC4), Oliveira Cave, and Almonda karstic system (Zilhão and McKinney, 1995; Neves et al., 2001; Lorenzo, 2007; López-García, 2008; Stringer et al., 2008; Zilhão et al., 2010; Pinto-Llona et al., 2012; Pérez et al., 2015). Most commonly found are *C. elaphus*, *P. pardus*, *U. arctos*, *C. lupus*, *R. pyrenaica,* and *M. giganteus* makes its appearance for the first time since MIS 6 (Cova del Rinoceront). The same is true of *C. antiquitatis* recorded for the first time in the entire time interval under consideration (Arenero del arroyo Culebro 1). The only locality that yielded *Palaeoloxodon* (straight-tusked elephant) remains is Cova del Muscle, dated by the fauna at 70–60 ka BP (López-García, 2008) and found together with *C. c. spelaea*, *E. hydruntinus, L. spelaea* and others (Canal and Carbonell, 1989).

The model of the assemblage evolution in MIS 6–MIS 4 has three independent components (the model coordinates). The first coordinate (BC1) correlates with the frequency of occurrence of the localities: *P. antiquus* (−0.80, 0.01), *E. ferus* (−0.80, 0.01), *C. elaphus* (−0.78, 0.01), and – at a level of tendency – with *D. dama* (−0.50, 0.16) (assemblage I), *R. pyrenaica* (0.74, 0.02), *C. alpinus* (0.88, <0.01), *P. pardus* (0.81, <0.01), and *U. arctos* (0.80, <0.01) (assemblage II). The model coordinate BC2 correlates with occurrence frequency of the following species: *S. hundsheimensis* (0.83, 0.006), *E. hydruntinus* (0.87, 0.002), *M. meles* (0.70. 0.04) (assemblage III) and *C. fiber* (−0.74, 0.03). The third coordinate (BC3) correlates with occurrence of *C. pyrenaica* localities (−0.86, 0.003).

The species which frequency correlatable with the model coordinates are indicators of basic components of the evolutionary changes in the composition of the regional large mammal assemblage. Variations in the occurrence of species correlatable with various coordinates of the model are controlled by unknown independent factors.

The basis for the assemblage I is formed by *P. antiquus*, *E. ferus, C. elaphus, D. dama*. The assemblage members were most widely distributed at the end of MIS 6, when the species richness of the whole fauna was at its minimum; the assemblage became the least spread in MIS 4 (Fig. 3B). The frequencies of *R. pyrenaica*, *C. alpinus*, *P. pardus*, *U. arctos* occurrence – the species marking the assemblage II – changes in the opposite direction.

The frequency of *C. fiber* and *C. pyrenaica* varies independently of the above listed taxa. Beaver is more common in the first half of MIS 6 and in MIS 4, while at the end of MIS 6 and at the beginning of MIS 4 it is absent or relatively scarce. The peak of *C. pyrenaica* occurrence falls on the middle of MIS 6, its minimum – on the Eemian Interglacial.

Fig. 3C illustrates chronological changes in the occurrence frequency of the localities yielding remains of relatively widespread species that do not belong to assemblages I and II. The diagram of the combined relative frequency of occurrence is similar to that of changes in species richness. Most of species, except for *B. primigenius* and *S. hemitoechus*, demonstrate a drop in their presence at the end of MIS 6. The environments became most favourable for all 8 species in MIS 5d–c.

It should be noted that the global temperature dynamics itself (as recorded in variations of δ^{18}O) does not influence directly the faunal assemblage evolution on the Iberian Peninsula.

There are three stages in the evolution of the South European Mediterranean Iberian Regional assemblages corresponding to MIS 6, MIS5, and MIS 4 (Fig. 3D). They are mostly different in the spatial distribution of species belonging to assemblages I and II.

3.1.2. Middle European Western region

The region is in the central part of Western Europe (Fig. 1A (III)) and borders directly on the Iberian Region in the south. It includes the Pyrenees and the northernmost part of the Iberia Peninsula extending along the Bay of Biscay coast. The sample taken from that region includes 237 localities dated to MIS 6–MIS 4 (Table S1). More than 54–55 species has been found there (Tables S3A and B). The notion of the regional fauna diversity at MIS 6 interval can be gained from local faunas recovered from the following localities: Lazaret, Romain-la-Roche (layers VI-VIII, 165–159 ka BP) (Guérin et al., 2010), for MIS 6–MIS 5 – Stuttgart-Untertürkheim (lower travertine, 133–105 ka BP) (Wenzel, 1998a, b; Kuznetsova, 2000), for MIS 5 – Crumstadt 1, la Baume Moula-Guercy, Grand Abri aux Puces (level 2) (Quilès and Crégut–Bonnoure, 2006; Slimak et al., 2010), Gatzarria Cave (layer Cj, 100 ka BP) (Ready, 2013), Ciota Ciara Cave (s.u. 13, 14) (Berto et al., 2016; Buccheri et al., 2016), Cotencher (layer 13, 72.5 ± 9.4 ka BP) (Deák et al., 2019), Caverna delle Fate (layer IIb, 78–72 ka BP) (Valensi and Psathi, 2004; Valensi, 2009), for MIS 4 – Villa Sekkendorff (Forsten and Ziegler, 1995; Ziegler, 1996), Combe Grenal (layer 55, 61 ± 7 ka BP) (Dibble et al., 2009; Maureille et al., 2011) and Arma delle Manie (layer VII base, 60 ± 9 ka BP) (Djerrab and Camps, 2010).

The complicated composition of the regional fauna in MIS 6 is quite fully represented in the materials obtained from the localities Lazaret (CII–III), Romain-la-Roche, and Stuttgart-Untertürkheim: *P. antiquus*, *M. intermedius*, *Coelodonta antiquitatis*, *S. hemitoechus*, *E. ferus*, *E. hydruntinus*, *Capra ibex*, *R. rupicapra*, *B. primigenius*, *B. priscus*, *C. elaphus*, *M. giganteus*, *D. dama*, *C. capreolus*, *Rangifer tarandus*, *S. scrofa*, *C. lupus*, *C. alpinus*, *Vulpes vulpes*, *V. lagopus*, *C. c. spelaea*, *F. silvestris*, *L. pardinus*, *P. pardus*, *P. spelaea*, *Gulo gulo*, *Meles meles*, *Martes martes*, *Mustela nivalis*, *Mustela putorius*, *U. spelaeus*, and *U. arctos*. A notion about the regional fauna in MIS 5 can be gained from species list of Moula-Guercy, Grand Abri aux Puces, and Gatzarria Cave. It includes: *P. antiquus*, *M. intermedius*, *C. antiquitatis*, *S. hemitoechus*, *E. ferus*, *B. priscus*, *C. ibex*, *R. rupicapra*, *R. pyrenaica*, *B. primigenius*, *C. elaphus*, *M. giganteus*, *D. dama*, *C. capreolus*, *R. tarandus*, *S. scrofa*, *C. lupus*, *C. alpinus*, *V. vulpes*, *C. c. spelaea*, *L. lynx*, *L. pardinus*, *F. silvestris*, *P. pardus*, *M. meles*, *L. lutra*, *M. erminea*, *M. putorius*, *Ursus thibetanus*, *U. spelaeus*, *U. arctos*, *C. fiber*, and *Hystrix brachyura*. The fauna of MIS 4 stadial was no less diversified, as is seen from the materials obtained from the localities Villa Sekkendorff, Combe Grenal, and Arma delle Manie: *Mammuthus primigenius/inermedius*, *C. antiquitatis*, *S. hemitoechus*, *E. ferus*, *E. hydruntinus*, *B. primigenius*, *B. priscus*, *C. ibex*, *C. elaphus*, *M. giganteus*, *D. dama*, *C. capreolus*, *R. tarandus*, *S. scrofa*, *C. lupus*, *V. vulpes*, *C. c. spelaea, P. spelaea*, *M. erminea*, *M. nivalis*, *M. putorius*, *U. spelaeus*, *U. arctos*, and *H. brachyura*.

43 mammal taxa have been recorded in the region at MIS 6 interval. The most widespread species were (in the descending order): *C. lupus*, *C. elaphus*, *E. ferus*, *V. vulpes*, *B. primigenius*, *R. rupicapra*, *U. spelaeus,* and *U. arctos*. Some thermophilic species (*P. antiquus*, *S. hemitoechus*, *D. dama*) were present in the regional faunal assemblage during the entire Saale interval. It is worth noting the presence of some rare species – *G. gulo*, *V. lagopus*, *H. mediterraneus*, and *Hemitragus* ssp. The species richness peaked (38–39 species) at the first third of MIS 6 (Fig. 4A). At the end of MIS 6 the species richness dropped to 28 species. At that time the most widespread species were *C. elaphus*, *B. primigenius, U. spelaeus,* and *C. lupus.* The interglacial MIS 5e was marked by a sharp increase of the species richness to 46-47 taxa. In common with MIS 6, the most widespread species were *C. elaphus*, *C. lupus*, *E. ferus*, and *B. primigenius.*

Among species widely distributed at that time were *C. capreolus*, *B. priscus*, *V. vulpes*, *U. spelaeus, S. scrofa*, and *P. spelaea*. The group of common species included not only thermophilic (*S. hemitoechus*, *D. dama*, *P. antiquus*), but boreal species as well (*R. tarandus* and *M. giganteus*). There were also rare species recorded in 1–3 localities, such as *C. antiquitatis*, *M. intermedius*, *H. cedrensis*, *H. bonali*, *S. tatarica*, *L. lynx*, *U. thibetanus*, *H. brachyura*, *C. fiber*, and *M. pachygnatha*. The species richness kept that level approximately to the substage MIS 5c. Later it decreased and varied around 44 species (Fig. 3A). At that background the composition of the most widely spread species kept practically unchanged in the region. Thus, during MIS 4 stage the group

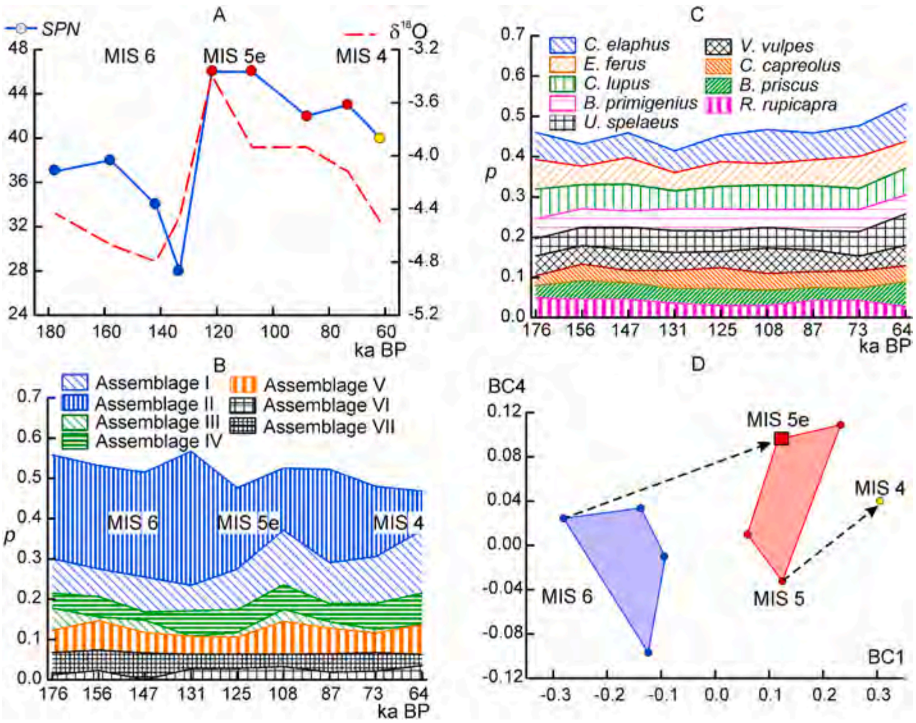

Fig. 4. Evolution of the Middle European Western large mammalian assemblage in MIS 6–MIS 4 stages. A – changes in species richness (*SPN*) against the background of global temperature changes ($\delta^{18}O$); B – “abundance” (relative frequencies of localities, *p*) of indicator species from the different ecological groups (assemblages I–VII); C – “abundance” (relative frequencies of localities, *p*) of most common species; D – the “portrait” of regional mammalian assemblage evolution in projection on two first coordinates of the model (BC1, BC4). This figure is available in colour online.

included *C. elaphus*, *U. spelaeus*, *E. ferus*, *C. lupus,* and *B. priscus*. At the time of the Middle Weichel some thermophilic species kept their nominal presence in the south of the region: *P. antiquus* – Madonna dell' Arma (43.826°N, 7.828°E (Valensi, 2009)), Coudoulous I (44.469°N, 1.690°E (Jaubert et al., 2005)), Barma Grande (43.784°N, 7.53°E (Onoratini et al., 2012)), *S. hemitoechus* – Arma delle Manie, and *H. amphibius* – Madonna dell' Arma.

The evolution of the regional assemblage at the end of Middle Pleistocene – in the first half of the Late Pleistocene is described by four independent variable values. The first coordinate of the model (BC1) correlated with the species richness (*SPN*; $r = 0.82$, $p = 0.06$, $n = 9$). BC1 displays a positive correlation with the frequency of occurrence of localities with *P. antiquus* (−0.96, <0.01), *S. hemitoechus* (−0.94, <0.001), *U. arctos* (−0.87, <0.01), *M. martes* (−0.81, <0.01), *D. dama* (−0.81, 0.009), *P. spelaea* (−0.79, 0.01) (assemblage I), *C. antiquitatis* (−0.75, 0.02), and *L. pardinus* (−0.74, 0.02) (*C. pyrenaica* (0.94, <0.001), *H. brachyura* (0.94, <0.001), *C. elaphus* (0.89, 0.001), *C. c. spelaea* (0.83, 0.006), *L. lynx* (0.80, 0.009) (assemblage II). The cited data means that the first coordinate of the model describes the general tendency towards the reduction of the range recorded for the species showing the negative correlation (assemblage I), while the species with the positive correlation enlarge their ranges (assemblage II).

Coordinate BC2 is correlated with the frequencies of *R. tarandus* (−0.74, 0.02), *C. ibex* (−0.73, 0.03) (assemblage III), *C. fiber* (0.89, 0.001), *H. mediterraneus* (0.70, 0.04), *H. cedrensis* (0.68, 0.04) (assemblage IV).

Coordinate BC3 is correlated with the frequencies of localities of *V. lagopus* (−0.73, 0.03), *V. vulpes* (−0.69, 0.04), *M. intermedius* (−0.67, 0.05) (assemblage V) and *B. primigenius* (0.73, 0.03).

Finally, coordinate CB4 displays correlation with the frequency of occurrence recorded for localities with *H. bonali* (−0.70, 0.04), *R. rupicapra* (−0.69, 0.04) (assemblage VI), *R. tarandus* (0.72, 0.02), *S. tatarica* (0.75, 0.02) (assemblage VII).

The "core" of the regional assemblage stays stable through the entire time interval under consideration (Fig. 3B). As to the entire time interval MIS 6–MIS 4, the assemblage included *C. elaphus*, *C. capreolus*, *B. primigenius*, *B. priscus*, *E. ferus*, *C. lupus*, *V. vulpes*, *U. spelaeus,* and *R. rupicapra*. The proportion of localities where remains of those species were found varies mostly around 40% and approached 50% in MIS 4 only (Fig. 4C).

The next in importance group of species with proportion of localities about 23% on average includes *L. pardinus*, *P. spelaea*, *P. pardus*, *U. arctos*, *S. scrofa*, and *C. ibex*. Changes in their occurrence often proceed in cycles, the peak values falling on the beginning and on the last third of MIS 6 and at the end of MIS 5 (*R. rupicapra*, *P. spelaea, U. arctos*, *P. pardus*, *L. pardinus*). The dynamics of *C. ibex* occurrence shows two rises corresponding to MIS 6a and MIS 5a. In the *S. scrofa* dynamics of occurrence there are two noteworthy periods – MIS 6 remarkable for a relatively low frequency of occurrence and MIS 5 (relatively high frequency, with a maximum in MIS 5a). All the listed species typically reduced their presence in MIS 4.

The "common" species group includes: *P. antiquus, S. hemitoechus, C. antiquitatis, E. hydruntinus, R. tarandus, M. giganteus, D. dama, C. c. spelaea, F. silvestris, M. martes, M. nivalis,* and *M. meles*. All of them demonstrate a synchronism in the changes with time. In general, they occur more often in the end of the Middle Pleistocene with a well pronounced maximum at boundary MIS 6–MIS 5. A decrease in the occurrence frequency in MIS 5a–MIS 4 time interval is characteristic of all those species.

The rest species belong the 'rare species' category. They were found in 9% of the regional localities only. There are some specific features in the occurrence of some species – they appear more or less synchronously, and – which is most noteworthy – they practically completely disappear from the regional fauna at the substage MIS 6a and then are restored at MIS 5e (*C. fiber, M. intermedius, S. kirchbergensis, C. alpinus, Hemitragus* ssp., and some others). It is that group of species which exerts mainly a control over the observed dynamics of the species richness in the region (Fig. 4A).

In a few species the variability of relative occurrence may be controlled by several independent factors (as follows from the results of multiple regression modelling). That group includes: *M. giganteus* (BC1, BC4), *R. tarandus* (BC2, BC4), *S. scrofa* (BC1, BC2, and BC3) and some others.

Fig. 4D presents a 'picture' of a faunal assemblage evolution in the model coordinates BC1 and BC4. With reference of to coordinate BC1, there is a hiatus between the states of the assemblage in MIS 6 and MIS 5, mostly caused by evolutionary changes in the occurrence frequency of the species belonging to assemblages I and II.

3.1.3. Middle European Atlantic region

The region lies to the north and west of the Middle European Western region (Fig. 1A (IV)) and borders on the North Sea. The modern zoogeographical subdivision of the European territory (that we use in this paper) suggests, however, that the bioregion extends westwards as far as the southern part of Great Britain Island, the area having been free of ice sheet at the Saale maximum. At the time of glaciations the insular part of the region was connected with the continent by the emerged shelf. For the last time such a connection took place in the Late Pleistocene.

The sample for the region includes 90 localities dated to MIS 6–MIS 4 (Table S1) that yielded about 46 species (Tables S4A and B). The practically complete regional list of species is presented in 16 local assemblages as follows: Biache-Saint-Vaast (layer IIA, 196–159 ka BP) (Poplin, 1978; Guipert et al., 2011), Abri Suard et Bourgeois-Delaunay (La Chaise) (layers 53′2, 53, 51, above 48, and 7, 171–71 ka BP) (David and Prat, 1965; Griggo, 1996), Abri Bourgeois-Delaunay (La Chaise) (layers 11–8, 151–130 ka BP) (David and Prat, 1965; Blackwell, 1980), Caours (lower part of the tufa sequence, 121.2 + 3.41/-3.29 ka BP) (Antoine et al., 2006), Scladina, layers 5–4 (Bocherens et al., 1997; Döppes et al., 2008; Abrams et al., 2014), Joint Mitnor Cave (Stuart, 1986; Currant and Jacobi, 2001), Taubach (layers 11, 7), Scladina (Sclayn) layers 3–5 (Bocherens et al., 1997; Döppes et al., 2008; Abrams et al., 2014), Weinberghöhlen bei Mauern (63 ± 13 ka BP) (Müller-Beck, 1974; Musil, 1980), Mont-Dol (layer 10, 60 ka BP) (Simonet and Monnier, 1991), and Zoolithenhöhle (Gailenreuth) (60 ± 15 ka BP) (Hofreiter et al., 2004; Hilpert et al., 2005).

A relatively high diversity of the regional large mammal fauna in the early Saale ice age is suggested by the materials from localities Biache-Saint-Vaast (IIA), Abri Suard (53) and Abri Bourgeois-Delaunay (11). The list of species recovered from the localities includes: *P. antiquus*, *M. intermedius*, *C. antiquitatis*, *S. hemitoechus*, *S. kirchbergensis*, *E. ferus*, *E. hydruntinus*, *B. primigenius*, *B. priscus*, *S. tatarica*, *C. elaphus*, *M. giganteus*, *C. capreolus*, *R. tarandus*, *S. scrofa*, *C. lupus*, *V. vulpes*, *C. c. spelaea*, *F. silvestris*, *P. spelaea*, *Cyrnaonyx antiqua*, *M. martes*, *U. spelaeus*, *U. arctos*, and *C. fiber*.

Most typical of MIS 5 in the faunal composition are local assemblages of Abri Bourgeois-Delaunay (8–10), Scladina (5–4), Taubach (11, 7), and Joint Mitnor Cave, which include: *P. antiquus*, *M. intermedius*, *C. antiquitatis*, *S. hemitoechus*, *S. kirchbergensis*, *E. ferus*, *Hippopotamus* spp., *B. primigenius*, *B. priscus*, *C. ibex*, *R. rupicapra*, *Alces latifrons*, *A. alces*, *C. elaphus*, *M. giganteus*, *D. dama*, *C. capreolus*, *R. tarandus*, *S. scrofa*, *C. lupus*, *C. alpinus*, *V. lagopus*, *V. vulpes*, *C. c. spelaea, F. silvestris*, *P. pardus*, *P. spelaea*, *M. meles*, *M. martes*, *L. lutra*, *U. spelaeus*, *U. arctos*, and *C. fiber*. Following three localities provide an idea of the regional fauna at MIS 4 stage: Weinberghöhlen, Mont-Dol, and Zoolithenhöhle. The species list includes: *M. primigenius*, *C. antiquitatis*, *E. ferus*, *E. hydruntinus*, *B. primigenius*, *B. priscus*, *C. ibex*, *A. alces*, *C. elaphus*, *M. giganteus*, *D. dama*, *C. capreolus*, *R. tarandus*, *S. scrofa*, *C. lupus*, *C. alpinus*, *V. lagopus*, *V. vulpes*, *C. c. spelaea, P. pardus*, *P. spelaea*, *M. meles*, *Martes foina*, *M. nivalis*, *U. spelaeus*, *U. arctos*, and *C. fiber*.

31 species dated to MIS 6 were discovered in the region. The most widespread of them were: *C. lupus*, *C. elaphus*, *E. ferus*, *C. antiquitatis*,

U. arctos, *V. vulpes*, and *U. spelaeus*. The common species group included: *B. priscus*, *C. c. spelaea*, *B. primigenius*, *P. spelaea,* and *M. intermedius*. There were both cold-tolerant species (*R. tarandus*, *M. giganteus*, *V. lagopus*), and thermophilic ones (*P. antiquus*, *S. hemitoechus*, *C. antiqua*), some of them were typical forest inhabitants (*C. fiber*, *M. martes*, *F. silvestris,* and some others), and others – open space dwellers (*S. tatarica* and *E. hydruntinus*) (Table S4A). The maximum diversity was recorded in the first half of MIS 6. At the end of the stage the large mammal species richness dropped (in common with the two above discussed regions) (Fig. 5A). The transition to the Eemian Interglacial was marked with more than twofold growth of species diversity (37 species) as compared with MIS 6a substage (16 species). Some new species joined the group of the most widespread ones: *C. elaphus*, *C. lupus*, *B. primigenius*, *U. arctos*, *D. dama*, *E. ferus*, *P. antiquus,* and *C. capreolus*. The presence of *S. kirchbergensis, S. hemitoechus,* and *P. pardus* in the fauna is worthy of notice.

Of the species attributable to the Middle Pleistocene relicts, in the deposits dated to MIS 5e–MIS 5c there were found otter, *C. antiqua* (= *Aonyx antiqua*) (Caours and Biache-Saint-Vaast, IIA), *Homotherium latidens* (d'Artenac (Delagnes et al., 1999)), and *A. latifrons* (Taubach, bed 11). The remains of hippopotamus dated approximately at MIS 5e and 5c (single cases) were found in Burtle Beds (Greylake), Milton Hill Fissure, Durdham Down Fissure, Eckington, Tornewton Cave, Joint Mitnor Cave, and Wotton Hill (Stuart, 1982, 1986; Gordo, 1987; Keen and Bridgland, 1986; Schreve, 1998, 2009; Currant, 2000; Gilmour et al., 2007).

At the end of MIS 5 and in MIS 4 the species richness was slightly lower, though still relatively high (Fig. 5A). The regional species composition changed gradually. During MIS 5c–a interval *C. lupus* and *C. elaphus* were most widespread; at the very end of MIS 5 they were replaced by *E. ferus*, *U. spelaeus*, *C. elaphus*, *R. tarandus,* and *B. priscus*, but in MIS 4 the assemblage is dominated by *R. tarandus*, *E. ferus*, and *C. lupus*. On the whole, 40 species of large mammals have been recorded in MIS 5d–a interval, and 34 ones – in MIS 4 stadial. The list of the regional fauna was noticeably reduced as a result of the extinction of *H. amphibious, S. hemitoechus, P. antiquus, M. intermedius*, *F. silvestris*, and *H. brachyura* (Table S4A).

The model of the regional assemblage evolution has three coordinates. The coordinate BC1 correlates with the frequency of occurrence of *S. hemitoechus* (−0.72, 0.028), *C. fiber* (0.75, 0.02), *F. silvestris* (−0.78, 0.014), and *P. antiquus* (−0.85, 0.004) (assemblage I), *C. ibex* (0.89, 0.002) and *R. tarandus* (0.77, 0.015) (assemblage II) (Fig. 5B). The next coordinate correlates with *SPN* (0.87, 0.002) and with the frequency of occurrence of *C. c. spelaea* (−0.67, 0.048), *C. antiquitatis* (−0.69, 0.038), *M. intermedius* (−0.80, 0.01) (assemblage III), *C. capreolus* (0.86, 0.003), *P. pardus* (0.75, 0.02), *C. alpinus* (0.74, 0.023) and *M. meles* (0.73, 0.025) (assemblage IV) (Fig. 5B). At last, BC3 correlates with the data on *R. rupicapra* (−0.80, 0.01) and *P. spelaea* (0.78, 013). The changes of the *C. ibex* and *R. tarandus* frequency are described by two coordinates BC1 and BC3 simultaneously. Each of the assemblages varies with time, though no regularities can be traced. The optimum conditions for species belonging to assemblage I (thermophilic) existed in MIS 5e and at the beginning of MIS 6; the members of assemblage II were most numerous in MIS 6a and in MIS 4 (cold adapted species); the species of assemblage III (species of open habitats) – in MIS 6 (and especially MIS 6a), and assemblage IV (species of forest habitats) – MIS 5–MIS 4. The changes in *P. spelaea* occurrence display fluctuations which are not related to the climate changes. On average, the cave lion occurs somewhat more often in MIS 5–MIS 4 as compared with MIS 6 (Fig. 5B). The chamois (*Rupicapra*) occurs in a small number of localities mostly dated to MIS 5, the maximum of its occurrence falling presumably on MIS 6a.

Fig. 5D shows changes in the occurrence frequency of species that, in all probability, were widely distributed in the region during MIS 6 to MIS 4 (except for *Hippopotamus* sp.), though not belonging to assemblages I–IV. The group includes species with different environmental preferences and differently responding to the glacial environments of MIS 6 and to interglacial ones of MIS 5e.

In MIS 4 species *P. antiquus*, *M. martes, F. silvestris, L. lutra*, *H. brachyura*, disappeared from the list of the regional fauna, which may be considered as a sign of essential degradation of forests. However, only a few species disappeared at boundary of MIS 5 and MIS 4: those are *S. hemitoechus*, *R. rupicapra* and probably, *M. intermedius*. That may be interpreted as indicator of a slow change in the regional fauna composition at the transition from Last Interglacial to the Weichsel Glaciation

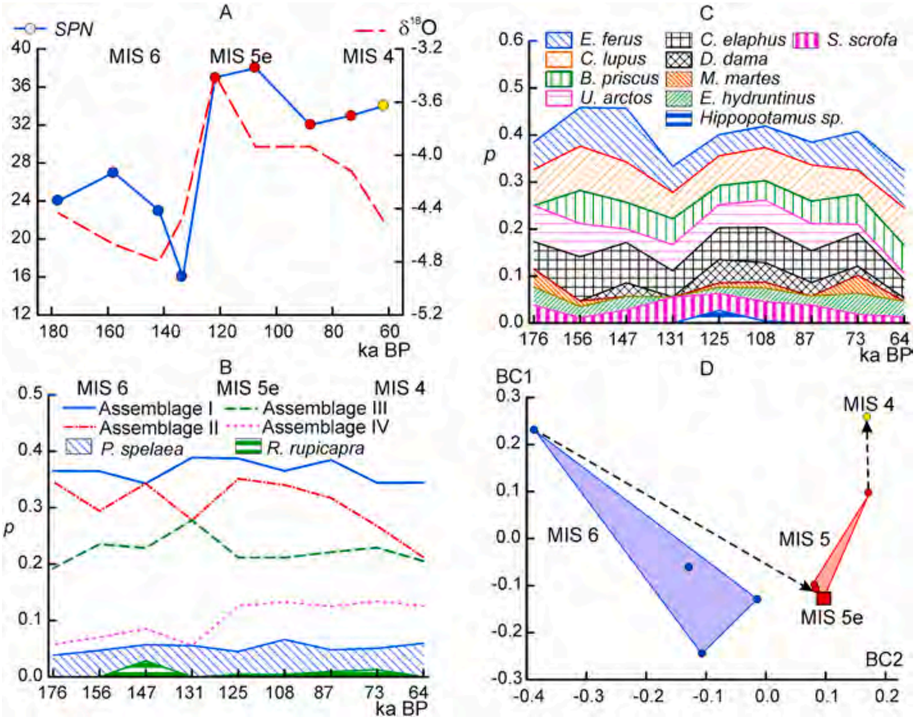

Fig. 5. Evolution of the Middle European Atlantic large mammalian assemblage in MIS 6–MIS 4 stages. A – changes in species richness (*SPN*) against the background of global temperature changes ($\delta^{18}O$); B – "abundance" (relative frequencies of localities, *p*) of indicator species from the different ecological groups (assemblages I–IV), *R. rupicapra* and *P. spelaea*; C - "abundance" (relative frequencies of localities, *p*) of most common species; D – the "portrait" of regional mammalian assemblage evolution in projection on two first coordinates of the model (BC1, BC2). This figure is available in colour online.

in Middle European Atlantic region.

The picture of the regional assemblage evolution has been constructed in coordinates BC2 (abscissa axis) and BC1 (Fig. 5F). In this case the coordinate BC2 demonstrates correlation with the species richness. In relation to it, there is a hiatus between the assemblage state in MIS 6 and that in MIS 5. The points corresponding to MIS 5e-b are set very densely, which suggests relatively small changes in the assemblage composition during MIS 5. A certain "movement" towards the state typical of MIS 4 became noticeable at the end of this isotope stage.

3.1.4. West European Atlantic Southern region

The region occupies the middle part of the Great Britain Island (Fig. 1A (V)). According to reconstructions (Ehlers et al., 2013, Fig. 5), no ice sheet existed in the region at the young (?) Saale (MIS 6). According to more recent data (Gibbard et al., 2018), however, there was a glaciation about 160 ka BP (Late Wolston) in Fenland (East Anglia) and periglacial/glacial climatic conditions were confirmed.

We selected 33 localities (Table 1) dated of time interval of interest for this study. During MIS 6–MIS 4, the remains of 29 species of large mammals were found in the region. Comprehensive information on species diversity can be obtained from the following locations (Tables S5A and S5B): College Farm, Lower Channel (layers 1 and 2) (Schreve, 1998; Murton et al., 2015), Crayford (Schreve, 1998), Balderton Sand and Gravel (150 ka BP) (Brandon and Sumbler, 1991; Schreve, 1998), Trafalgar Square (London) (51.508N, −0.128W) (Franks, 1960; Stuart, 1974; Stuart, 1976), Brentford (Juby, 2011), Barrington Chalk Pit (122 ka BP) (Stuart, 1995), Kirkdale Cave (Boylan, 1981; McFarlane and Ford, 1998), Victoria Cave (Lower Cave Earth, 112–102 ka BP) (Dawkins, 1872; Gascoyne et al., 1981; Gilmour et al., 2007), Stump Cross Cave (flowstone enclosing the cranial remains of wolverine, 73.9 + 12/-11.9 ka BP) (Gilmour et al., 2007; O'Connor and Lord, 2013), Ash Tree Cave (Basal Clay, > 58 ka BP) (Dinnis et al., 2016), and Lynford Quarry (deposit near base, main channel deposits, 83–64 ka BP) (Boismier et al., 2003; Schreve, 2006; Donoghue, 2006; Schreve et al., 2012).

It should be noted that some of the local faunas recovered from fluvial deposits may be mixed: the mammal remains found together often belong to species with contrary environmental (and first of all, climatic) requirements. Besides, there is a gap in the record between MIS 5e and MIS 5b. The fauna composition attributable approximately to MIS 6 described in College Farm, Balderton Sand and Gravel, and Crayford localities. The list of the species recovered from those localities is as follows: *P. antiquus*, *M. intermedius*, *C. antiquitatis*, *S. hemitoechus*, *S. kirchbergensis*, *E. ferus*, *B. primigenius*, *B. priscus*, *Ovibos moschatus*, *C. elaphus*, *M. giganteus*, *R. tarandus*, *C. lupus*, *C. alpinus*, *V. vulpes*, *C. c. spelaea, P. spelaea*, and *U. arctos*. In the Ipswichian Interglacial the regional mammal fauna (Trafalgar Square (London), Victoria Cave, Brentford, Barrington Chalk Pit and Kirkdale Cave) included: *P. antiquus*, *M. intermedius*, *S. hemitoechus*, *E. ferus*, *Hippopotamus* ssp., *B. primigenius*, *B. priscus*, *C. elaphus*, *M. giganteus*, *D. dama*, *C. capreolus*, *S. scrofa*, *C. lupus*, *V. vulpes*, *C. c. spelaea, P. spelaea*, *M. meles*, *M. erminea*, and *U. arctos*. The regional fauna datable to MIS 4 is completely devoid of thermophilic species, as follows from the studies of local faunas in localities Stump Cross Cave, Ash Tree Cave, Lynford Quarry; the faunas are dominated by *M. primigenius*, *C. antiquitatis*, *E. ferus*, *B. priscus*, *R. tarandus*, *C. lupus*, *C. c. spelaea*, *V. vulpes*, *G. gulo*, and *U. arctos*.

The most widespread species were as follows: in MIS 6 – *Mammuthus* sp., *E. ferus*, *U. arctos*, and *C. lupus*, in MIS 5e – *B. priscus*, *Hippopotamus* ssp., *P. antiquus*, *U. arctos*, and *C. elaphus*, in the second half of MIS 5 – *B. priscus*, *R, tarandus*, *C. lupus* and *M. primigenius*. As to MIS 4 stage, the data available at present are insufficient for estimating relative frequency of occurrence of 9 species recorded at that time. The maximum of species richness is definitely confined to the Ipswichian Interglacial (Fig. 6A). If we exclude the short-term Ipswichian Interglacial from consideration, the regional faunal assemblage appears to include mostly species well adapted to cold climate (Fig. 6B). Thermophilic species,

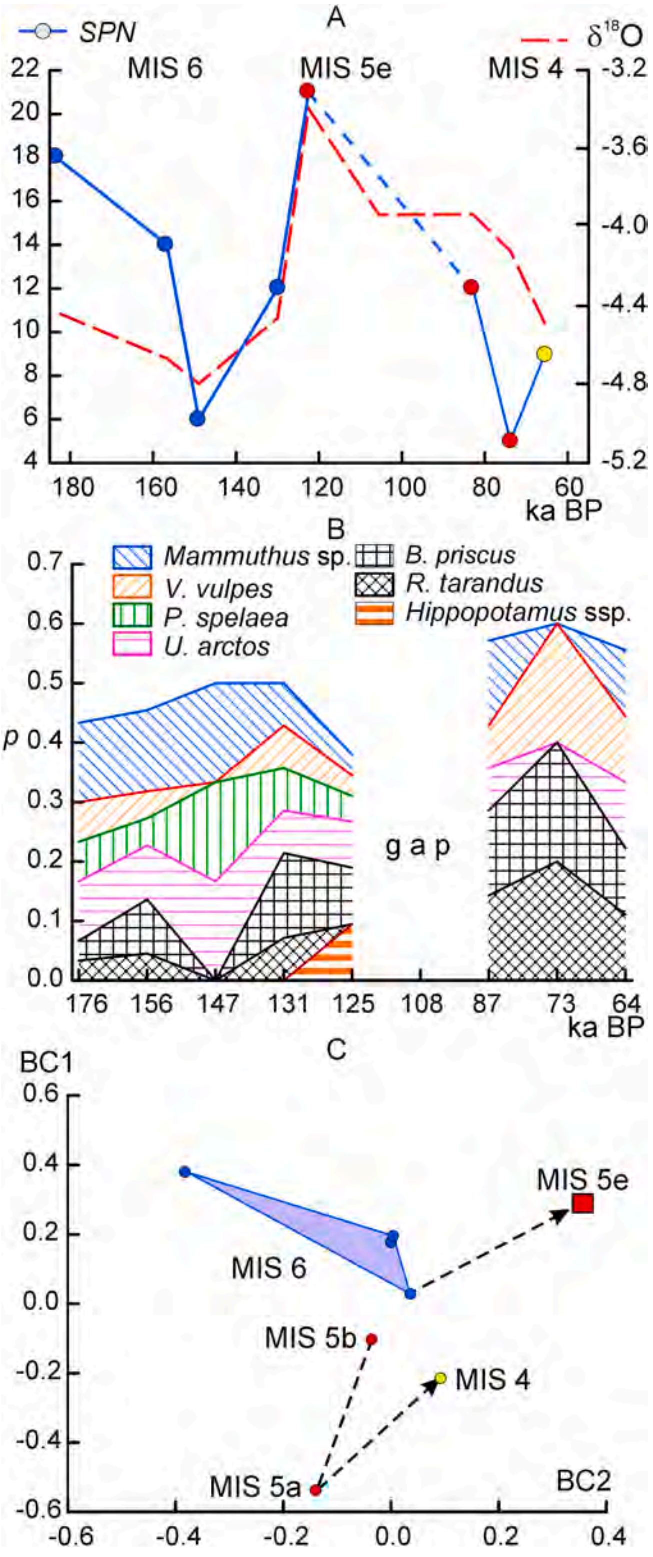

Fig. 6. Evolution of the West European Atlantic Southern large mammalian assemblage in MIS 6–MIS 4 stages. A – changes in species richness (*SPN*) against the background of global temperature changes ($\delta^{18}O$); B – "abundance" (relative frequencies of localities, *p*) of the selected species; C – the "portrait" of regional mammalian assemblage evolution in projection on two first coordinates of the model (BC1, BC2). This figure is available in colour online.

including forest ones, appear for a short time in the Ipswichian Interglacial and disappear immediately after.

In spite of a small volume of the starting data, we made an attempt at describing the regional assemblage evolution with the use of a model. The model thus obtained has only two coordinates. The BC1 coordinate shows a correlation with geological age ($r = 0.78$, $p = 0.02$) and frequency of occurrence of *R. tarandus* (−0.97, <0.01), *V. vulpes* (−0.96), *B. priscus* (−0.85, <0.01), *U. arctos* (0.74, 0.03), and *P. spelaea* (0.74, 0.03). The second coordinate is correlatable with the number of species only (0.77, 0.03). Fig. 6C displays irreversible (evolutionary) transformations of the entire assemblage, an isolated position of the Ipswichian interglacial (MIS 5e) and the return to lower values of the species richness (though with changed relationship between various species occurrence) at the end of MIS 5 and during MIS 4.

3.1.5. *West European Atlantic northern region*

The region includes the northern part of the Great Britain Island and a small part in the east of the island of Ireland (Fig. 1A (VI)). The attribution of the part of Ireland Island into the region resulted probably from the too large size of the grid cell and too small distance between the islands.

Two localities have been chosen in the region, both confined to the interval ~ MIS 5c – MIS 4 (?): Aghnadarragh (layer 5, 109–74 ka BP) (Lister and Grün, 2015), North Sea, north of Aberdeen, >50–47 ka BP) (Lister and Stuart, 2019). The antler of *M. giganteus* from the North Sea shelf yielded infinite radiocarbon dates. We suppose that the real age of the remains falls within the time interval under study. The interglacial interval, however, is excluded from consideration (because of a high stand of the sea level). As has been published not long ago (Lister and Grün, 2015), the remains of *M. primigenius* and *O. moschatus* were dated by ESR method. The dates fall in the range 109 to 74 ka BP, which corresponds to the later part of MIS 5. The presences of *O. moschatus*, as well as remains of cold-adapted flora are indicative of the cold climatic condition during the end MIS 5 in the region.

3.1.6. *South European Mediterranean Apennine region*

The region includes the entire Apennine peninsula (Fig. 1A (VII)). For the analysis, we selected 33 geographical sites with 36 localities (Table 1). The complete list of mammal fauna contains 33 species (Tables S6A and S6B). The composition of local faunas is shown taking the following localities as examples: Riparo del Molare (middle Palaeolithic layer 10 m thick) (Arobba et al., 2004), Montignoso (Mann and Vandermeersch, 1997), Grotta Grande of Scario (trench A and F, 135 ± 11 ka BP) (Ronchitelli et al., 2011), Grotta degli Orsi Volanti (Mazza et al., 2005), Melpignano-Cursi and San Sidero area (Bologna et al., 1994; Petronio et al., 2008), Cava Nuzzo (Bologna et al., 1994; Petronio et al., 2007; Pandolfi et al., 2017), Grotta Cucigliana (layer A) (Farina, 2011,; 2013), San Sidero 3 (De Giuli, 1983; Bologna et al., 1994; Iurino et al., 2013), Torre Talao (Marra, 2009), Carnello (Petronio et al., 2011), and Canale delle Acque Alte (layers C2, E2, E3; 59–57 ka BP) (Farina, 2011).

A typical MIS 6 fauna of the region may be illustrated with the data from localities Riparo del Molare, Montignoso, Grotta Grande of Scario (A, F): *P. antiquus*, *S. hemitoechus*, *E. ferus*, *Hippopotamus* spp., *B. primigenius*, *B. priscus*, *C. elaphus*, *D. dama*, *C. capreolus*, *S. scrofa*, *C. lupus*, *V. vulpes*, *C. c. spelaea*, *L. lynx*, *F. silvestris*, *P. pardus*, *U. arctos*, and *H. brachyura*. The local faunas of Grotta degli Orsi Volanti, Melpignano-Cursi and San Sidero area and Grotta Cucigliana show specific features of regional fauna in MIS 5; they include: *P. antiquus*, *S. hemitoechus*, *E. ferus*, *E. hydruntinus*, *Hippopotamus* spp., *B. primigenius*, *B. priscus*, *C. elaphus*, *D. dama*, *C. capreolus*, *S. scrofa*, *C. lupus*, *Canis aureus*, *V. vulpes*, *C. c. spelaea*, *L. lynx*, *P. spelaea*, *M. meles*, *U. spelaeus*, *U. arctos*, and *M. sylvana*. The large mammal fauna diversity on the peninsula in MIS 4 stage may be illustrated with the list of species recovered from Carnello, San Sidero 3, Torre Talao and Canale delle Acque Alt localities: *P. antiquus*, *S. hemitoechus*, *E. ferus*, *E. hydruntinus*, *Hippopotamus* spp., *B. primigenius*, *B. priscus*, *C. ibex*, *C. elaphus*, *M. giganteus*, *D. dama*, *C. capreolus*, *S. scrofa*, *C. lupus*, *V. vulpes*, *C. c. spelaea*, *L. lynx*, *P. pardus*, *P. spelaea*, *M. martes*, *U. spelaeus*, and *U. arctos*.

It should be noted that the cold-adapted species are practically absent from the regional list. The species most widely spread in MIS 6 here were *D. dama, C. elaphus, B. primigenius, S. scrofa, C. lupus, E. ferus, P. antiquus,* and *S. hemitoechus*. In common with the above discussed regions the species richness was conspicuously reduced here at the end of MIS 6 (Fig. 7A) and, unlike the above cases, in the Apennines it did not practically increase in the subsequent interglacial. In MIS 5e the large mammal fauna in the region was as follows: *D. dama*, *C. elaphus*, *C. ibex*, *B. primigenius*, *S. scrofa*, *P. antiquus*, *C. capreolus*, *U. arctos*, *B. priscus*, *Hippopotamus* spp., and *V. vulpes*. *Hippopotamus* spp. appeared often enough in the faunal lists of MIS 6–MIS 4. The same is true of the narrow-nosed rhinoceros (*S. hemitoechus*), which is constantly present in the regional fossil record except, probably, for interglacial.

The faunal diversity increased in MIS 5d-c. Such a relatively high level of the species richness persisted until MIS 4 (probably, except for the very end of MIS 5). At that, the set of dominant species stayed more or less the same. Among the species most widespread during the entire MIS 6–MIS 4 there were *D. dama*, *C. elaphus*, *B. primigenius*, *S. scrofa*, and *C. capreolus.*

The evolutionary model of the regional assemblage has three coordinates. The first one, BC1, correlates with the species richness (0.81, <0.01) and with its frequency of occurrence: *C. ibex* (−0.81, <0.01), *C. elaphus* (−0.75, 0.02), *C. capreolus* (−0.69, 0.04) (assemblage I), *P. spelaea* (0.72, 0.03), *E. hydruntinus* (0.76, 0.02), and *C. c. spelaea* (0.83, <0.01) (assemblage II). The differences between the two assemblages manifest themselves in differently directed response to (most probably) environmental changes in the region between MIS 6a and MIS 5d. It was at that time that *P. spelaea*, *E. hydruntinus* and *C. c. spelaea* disappeared for a while from the palaeontological records, and the frequencies of the other three species occurrence became essentially greater (Fig. 7B). The second coordinate of the model correlated with occurrence frequency of *P. antiquus* (−0.72, 0.03), *P. pardus* (0.68, 0.04), and *L. lynx* (0.73, 0.03) (assemblage III). Coordinate BC3 shows a poorly pronounced correlation with *S. scrofa* (−0.68, 0.04).

Fig. 7C displays variability in occurrence of the most commonly encountered species (besides those included into assemblages I–III). Relative dominant of the regional assemblage – *D. dama,* in common with *B. primigenius,* displays the frequency variability not unlike to that of species belonging to assemblage I (noted for a frequency rise in the interglacial). The occurrence of *C. lupus* is similar to the species of assemblage II. Quasi-cyclic changes are characteristic of *U. arctos* and *B. priscus* (their frequency of occurrence rises at the end of MIS 6, decreases during the interglacial, and rises again in the middle of MIS 5 and in MIS 4).

Changes in the relative frequency of occurrence of *S. hemitoechus* localities are similar in general to the dynamics of species of assemblage III and that of *P. antiquus*. It seems possible that ranges of many species at least shrank during the interglacial; *M. martes* was recorded at the end of MIS 5 and in MIS 4 only. *H. brachyura* is recorded in the middle of MIS 6 and in MIS 5a.

The analysis of the fauna in the region revealed relatively weak variations in the occurrence frequency of the most widespread species localities in MIS 6a–MIS 5e. The transition of the faunal assemblage state at the end of MIS 6 to its new state in MIS 5 occurred after the interglacial time (Fig. 7D). The transition to MIS 4 manifested itself in changes of ranges of a few relatively rare species, and did not practically affect the dominants of the assemblage.

3.1.7. *South European Mediterranean Balkan region*

That bioregion is confined to the Balkan Peninsula (except for a small area adjacent to the Sea of Marmara (Fig. 1A (VIII)). The information on the large mammal fauna in MIS 6–MIS 4 was obtained mainly from three sites (Tables S7A and 7B): Crvena Stijena (layers XXXI-XXVII, XXIII-XX,

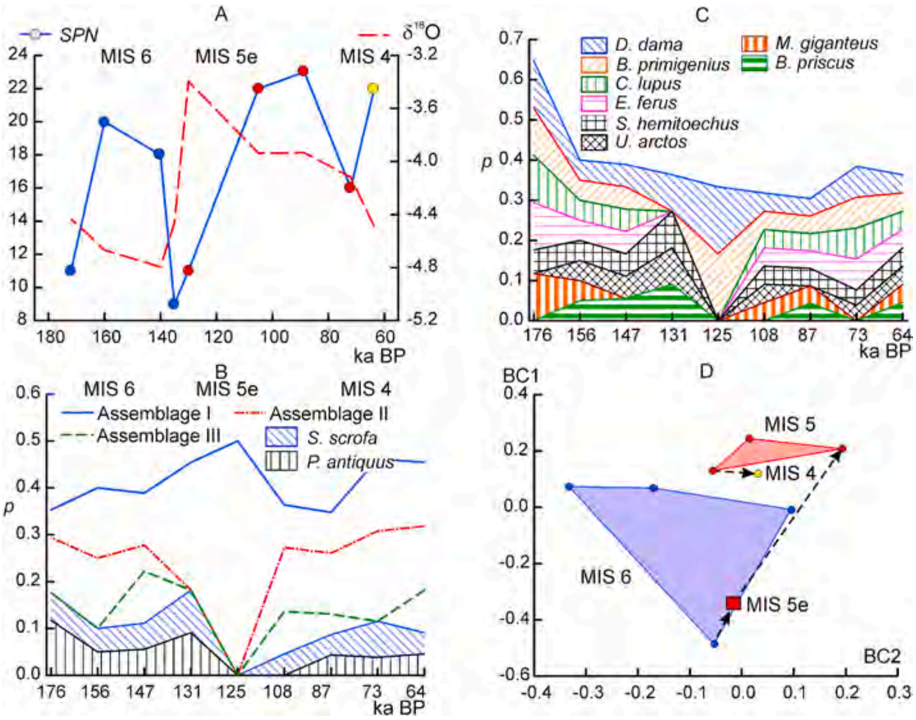

Fig. 7. Evolution of the South European Mediterranean Apennine region large mammalian assemblage in MIS 6–MIS 4 stages. A – changes in species richness (*SPN*) against the background of global temperature changes ($\delta^{18}O$); B – "abundance" (relative frequencies of localities, *p*) of indicator species from the assemblages I-III, *S. scrofa*, *P. antiquus*; C – "abundance" (relative frequencies of localities, p) of the most common species; D – the "portrait" of regional mammalian assemblage evolution in projection on two first coordinates of the model (BC1, BC2). This figure is available in colour online.

XIX-XIV, MIS6 – MIS 4) (Basler et al., 1966; Morin and Soulier, 2017), Kalamakia Cave (layer III, 97–43 ka BP) (Lecervoisier, 2003; Harvati et al., 2013), and the Klissoura (Klisoura) Cave 1 (layers XVII, dripstone layer (unit "a"), 81.6–60.3 ka BP) (Koumouzelis et al., 2001; Starkovich, 2012, 2017).

The regional list includes ~24 species. The most diversified fauna dated to MIS 6 was recovered from the multi-layered locality Crvena Stijena. Layers XXXI–XXVII yielded remains of *E. ferus*, *C. ibex*, *Ovis orientalis musimon, C. elaphus*, *M. giganteus*, *D. dama*, and *C. capreolus*. Layer III of the Kalamakia Cave and layers XXVI-XXV of Crvena Stijena locality (both corresponding to MIS 5) yielded *P. antiquus*, *S. kirchbergensis*, *E. ferus*, *B. primigenius*, *C. ibex*, *C. elaphus*, *D. dama*, *C. capreolus*, *S. scrofa, C. lupus*, *V. vulpes*, *L. lynx*, *F. silvestris*, *P. pardus*, *Martes* sp., *Mustela* sp., *U. thibetanus*, and *U. arctos*. Local faunas from Crvena Stijena (layer XXIV) and Klissoura Cave 1 (layers XVII, XX) give an idea of their diversity during stadial MIS 4. The species list for that interval includes: *E. ferus, E. hydruntinus*, *C. ibex*, *B. primigenius, B. priscus, C. elaphus*, *D. dama, C. capreolus*, *S. scrofa*, *C. lupus*, *V. vulpes*, and *C. c. spelaea.*

The maximum amount of localities dated to MIS 6 yielded remains of cold-adapted species *M. giganteus* and *O. orientalis*.

Among the species typically found in the region in the period under consideration (MIS 6–MIS 4), there are *C. elaphus, C. capreolus, C. ibex* and *S. scrofa*, *S. kirchbergensis* (MIS 6–MIS 5)*, B. primigenius* (MIS 5–MIS 4)*, E. ferus*, *C. lupus* (MIS 5–MIS 4), and *U. arctos*.

The scarcity of data prevents us from the development of the evolution model for the considered regional assemblage.

3.1.8. Middle European Central – southern region

The region under consideration occupies a large area north of the Balkan Peninsula in the central and Eastern Europe (Fig. 1A (IX)). The region was not glaciated during the Saale glacial time (MIS 6). For the region characteristic, we selected 59 sites with 101 localities (Table 1). The complete list contains about 47 species (Table S8A). The composition of local faunas (Table S8B) is considered taking the following localities as the examples: Kozarnika (Tillier et al., 2017), Vindija Cave (Musil, 2010; Miracle et al., 2010), Mishik (Mishin) Kamik cave (150–130 ka BP) (Gyurova et al., 2015; Spassov et al., 2017), Ihrovytsya or Ihrovytsia (Gorokhov soil, layer II, 150 ± 16, 83 ka BP) (Krajcarz et al., 2013; Łanczont et al., 2014), Krapina (units 1–9, 130–87 ka BP) (Döppes et al., 2008; Musil, 2010), Mala Balanica (layers 2 a-c, 113 + 74/-43 ka BP) (Roksandić et al., 2011; Rink et al., 2013; Cvetković and Dimitrijević, 2014), Gánovce-Hrádok (complex III, Taubachian; vertebrate assemblage B (cold phase), layer 3, vertebrate assemblage "Early" Weichsel (vertebrate assemblage E), 131–85.2 ka BP) (Sabol et al., 2017), Pešturina Cave (layers 4a–b, 103.5–67 ka BP) (Blackwell et al., 2014; Majkić et al., 2018), Kalman Lambrecht (Jánossy, 2001; Musil, 2010), Baranica Cave (layer II, >53100 BP, OxA-13946) (Dimitrijević, 2011), Hijenska Pećina (Pičuljan, 2012), Odessa-Nerubaj Caves (>52450 BP, VERA-2761) (Kurtén, 1969; Nagel et al., 2005; Ridush, 2009), and Molodovo 1 (Ivanova, 1982; Demay et al., 2012).

The regional fauna composition in MIS 6 may be illustrated with list of species obtained from several localities (Vindija Cave, Mishik Kamik Cave and Ihrovytsya); the list includes: *M. intermedius*, *C. antiquitatis*, *S. kirchbergensis*, *E. ferus*, *E. hydruntinus*, *B. priscus*, *C. elaphus*, *M. giganteus*, *D. dama*, *C. capreolus*, *R. tarandus*, *S. scrofa*, *C. lupus*, *V. lagopus*, *V. vulpes*, *C. alpinus*, *C. c. spelaea, P. spelaea*, *M. meles*, *M. nivalis*, *M. erminea*, *U. thibetanus*, *U. spelaeus*, and *H. brachyura*. The species list from localities Krapina, Mala Balanica, Pešturina Cave, Kalman Lambrecht Cave and Baranica Cave shows clearly a highly diversified fauna in MIS 5 including *P. antiquus*, *M. intermedius*, *C. antiquitatis*, *S. hemitoechus*, *S. kirchbergensis*, *E. ferus*, *E. hydruntinus*, *Hippopotamus* ssp., *B. primigenius*, *B. priscus*, *C. ibex*, *R. rupicapra*, *A. alces*, *C. elaphus*, *M. giganteus*, *D. dama*, *C. capreolus*, *S. scrofa*, *C. lupus*, *V. vulpes*, *C. alpinus*, *C. c. spelaea*, *L. lynx*, *F. silvestris*, *P. pardus*, *P. spelaea*, *G. gulo*, *L. lutra*, *M. martes*, *M. meles*, *Mustela eversmanii*, *M. putorius*, *U. spelaeus*, *U. arctos*, *H. brachyura*, *Hystrix cristata*, and *C. fiber*.

The materials recovered from the well-known Molodovo 1 (MIS 4, layer 4, approximately) locality fill that gap only partially. Among large mammals from that locality include *M. primigenius*, *C. antiquitatis*, *A. alces*, *C. elaphus*, *R. tarandus*, *C. lupus*, *M. nivalis*, and *U. arctos*.

The large mammal fauna of the region is highly diversified. On the whole, there are 32–33 species recorded in MIS 6. Most common are localities with *U. spelaeus*, *E. ferus*, *C. lupus*, *C. elaphus*, *B. primigenius*, *M. intermedius*, *M. giganteus,* and *P. spelaea*. There are some other species in the list, such as *S. kirchbergensis* (Velika Balanica, Vindija Cave), *C. antiquitatis* (Hôrka-Ondrej, Gánovce-Hrádok, Ihrovytsya), *C. alpinus* (Mishik Kamik Cave), *V. lagopus* (Ihrovytsya, Mishik Kamik Cave), *U. rossicus* (Mishik Kamik cave (Spassov et al., 2017)). Characteristic is the absence of *U. arctos* remains throughout this isotope stage in the region. The maximum species diversity (28 species) in MIS 6 falls approximately on ~ MIS 6c (Fig. 8A). It is approximately on this cold interval that fall occasional finds such species as *A. alces* (Betalov podmol (Musil, 2010)), *D. dama* (Velika Balanica, Mishik Kamik Cave), *F. silvestris* (Velika Balanica), *U. thibetanus* (Mishik Kamik Cave) and *H. brachiura* (Hôrka-Ondrej, 43.463°N, 22.886°E (Kaminská, 2000) and the Mishik Kamik Cave).

The species richness decreases at the end of MIS 6 and increases sharply again (up to 39 species) in the interglacial (Fig. 8A). In MIS 5e the most widespread species were *U. spelaeus*, *P. spelaea*, *C. lupus*, *C. elaphus*, and *V. vulpes*. The maximum number of *P. antiquus*, *S. kirchbergensis*, *F. silvestris* remains falls on that time. There are recorded also findings of *Hippopotamus* ssp. (Krapina), *P. pardus* (Krapina and Veternica (Miracle and Brajković, 2010; Miracle et al., 2010)) *U. arctos* (Gánovce-Hrádok, Krapina and other), *M. martes* (Schwabenreith-Höhle (Döppes and Rosendahl, 2009; Döppes et al., 2016; Spötl et al., 2019)), *L. lutra* (Krapina), *C. fiber* (Krapina).

A high level of the species richness persisted through the entire stage MIS 5 and reduced a little in MIS 4 (31 species). The list of most common species changed insufficiently as compared with the interglacial and included *U. spelaeus, C. elaphus, C. lupus, P. spelaea*, *V. vulpes*, and *E. ferus*. The occurrence frequency of *B. primigenius* and *C. c. spelaea* increased. The remains of straight-tusked elephant (*P. antiquus*) found in Krapina, Gánovce-Hrádok, Karagash quarry and Kůlna Cave, and *Hippopotamus* ssp. – not far from Krapina, in Grotta dei Moscerini (David and Lungu, 1972; Stiner, 1992; Musil, 2010). *R. tarandus* reappeared in the regional fauna.

In MIS 4 the list of the most widespread species included *U. arctos* along with c *U. spelaeus, C. lupus,* and *P. spelaea*. Noteworthy is the presence of *S. kirchbergensis* (Kůlna cave) and *S. hemitoechus* (Grotta dei Moscerini), *C. fiber* (Romualdova pećina), and *V. lagopus* (Divje babe I (Toškan, 2007). *C. antiquitatis* was constantly present in the north and northeast of the region (49.69°N – 47.6°N, 17.2°E – 29.0°E) in MIS 5–MIS 4.

The model of the assemblage evolution has only two coordinates. The coordinate BC1 shows a close correlation with *SPN* (0.92, <0.01). Coordinates BC1 and BC2 display the locality occurrence for the four groups of species. Relative to the first coordinates, assemblage I includes *M. giganteus* ($r = -0.84$, $p < 0.01$), *C. elaphus* (−0.71, 0.03), and *S. kirchbergensis* (−0.68, 0.04). The assemblage II includes species not found in MIS 6 at all, or occur there only occasionally (mostly in ~MIS 6b), though they are constantly present in MIS 5: *V. vulpes*, *F. silvestris*, *P. pardus*, *M. meles*, *A. alces*, *R. rupicapra*, *C. antiquitatis*, and *E. hydruntinus*. On the whole, the dynamics of the relative frequency of occurrence calculated for species belonging to different assemblages shows a similarity (Fig. 8B). The species belonging to assemblage I display a tendency towards a decrease of relative presence from MIS 5e to MIS 5a. The species of assemblage II also display a drop of the occurrence frequency after MIS 5e, but later it grows a little towards MIS 5a.

Coordinate BC2 correlates with occurrence of species that occurred relatively more frequently in some substages of MIS 6 than in MIS 5 (*U. spelaeus, C. alpinus, D. dama*), or were confined to MIS 6 only (*U. rossicus?*). Changes in the relative frequency of the above listed species that control the regional evolution pattern are shown in Fig. 8B.

Fig. 8C displays a relative occurrence frequency of localities of the common regional species that exerted an essential influence (by their presence or absence) on the fauna composition and *SPN*. A few of them (*E. ferus, B. primigenius, B. priscus*) had local maximum at the beginning of MIS 6, others (*C. lupus*, *P. spelaea*, *C. c. spelaea*, *S. scrofa*) – in ~MIS 6c. At the maximum cooling of the Saale ice age some species (*S. scrofa*, *B. primigenius* or *C. capreolus*) disappeared from the palaeontological records, and reappeared in the Eemian interglacial. Total increase in the relative occurrence of the species localities coincides with the beginning of Weichsel Glaciation (MIS 5d-c and MIS 4).

The low-dimensional model of the evolution in the regional assemblage showed that there were four different states of assemblage: I – MIS 6e–c, II – MIS 6b, III – MIS 6a, and IV – MIS 5–MIS 4 (Fig. 8D). The states differ, first of all, in their species richness which varied essentially during MIS 6 (probably due to incompleteness of the palaeontological

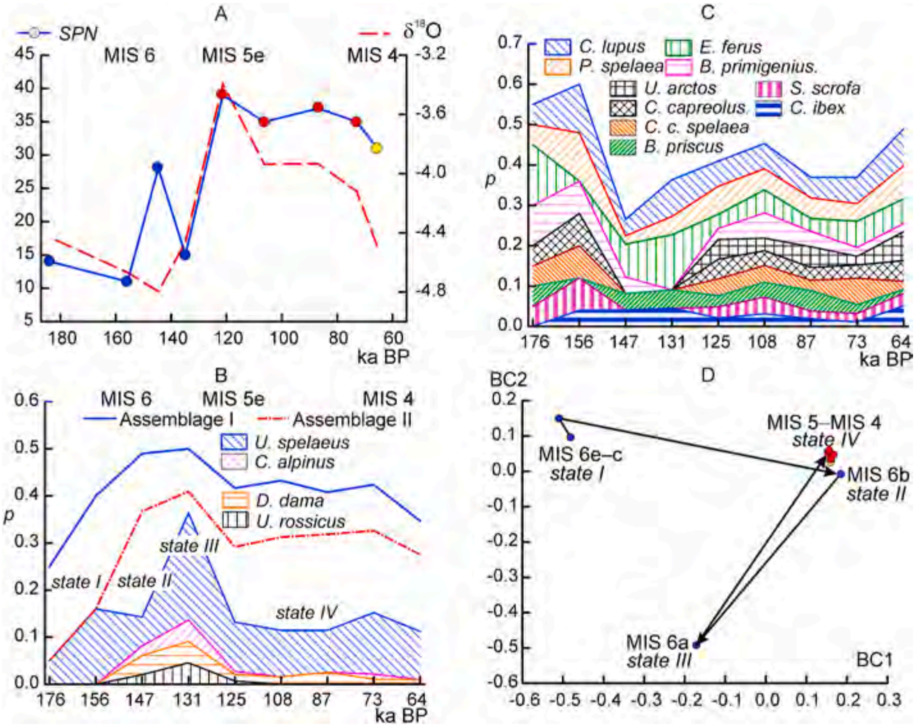

Fig. 8. Evolution of the Middle European Central – Southern region large mammalian assemblage in MIS 6–MIS 4 stages. A – changes in species richness (*SPN*) against the background of global temperature changes ($\delta^{18}O$); B – "abundance" (relative frequencies of localities, *p*) of indicator species from the assemblages I and II, *U. spelaeus*, *U. rossicus*, *C. alpinus*, and *D. dama*; C – "abundance" (relative frequencies of localities, p) of the most common species; D – the "portrait" of regional mammalian assemblage evolution in projection on two first coordinates of the model (BC1, BC2). This figure is available in colour online.

record) and stays practically constant in MIS 5–MIS 4.

3.1.9. Middle European Central – northern region

That is a large European region positioned on the territory of Central and Eastern Europe north of the Middle European Central – Southern region. At the maximum extent of the younger Saale (Warthe or Warthe II, Moscow stage) glaciation, especially at the end of MIS 6, the ice sheet covered a considerable part of this region (Fig. 1A (X)) (Ehlers et al., 2011, 2013).

We have studied the regional faunal assemblage on a basis of materials recovered from 31 geographical sites with 46 localities ("units", "layers" and etc.) (Table 1). 39 species of large mammals have been recorded in MIS 6–MIS 4 (Table S9A). Practically complete assortment of the regional large mammal fauna was recovered from the following localities (Table S9B): "Chetveria" quarry ("Sozh stage of the Pripyat glaciation") (Motuzko, 2013), Deszczowa Cave (layers I–IV, VI) (Wojtal, 2007; Stefaniak et al., 2009; Krajcarz and Cyrek, 2011), Biśnik Cave (layers 15–7, 5/6, 196–67 ka BP) (Asperen and Stefaniak, 2011; Krajcarz and Cyrek, 2011; Marciszak et al., 2011; Marciszak and Socha, 2014; Stefaniak, 2015; Tomek et al., 2012), Nietoperzowa Cave (Krajcarz and Madeyska, 2010; Musil, 2010), Schönfeld (van Kuznetsova, 2000), Schronisko Wylotne (layers 5–7) (Nadachowski et al., 2015), Jaskinia Ciemna (layers 15–16, 13, 11.2) (Valde-Nowak et al., 2014), Zwoleń (layers I, V, VI, VIII, X, 95–65 ka BP) (Schild, 2006), Niedźwiedzia Cave (below Jaskinia Miniaturka, 87 ± 6 ka BP, > 40000 BP, Gd-15344) (Baca et al., 2014; Marciszak et al., 2019b), Hallera Avenue (Wroclaw) (complex A/B; C, D, 80.4–59.1 ka BP) (Wiśniewski et al., 2013).

The deposits of "Chetveria" quarry and Deszczowa Cave yielded the remains of a fauna dated to MIS 6 stage. A relatively short list of the species consists of *M. intermedius*, *C. antiquitatis*, *E. ferus*, *B. priscus*, *C. elaphus*, *M. giganteus*, *R. tarandus*, *V. praeglacialis*, *P. spelaea*, and *Gulo schlosseri*. The regional fauna in the Eem interglacial can be judged by the composition of local faunas recovered from localities Biśnik Cave (layers 13–14), Schronisko Wylotne, Jaskinia Ciemna, and Niedźwiedzia Cave: *M. intermedius*, *C. antiquitatis*, *E. ferus*, *B. primigenius*, *B. priscus*, *R. rupicapra*, *A. alces*, *C. elaphus*, *M. giganteus*, *C. capreolus*, *R. tarandus*, *C. lupus*, *V. lagopus*, *V. vulpes*, *C. c. spelaea*, *L. lynx*, *F. silvestris*, *P. pardus*, *P. spelaea*, *M. martes*, *M. meles*, *M. erminea*, *M. eversmanii*, *M. nivalis*, *M. putorius*, *G. gulo*, *U. spelaeus*, *U. arctos*, and *C. fiber*. The layer 7 of Biśnik Cave related to MIS 4 stage contains fauna as follows: *C. antiquitatis*, *E. ferus*, *B. priscus*, *O. moschatus*, *R. rupicapra*, *C. elaphus*, *M. giganteus*, *R. tarandus*, *C. lupus*, *V. lagopus*, *V. vulpes*, *C. c. spelaea, F. silvestris*, *P. spelaea*, *M. martes*, *M. erminea*, *M. nivalis*, *M. putorius*, *U. spelaeus*, and *C. fiber*. Remains of *M. primigenius* and *S. kirchbergensis* dated to the same stadial were found in the locality Hallera Avenue (Wroclaw).

The regional fauna dated to MIS 6 includes 13 species only. Most of localities yielded remains of the following species (in decreasing order): *P. spelaea, E. ferus, M. intermedius, B. priscus,* and *R. tarandus*. Besides, remains of *C. antiquitatis, G. schlosseri, C. elaphus, D. dama* and *Crocuta* sp. were found occasionally. The maximum of species diversity is recorded at the very beginning of MIS 6 (10 species, Fig. 9A). The total number of species in the localities of the region did not exceed 3–4 up to the Eem Interglacial.

Their number rises sharply in the localities dated at the interglacial – up to 32 species. The most widely distributed taxa are as follows (in descending order): *C. elaphus, P. spelaea, E. ferus, R. tarandus, C. capreolus, M. intermedius, A. alces*, and *C. lupus*. The "rare" species group (present in one or two localities) includes mammalian species different in their environmental preferences, such as *F. silvestris, M. martes, P. antiquus, Castor fiber, P. pardus, S. kirchbergensis, U. spelaeus, C. antiquitatis, M. giganteus,* and some others (Table S9A).

Immediately after MIS 5e the species richness in the region falls down approximately to 27 species (Fig. 9A). Certain changes appeared in the list of the most widespread species (in the order of decreasing number of localities): *E. ferus, P. spelaea, M. intermedius/M. primigenius, C. fiber, R. tarandus*, and *C. capreolus*. The regional fauna in the middle of MIS 5 included both thermophilic and cold-adapted species. Noteworthy is the complete disappearance (extinction) of *P. antiquus* and *P. pardus* from the region. Quite possible (though we have not enough data for a confident statement) that by the end of MIS 5 the species richness descended to a level typical of MIS 6 (8 species altogether: *Mammuthus* sp., *E. ferus, C. fiber, R. tarandus, C. capreolus, C. antiquitatis, B. priscus*, and *A. alces*).

MIS 4 stadial is distinctly dominated by cold-adapted species against the background of relatively high species richness (26 species). The most

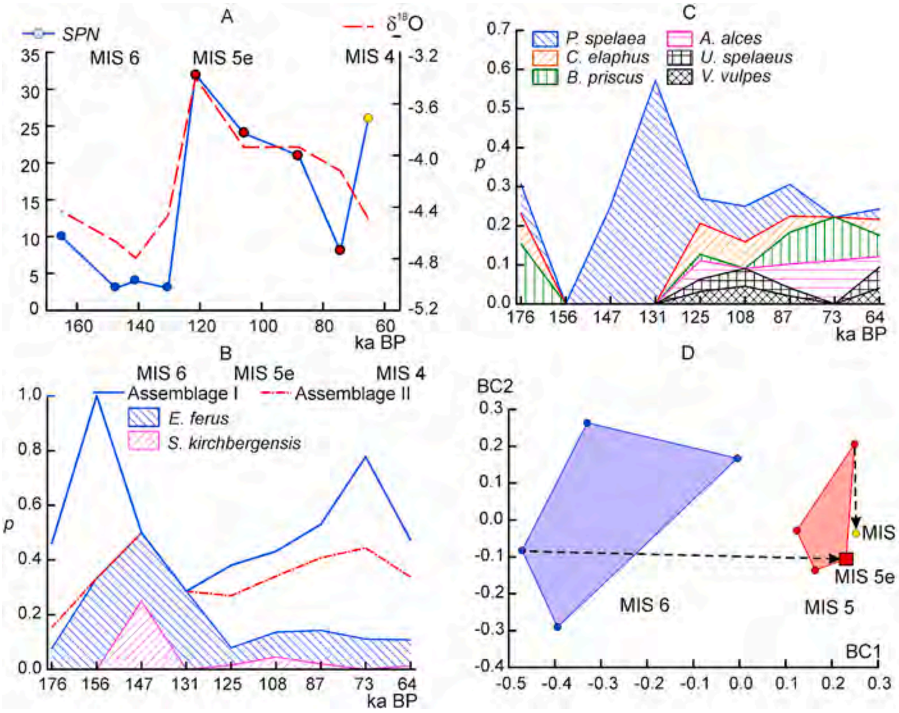

Fig. 9. Evolution of the Middle European Central –Northern region large mammalian assemblage in MIS 6–MIS 4 stages. A – changes in species richness (*SPN*) against the background of global temperature changes ($\delta^{18}O$); B – "abundance" (relative frequencies of localities, *p*) of indicator species from the assemblages I and II, *E. ferus* and *S. kirchbergensis*; C – "abundance" (relative frequencies of localities, p) of the most common species; D – the "portrait" of regional mammalian assemblage evolution in projection on two first coordinates of the model (BC1, BC2)This figure is available in colour online.

widely spread in the region were *E. ferus, R. tarandus, C. antiquitatis, M. primigenius, B. priscus, C. lupus*, and *U. spelaeus*. The cited list is quite close to the core of the so-called "Mammoth steppe" faunal assemblage ("*Mammuthus – Coelodonta*") that would be most widespread in the Late Pleistocene (MIS 3–MIS 2).

During MIS 4 the regional fauna is still diversified in its environmental preferences. It includes, on one hand, *M. giganteus, V. lagopus, P. spelaea, C. c. spelaea, S. tatarica, O. moschatus* (Biśnik Cave), and on the other – *C. fiber* (Zwoleń, Biśnik Cave), probably *S. kirchbergensis* (Hallera Avenue (Wroclaw)), *F. silvestris* and *M. martes* (Deszczowa Cave, Biśnik Cave).

The model of the Middle European Central –Northern regional assemblage evolution has two coordinates. Coordinate BC1 shows a positive correlation with species richness *SPN* ($r = 0.79$, $p = 0.01$) and with variable δ^{18}O (0.68, 0.04). Therefore, the evolution of that regional assemblage of large mammals demonstrates a direct dependence on the global temperature fluctuations. Quite clear that it depends primarily on the region position in the periglacial zone during MIS 6 and on its geographical position in general.

BC1 correlates with relative frequency of *E. ferus* (−0.90, 0.001), *C. fiber* (0.69, 0.04), *M. martes* (0.69, 0.04), *C. capreolus* (0.80, 0.01) (assemblage I). Besides, a positive correlation was obtained for *C. lupus* (0.69, 0.04), and *C. antiquitatis* (0.74, 0.02). That may be attributed to the fact that both species are practically absent from our sample for MIS 6 (except for the rhinoceros that appeared at the very beginning of the stage), their 'appearance' coinciding with the interglacial. The second coordinate of the model demonstrates a correlation with relative occurrence frequency of *S. kirchbergensis* (−0.68, 0.04), *R. tarandus* (0.76, 0.02) and *M. intermedius/M. primigenius* (0.92, <0.01) (assemblage II). Representatives of assemblage I displayed the maximum relative frequency in the middle of MIS 6 and at the end of MIS 5; the maximums of assemblage II fall on the second half of MIS 6 and the end of MIS 5 (Fig. 9B). The diagram of a relative frequency of the caballoid horse occurrence is similar to the same graph constructed for Merck's rhinoceros, with the relative frequency maximum falling on the second half of MIS 6; the horse, however, does not display a drop of frequency at the end of MIS 5 and in MIS 4.

Some most widespread species in the region do not show any correlation of the frequency of their occurrence with the model coordinates. The general character of changes in their relative occurrence differs essentially from that presented in Fig. 9C. For instance, at the background of very low species richness *P. spelaeus* became absolutely dominant by the end of MIS 6. Since the MIS 6 beginning, *C. elaphus* and *B. priscus* first appeared in the palaeontological records in MIS 5e, but their subsequent dynamics differs essentially. The relative frequency of *A. alces* reached its maximum at the end of MIS 5, when *C. elaphus* practically disappeared, while the greatest abundance of *U. spelaeus* in the region falls on the middle of MIS 5 and on the MIS 4 stadial.

Fig. 9D presents the evolutionary dynamics of those faunal assemblages in coordinates BC1 and BC2. It is noteworthy that the state with low species richness in MIS 6 changes abruptly to the high species richness in MIS 5 relative to the first coordinate of the model, while the transition from MIS 5 to the MIS 4 stadial is practically indistinct.

3.1.10. North European Scandinavian, middle European boreal, North European polar, and Asian North-Siberian Western regions

The four bioregions in the north of Europe and partly in the north of West Siberia (Asian North-Siberian Western) were covered (completely or over the greater part) with the ice sheet (Fig. 1A (XI, XII, XIII, and XVIII)).

We know of four localities only on that vast territory. In the North European Scandinavian region the Nordcemgrotta Cave site (Kjæpsvik) is situated near the modern Atlantic coastline of the Scandinavian Peninsula. This site yielded remains of *U. maritimus* dated to ~ MIS 5d (>70 ± 8.5 ka BP) (Crockford, 2012). The presence of the polar bear in this area suggests at least subarctic climatic conditions at the end of the last interglacial.

The Middle European Boreal region features a well-known Cheremoshnik (= Cheremoshnya) locality (layer Tb/IV (4.3–4.0 m), 115.5–114.2 ka BP), which is the stratotype of the Mikulino Interglacial (Agadjanian and Erbaeva, 1983; Rusakov et al., 2015). The locality is known for the presence of small mammal fauna including a rich set of steppe species (*Microtus gregalis, Eolagurus luteus, Cricetus cricetus* and others) along with *Apodemus* (*Sylvaemus*) *sylvaticus* (probably *A.* (*S.*) *uralensis*), *Clethrionomys* (= *Myodes*) *glareolus*. Judging from the small mammal fauna, the interglacial interval was marked by predominantly forest-steppe and steppe biotopes. The only remains of a large mammal found there were those of a caballoid horse.

The North European Polar region are known for a finding of *Mammuthus* sp. (probably *M. intermedius*) recovered from marine clayey sands in Varzuga River basin, the southern Kola Peninsula (>103.5 ka BP) (Molodkov and Yevzerov, 2004).

The locality Gornokazymsk is situated in the Asian North-Siberian Western region and dated approximately to MIS 4 stage (Smirnov et al., 1986). The locality yielded remains of *E. ferus* and *Mammuthus* sp. (most probably *M. primigenius*). The composition of the micromammal assemblage (*Microtus middendorffi, M. gregalis, Dicrostonyx gulielmi*, and *Lemmus sibiricus*) strongly suggests a cold (arctic/subarctic) climatic condition.

3.1.11. East European – Asian West-Siberian Central region

The region is situated in the Eastern Europe and West Siberia (Fig. 1A (XIV)) and includes the Middle and Southern Urals. In MIS 6 the northern part of the region was covered with the ice sheet. In the region there was described 28 sites with 39 localities (Tables 1 and S1) dated to MIS 6 –MIS 4 interval and unevenly distributed over the territory. The most of the sites concentrates in the west, near the Ural Mountains, and in the east, in the Ob' upper reaches and in the Altai-Sayan forelands.

The large mammal fauna in the region in MIS 6–MIS 4 included about 40 species (Table S10A). One can gain an impression of its diversity from the list of species found in the following localities: Mokhovo (Berezovo Formation and loess-like loams of the overlying Berezovo Formation) (Billia, 2007; Foronova, 2014), Zhilische Sokola (pit 2) (Bachura and Kosintsev, 2007; Bachura, 2008), Makhnevskaya Ice (Ledyanaya) Cave (Kosintsev et al., 2016; Kuzmin et al., 2017; Fadeeva et al., 2020), Idrisovsky grotto (Idrisovo Cave) (Kuzmin et al., 2017), Ignatievskaya Cave (Gimranov and Kosintsev, 2015; Kosintsev et al., 2016; Fadeeva et al., 2018), Bobylek (Kosintsev et al., 2016; Danukalova et al., 2020), Barsuchiy Dol (Kuzmin et al., 2017), Krasny Yar Village (layer 6, 80 ± 10 ka BP) (Vasiliev, 2002; Shpansky, 2017), Sikiyaz-Tamak 7 ("Kaminnaya" (layers 17–13 (MIS 5e-c), 11 (upper part) and 9 (upper part), >57300 BP, OxA-10916) (Kuz'mina, 1975; Kosintsev et al., 2016; Danukalova et al., 2018, 2020), Ust'-Katavskaya Cave (Kosintsev et al., 2016), Smelovskaya 2 cave (layer IV, > 60800 BP, OxA-19534) (Kuzmina, 2000; Kosintsev et al., 2016, 2019), "Tobolsk" region (Kosintsev et al., 2019).

A relatively diversified fauna that existed in the region at MIS 6 stage was described in Mokhovo and Zhilische Sokola localities: *M. intermedius*, *C. antiquitatis*, *S. kirchbergensis*, *E. ferus*, *B. priscus*, *S. tatarica*, *A. alces*, *C. elaphus*, *M. giganteus*, *R. tarandus*, *C. lupus*, *V. lagopus*, *V. vulpes*, *P. spelaea*, *Martes zibellina*, *Meles leucurus*, *M. erminea*, *M. nivalis*, *M. eversmanii*, *U. arctos*, *C. fiber*, and *M. bobac*. Relatively numerous localities in the region are dated by the fauna composition to the beginning of Kazantsevo Interglacial (MIS 5e). The richest local faunas were recovered from the localities Makhnevskaya Ice (Ledyanaya) Cave, Ignatievskaya Cave, and Barsuchii Dol Cave. The list of species found there includes *M. intermedius*, *C. antiquitatis*, *S. kirchbergensis*, *E. ferus*, *B. priscus*, *Ovis ammon*, *S. tatarica*, *A. alces*, *C. elaphus*, *M. giganteus*, *R. tarandus*, *C. lupus*, *V. lagopus*, *V. vulpes*, *C. c. spelaea*, *L. lynx*, *P. spelaea*, *M. meles*, *M. leucurus*, *G. gulo*, *M. martes*, *Mustela lutreola*, *M. erminea*, *M. nivalis*, *U. thibetanus*, *Ursus kanivetz*, *U. rossicus*, *U. arctos*, *M. bobac*, *C. fiber*, and *H. brachyura*. The transition to MIS 4 stadial may be illustrated with local faunas from Ignatievskaya Cave (layers 8–9) and "Tobolsk" region where the following species were recorded: *M. primigenius*, *Elasmotherium sibiricum*, *C. antiquitatis*, *E. ferus*, *B. priscus*, *S. tatarica*, *C. elaphus*, *R. tarandus*, *C. lupus*, *C. alpinus*, *V. lagopus*, *V. vulpes*, *C. c. spelaea, L. lynx*, *G. gulo*, *M. martes*, *M. erminea*, and *U. kanivetz*.

Note that the mammal sites of reliably dated as MIS 4 stadial in the region has not yet been discovered.

In MIS 6–MIS 4 the large mammal species richness in the region varied over wide limits – from 7 to 27 species. The data on mammals in MIS 6 do not cover the entire time interval (Fig. 10A). The maximum of species richness (22 species) falls approximately on the MIS 6d–c. According to the data available, the widespread in the region at that time were: *E. ferus*, *C. elaphus*, *B. priscus*, *U. arctos,* and *M. intermedius*. The presence of such species as *S. kirchbergensis*, *C. antiquitatis*, *M. giganteus*, *R. tarandus*, and *V. lagopus* should be noted in MIS 6. After the number of species had been probably lowered to 7 at the end of MIS 6 their number increased again to 27 in the Kazantsevo Interglacial. At that time cave bears *U. kanivetz* became widely spread over the Ural region. The group of species noted for a relatively wide range in the interglacial includes *C. lupus*, *V. vulpes*, *M. leicurus/M. meles*, *U. rossicus*, *P. spelaea,* and *H. brachyura*. Noteworthy is that the porcupine occurred both in the west (the Urals) and in the southeast of the region (the Altai Mountains) (Kuzmin et al., 2017). There are also some species indicative of forests and dated to the interglacial: *U. thibetanus* (Makhnevskaya Ice (Ledyanaya) Cave), *L. lynx* (Barsuchii Dol cave, Ignatievskaya cave), *C. fiber* (Idrisovo cave), *A. alces* (Makhnevskaya Ice (Ledyanaya) Cave), *M. martes* (Ignatievskaya Cave and Krasnyi Bor (Yakovlev, 1996)), *M. zibellina* (Bobylek). It is interesting that argali (*O. ammon*) penetrated from the southeast of the region to the Urals (lgnatievskaya cave).

In the middle of MIS 5 a sharp decrease in the species richness is recorded in the region (Fig. 10A), which in all probability may be attributed to the lack of palaeontological information. The regional species richness stayed stable and rather high at the end of MIS 5 and through MIS 4, though some changes took place time and again in the list of the most frequent species. Among the species most widely spread after the interglacial there were: *U. kanivetz, C. lupus, V. lagopus, V. vulpes, E. ferus, B. priscus, C. elaphus, P. spelaea, C. antiquitatis* and *S. tatarica*. Worth mentioning is the presence of rhinoceros *E. sibiricum* (assigned usually to the group of rare species) that appeared in the fossil records at the end of MIS 5 and persisted through MIS 4 (Kosintsev et al., 2019). The species widespread in MIS 4 were *B. priscus*, *S. tatarica*, *M. giganteus*, *U. kanivetz*, *C. antiquitatis,* and *M. primigenius*. Some others – *R. tarandus, U. arctos, C. elaphus*, and *E. ferus* – should be probably added to the list. *O. moschatus* and *C. alpinus* made their appearance in the regional species list of that stadial.

The model of evolution of the regional assemblage includes three coordinates. None of them shows a correlation with the variable of temperature ($\delta^{18}O$). Variable BC1 correlates with the relative frequency of occurrence of a number of species: *V. lagopus* ($r = -0.95$, <0.01), *M. erminea* (-0.92, 0.01), *P. spelaea* (-0.64, at a trend level), *G. gulo* (-0.61, at a trend level), *U. rossicus* (-0.61, at a trend level) (assemblage I), *M. intermedius* (0.72, 0.04), *R. tarandus* (0.75, 0.03), *M. giganteus* (0.82, 0.01), *E. ferus* (0.84, <0.01), *U. arctos* (0.90, <0.01), and *B. priscus* (0.95, <0.01) (assemblage II). The general feature of the occurrence dynamics of all the above listed species is that they don't increase their frequency in the interglacial. The species showing a positive correlation with BC1 are noted for maximums of the relative occurrence frequencies falling on the middle of MIS 6, MIS 5b-a, and more rarely – MIS 4; there is also a general trend towards a decrease in relative occurrence from MIS 5d-c to MIS 4. Species, which belonging to assemblage I, are noted for a stable relative frequency of occurrence and a noticeable growth of their total relative proportion in MIS 5d-c (Fig. 10B). Coordinate BC2 is positive correlatable with the species richness value (0.88, 0.04) and describes the relative frequency of *U. kanivetz* (0.88, 0.04). Coordinate BC3 shows a correlation with occurrence of *C. elaphus* localities ((-0.73, 0.04). Typically, the named species display a decrease in the relative occurrence in ~MIS 5d-c and a rise at the end of MIS 5. In MIS 6 *C. elaphus* demonstrates the relative occurrence maximum, while *U. kanivetz* makes its appearance in the record in the interglacial.

Fig. 10C presents the dynamics of the relative occurrence frequency of localities with the species most widely spread in the region during the entire time interval under consideration. Many of the species were notably reduced in occurrence at the interglacial time. A positive

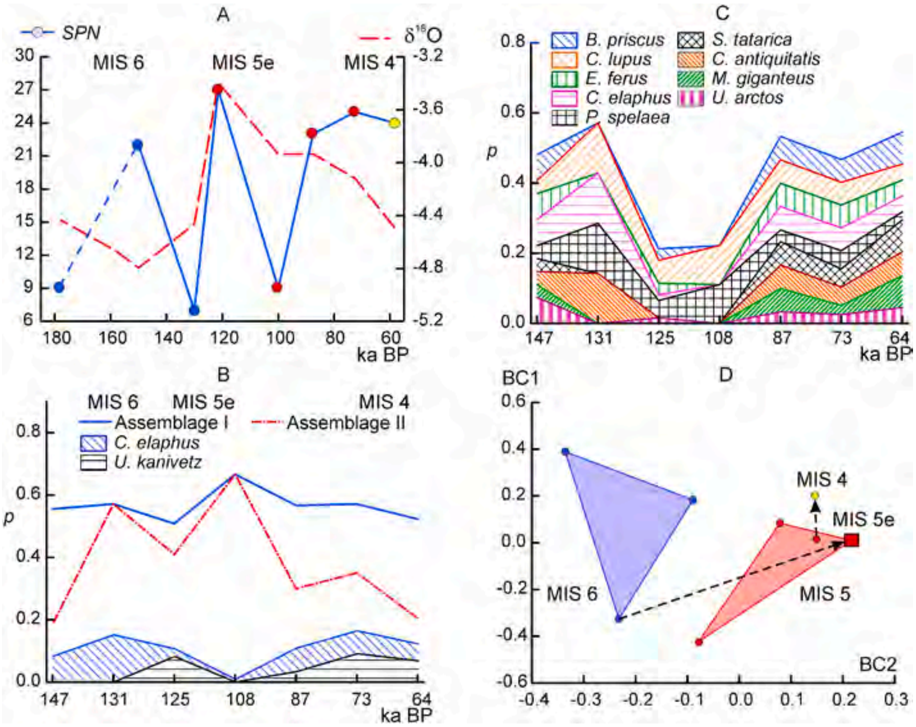

Fig. 10. Evolution of the East European – Asian West-Siberian Central large mammalian assemblage in MIS 6–MIS 4 stages. A – changes in species richness (*SPN*) against the background of global temperature changes ($\delta^{18}O$); B – "abundance" (relative frequencies of localities, *p*) of indicator species from the assemblages I and II, *C. elaphus* and *U. kanivetz*; D – relative "abundance" (*p*) of the most common species; D – the "portrait" of regional mammalian assemblage evolution in projection on two first coordinates of the model (BC1, BC2). This figure is available in colour online.

response to the interglacial conditions was shown by *B. priscus*, *E. ferus*, and *U. arctos*, while other species (*C. elaphus*, *P. spelaea*, *C. antiquitatis*, *M. giganteus* and *C. lupus*) responded negatively.

In common with many above-considered regions, the regional assemblage transition from MIS 6 to MIS 5 (Kazantsevo Interglacial) was abrupt and irreversible, though it was not accompanied by any species extinction (Fig. 10D). Quite possibly, its state was not stable in MIS 5, though the data available at present are insufficient for substantiation of the hypothesis. The transition to MIS 4 stadial was accompanies by the assemblage restructuring, when some species changed their relative frequency of occurrence and others dropped out of the assemblage. The restructuring, however, did not have any material effect on the species richness as a whole.

3.1.12. *Asian West-Siberian South-Eastern region*

The region is situated in the southeast of West Siberia and occupies, besides the plain, a considerable area in the west of the Altai-Sayan Mountains region (Fig. 1A (XV)). It is similar in the fauna composition to the subregions included into East European – Asian West-Siberian Central region. That is why we included it into our analysis.

On the whole, the presence of 44 species is recorded in 19 sites and 60 localities datable to MIS 6–MIS 4 (Tables S11A and S11B). In the recent years the principal volume of data on the mammals that inhabited the region at the end of Middle Pleistocene and in the Late Pleistocene was obtained from the multi-layered deposits of the Denisova Cave (Derevianko et al., 2003; Druzhkova et al., 2017; Jacobs et al., 2019), where remains of the ancient hominids (Denisovans and Neanderthals) have been found. Apart from Denisova Cave, there are a number of other sites yielding materials that give an insight into the regional fauna richness: Tatarka Faunal Comlex (Vasil'ev, 2003), Krasny Yar Village (Novosibirsk district) (layer 6) (Vasiliev, 2002; Shpansky, 2017), Ust'-Izhul' 1 (layers 25-26, 125–105 ka BP) (Laukhin et al., 1999; Chlachula et al., 2003; Foronova, 2014), Strashnaya cave (Kuzmin et al., 2017; Krivoshapkin et al., 2018), Kurtak (Berezhekovo) (layer 7, 118 ± 23 ka BP) (Chlachula, 2001), Ust'-Karakol 1 (pit 18, 130–90 ka BP) (Maloletko and Panychev, 1990; Derevianko et al., 1998; 2003; Orlova et al., 2004; Agadjanian et al., 2006), Kurtak 4 (Chlachula, 2001; Zander et al., 2003).

The deposits studied in the Denisova Cave and dated to the interval 184–131 ka BP (MIS 6) yielded remains of the following species: *P. antiquus/nomadicus*, *M. intermedius*, *C. antiquitatis*, *E. ferus*, *Equus ovodovi*, *Bos mutus baicalensis*, *B. priscus*, *Capra sibirica*, *O. ammon*, *Procapra gutturosa*, *S. tatarica*, *A. alces*, *C. elaphus*, *M. giganteus*, *Capreolus pygargus*, *R. tarandus*, *C. lupus*, *C. alpinus*, *V. vulpes*, *V. corsac*, *V. lagopus*, *C. c. spelaea*, *L. lynx*, *P. spelaea*, *M. zibellina*, *Mustela altaica*, *M. nivalis*, *M. erminea*, *M. eversmanii*, *U. rossicus*, and *U. arctos*. In the deposits described in the same cave and dated to the Kazantsevo interglacial time (129–113 ka BP), as well as in the Krasny Yar Village and Strashnaya Cave localities the following mammal remains were described: *M. primigenius/intermedius*, *C. antiquitatis*, *S. kirchbergensis*, *E. ferus*, *E. ovodovi*, *B. m. baicalensis*, *B. priscus*, *Soergilia elisabethae*, *C. sibirica*, *O. ammon*, *P. gutturosa*, *S. tatarica*, *A. alces*, *C. elaphus*, *M. giganteus*, *C. pygargus*, *R. tarandus*, *C. lupus*, *C. alpinus*, *V. vulpes*, *V. corsac*, *V. lagopus*, *C. c. spelaea*, *L. lynx*, *Otocolobus manul*, *Uncia uncia*, *P. spelaea*, *M. leucurus*, *M. zibellina*, *Mustela sibirica*, *M. altaica*, *M. nivalis*, *M. erminea*, *M. eversmanii*, *U. thibetanus*, *U. rossicus*, *U. arctos*, *H. brachyura*, and *C. fiber*.

Local fauna recovered from the Denisova Cave and attributable to the end of MIS 5 – MIS 4 The deposits dated to ~75 and 69–62 ka BP) included: *M. primigenius/intermedius, C. antiquitatis, E. ferus, E. ovodovi, B. m. baicalensis, B. priscus, C. sibirica, O. ammon, P. gutturosa, S. tatarica, A. alces, C. elaphus, M. giganteus, C. pygargus, R. tarandus, C. lupus, C. alpinus, V. corsac, V. vulpes, C. c. spelaea, O. manul, U. uncia, P. spelaea, G. gulo, M. zibellina, M. sibirica, M. eversmanii, M. altaica, M. nivalis, M. erminea, U. rossicus, U. arctos, M. baibacina,* and *C. fiber.*

The region as a whole is distinct for an exceedingly high and persistent species richness (25–21 species) through MIS 6. During MIS 5 and MIS 4 the number of the recovered species varies from 40 (MIS 5e) to 31 (MIS 4). The only exception is an interval corresponding approximately to substage MIS 5b with a small number of localities that yielded only 4 species of large mammals (Fig. 11A).

In MIS 6 the species most often found in the region were following: *C. c. spelaea, C. lupus, V. vulpes, O. ammon, C. sibirica, B. priscus, C. elaphus, P. gutturosa, C. antiquitatis, C. pygargus, E. ovodovi*, and *C. alpinus*. As can be seen from this short list, it includes several species typical of mountains and arid plains of Asia. Among common species, *V. corsac*, *M. eversmanii*, *M. intermedius, S. tatarica,* and *U. rossicus* should be mentioned. Rare species dated to MIS 6 are *P. namadicus* (?) (the only find from the Denisova Cave), *R. tarandus*, *A. alces*, and *B. m. baicalensis*.

In the Kazantsevo Interglacial the list of most common species includes: *B. priscus, E. ferus, M. intermedius, C. c. spelaea, O. ammon, C. antiquitatis, C. pygargus, E. ovodovi*, and *C. alpinus*. The species definitely indicative of interglacial environments are *U. thibetanus* (Strashnaya Cave), *H. brachyura* (Strashnaya Cave), *S. elisabethae* (Krasny Yar Village) *S. kirchbergensis* (Krasny Yar Village). In all the cases we are dealing with occasional (single) finds. There have been recorded species indicative of forests; as a rule, they belong to 'common' and 'rare' categories. In MIS 5e that group included *A. alces, C. fiber, M. leucurus, M. zibellina*, and *L. lynx*. The transition to the last glaciation beginning was marked by a relatively small decrease in the species richness. In MIS 5d-a, the group of most widespread species included those of open space, as well as mountain animals and eurytopic species: *O. ammon, C. lupus, C. c. spelaea, C. antiquitatis, C. pygargus, C. elaphus, B. m. baicalensis, B. priscus*, and *C. sibirica*.

During MIS 4 the list of the most widespread animals consisted of *O. ammon, C. antiquitatis, E. ferus, E. ovodovi, C. lupus, V. vulpes, C. c. spelaea, B. priscus,* and *M. primigenius/intermedius*. The species commonly found in the region were *C. pygargus*, *C. elaphus*, *C. sibirica*, *P. gutturosa*, *U. rossicus*, and *S. tatarica*.

On the whole, at least during MIS 6–MIS 5, the species composition of the large mammal assemblage in the considered region was kept relatively constant. A drop of species diversity recorded in MIS 5b is most probably attributable to a gap in the palaeontological records. A prevalence of open landscape species and a relatively low occurrence of forest species suggest the landscapes being dominated by arid steppes and forest-steppes at the end of Middle Pleistocene and in the first half of the Late Pleistocene. An increase of the forested area proportion could occur in MIS 5. A relatively high level of the species richness in the region persisted also due to a high habitat diversity in the Altai Mountains.

The model of the evolution of the Asian West-Siberian South-Eastern regional assemblage has three coordinates none of which correlates with δ^{18}O variable (the data on the of time scale s4 interval were excluded from calculations). Coordinate BC1 correlates with the relative occurrence frequency of *L. lynx* ($r = 0.90$, $p < 0.01$), *M. zibellina* (0.84, <0.01) and *V. corsac* (0.72, 0.04) (assemblage I) (Fig. 11B). These three species are noted for a relatively high frequency in the first half of MIS 6 and the absence of 'positive response' to MIS 5e event. The second coordinate correlates with species richness (0.84, <0.01) and with species of common or rare occurrence, mostly *V. lagopus* (−0.92, <0.01), *V. vulpes* (−0.83, 0.01), *C. c. spelaea* (−0.80, 0.02) (assemblage II), *E. ferus* (0.74, 0.04), *U. uncia* (0.75, 0.03), *R. tarandus* (0.79), *A. alces* (0.80, 0.02), *C. antiquitatis* (0.83, 0.01) (assemblage III). Species belonging to assemblage II are rather stable in their frequency, all of them displaying maximums in the first half of MIS 6, in MIS 5e and MIS 4. Species of assemblage III show a tendency of increasing occurrence frequency from MIS 6 to MIS 4. Against the background of this general trend there are local maximums in the middle of MIS 6, in MIS 5 and MIS 4. Coordinate BC3 shows a correlation with occurrence frequency of species responding differently to the interglacial environments – *U. rossicus* (−0.82, 0.01), *M. leucurus* (0.75, 0.03). Badger and similar species (*H. brachyura*, *U. thibetanus*, *Soergelia* sp., and some others) occur mostly or exclusively in the Kazantsevo interglacial stage. In contrast to them,

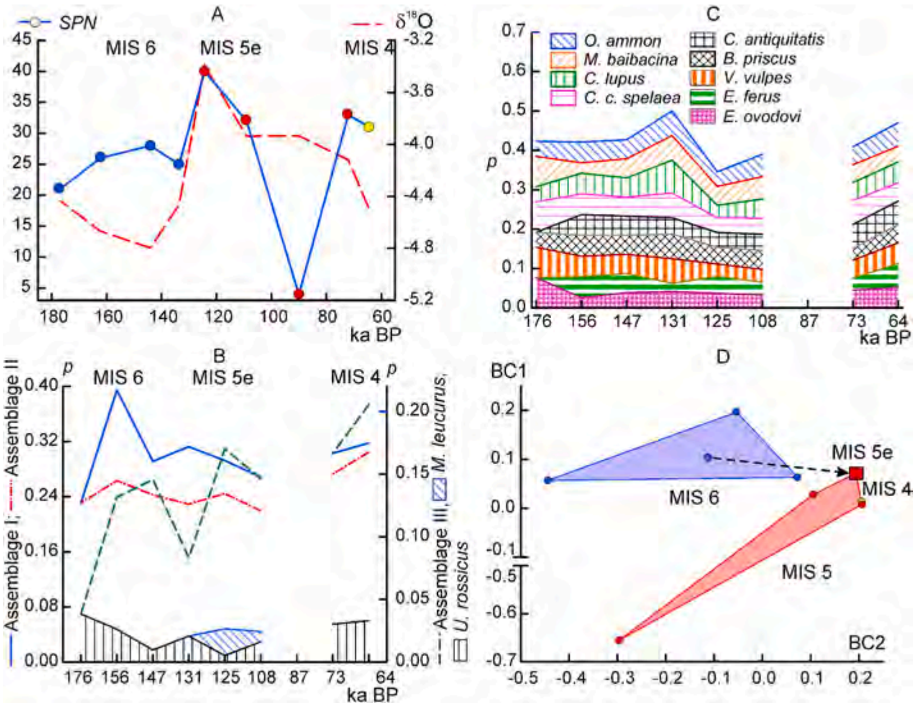

Fig. 11. Evolution of the Asian West-Siberian South-Eastern large mammalian assemblage in MIS 6–MIS 4 stages. A – changes in species richness (*SPN*) against the background of global temperature changes ($\delta^{18}O$); B – "abundance" (relative frequencies of localities, *p*) of indicator species from the assemblages I–III, *M. leucurus* and *U. rossicus*; C – relative "abundance" (*p*) of the most common species; D – the "portrait" of regional mammalian assemblage evolution in projection on two first coordinates of the model (BC1, BC2). This figure is available in colour online.

U. rossicus makes its presence less pronounced in the interglacial, while its maximum proportion in the regional assemblage is recorded at the very beginning of MIS 6 and in MIS 4. In the middle of the Late Pleistocene the region was undoubtedly refugia for that species.

A relative stability of the entire large mammal assemblage throughout MIS 6–MIS 4 time interval is seen in the dynamics of species having widest ranges within the region (Fig. 11C). The list of those species (*O. ammon*, *E. ovodovi* and other) emphasizes specificity of the regional fauna in comparison with the above-discussed faunal assemblages of the European–Asian origin. It is noteworthy that all those species are cold-adapted or tolerant species, which accounts for their neutral or negative response to the interglacial warming. The "connection" between the considered assemblage and those in the Ural region amounted to the penetration to the latter (to the northwest) of some species, such as *O. ammon, H. brachyura, U. thibetanus*, and probably (in the first half of the Late Pleistocene) also *U. rossicus, C. alpinus,* and *C. c. spelaea*.

A relative stability of the species richness typical of the regional assemblage is reflected in its evolutionary model, where the states of the assemblage at different isotope stages (MIS) practically do not differ

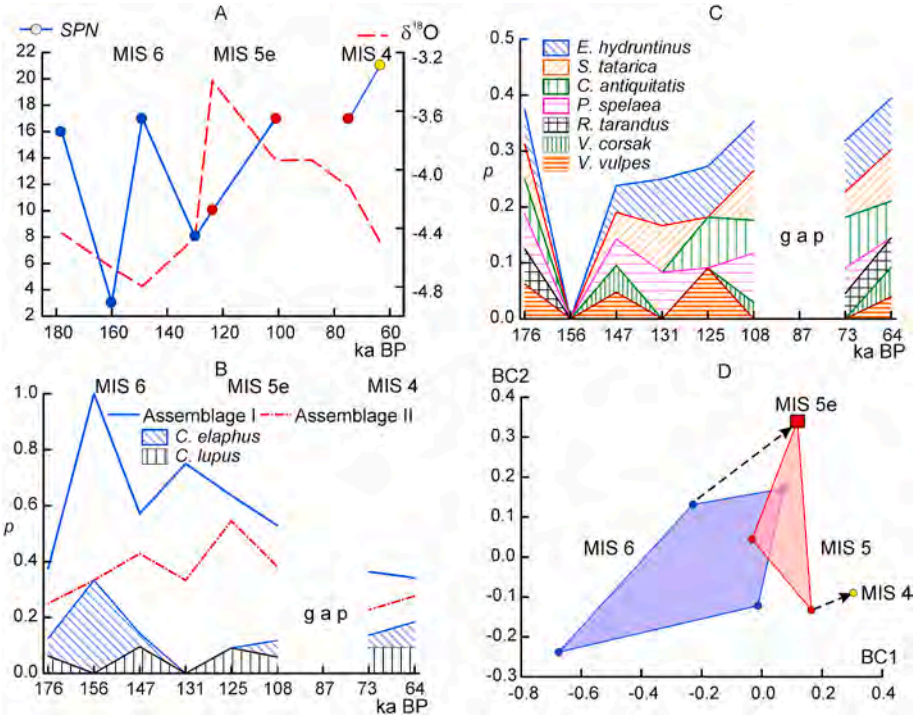

Fig. 12. Evolution of the East-European-Asian Ponto-Caspian large mammalian assemblage in MIS 6–MIS 4 stages. A – changes in species richness (*SPN*) against the background of global temperature changes ($\delta^{18}O$); B – "abundance" (relative frequencies of localities, *p*) of indicator species from the assemblages I and II, *C. elaphus* and *C. lupus*; C – relative "abundance" (*p*) of the common species; D – the "portrait" of regional mammalian assemblage evolution in projection on two first coordinates of the model (BC1, BC2). This figure is available in colour online.

with reference to the principal coordinate BC1 (Fig. 11D). There are some differences between stages relative to coordinate BC2, most probably due to dynamics of species of assemblages II and III and close to them. The transition to the MIS 4 stadial did not result in essential changes in the composition and species richness of the region.

3.1.13. East-European-Asian Ponto-Caspian region

The region lies in the southeast of Europe between the Black and Caspian seas (Fig. 1A (XVI)). It is noted for a relatively low species richness, which varies with time essentially (most probably, because of a scarcity of the palaeontological materials) (Fig. 12A). During MIS 6 the number of large mammal species varies from 17 to 3 (23 species altogether), 10 species was found in MIS 5e, 17 species is identified in MIS 5d-c, the same (17) in MIS 5a and 21 species in MIS 4. Overall 34 species were recorded in the region (Tables S12A and S12B), distributed over 24 palaeontological sites. There is a gap in the palaeontological record correlatable approximately with stage MIS 5b.

The most representative local faunas were recovered from the following localities: Veshenskaya (Litvinenko and Titov, 2005; Baigusheva et al., 2014), Chernyi Yar and Nizhnee Zaimishe (Sotnikova and Kirillova, 2017; Titov and Golovachev, 2017; Zastrozhnov et al., 2017; Golovachev and Titov, 2018, 2019), Zaikino pepelishe (147–125 ka BP) (Kuznetsova, 2000), Shkurlat (Markova, 1985; Shevyrev et al., 1985), Emine-Bair-Khosar Cave (layers Ba2 (unit I), Bc) (Ridush et al., 2018), Rozhok 1 (Baigusheva and Titov, 2007), Kodak 1 (Pidoplichko, 1936), Zaskal'naya (45.131N, 34.609E; layers II, IV–VI, > 46000 BP, GrA-13916) (Kolosov et al., 1993), Kiik-Koba (Kolosov et al., 1993), Prolom II (layer 4) (Kolosov et al., 1993; Stepanchuk, 1998; Baryshnikov, 2003a, 2003b), and Kabazi V (layers 3/1-3/1a, 73.3–59.1 ka BP) (Burke, 1999; Markova, 2007).

The local faunas datable to MIS 6 are recorded in the Veshenskaya and Chernyi Yar sites, with the species list as follows: *M t. chosaricus/M. intermedius*, *C. antiquitatis*, *S. kirchbergensis*, *E. ferus*, *E. hydruntinus*, *Camelus knoblochi*, *B. primigenius*, *B. priscus*, *S. tatarica*, *Alces* sp., *C. elaphus*, *M. giganteus*, *R. tarandus*, *C. lupus*, *Vulpes* sp., *P. spelaea*, *M. nivalis*, *U. rossicus*, and *C. fiber*. The regional assemblage dated to MIS 5 is most fully presented in the local faunas of Nizhnee Zaimishe, Zaikino pepelishe, Shkurlat, Emine-Bair-Khosar Cave, and Rozhok 1 localities. The total species list includes: *P. antiquus*, *M. t. chosaricus/M. intermedius*, *E. sibiricum*, *C. antiquitatis*, *S. kirchbergensis*, *E. ferus*, *E. hydruntinus*, *B. primigenius*, *B. priscus*, *S. tatarica*, *C. elaphus*, *M. giganteus*, *S. scrofa*, *C. lupus*, *V. vulpes*, *V. corsac*, *P. spelaea*, *M. nivalis*, and *C. fiber*. A general idea of the large mammal fauna at the end of MIS 5 – in MIS 4 in the west of the region (Crimean Peninsula) can be had from local faunas described in the localities Kodak 1, Zaskal'naya, KiiK-Koba, Prolom II and Kabazi V. Therehad been found mammal species as follows: *M. primigenius*, *M. t. chosaricus/M. intermedius*, *C. antiquitatis*, *E. ferus*, *E. hydruntinus*, *B. primigenius*, *B. priscus*, *S. tatarica*, *C. elaphus*, *M. giganteus*, *R. tarandus*, *S. scrofa*, *C. lupus*, *C. alpinus*, *V. vulpes*, *V. corsac*, *V. lagopus*, *C. c. spelaea*, *P. spelaea*, *U. spelaeus*, and *U. arctos*.

The species most widely spread in the region in MIS 6 are: *M. t. chosaricus, M. giganteus*, *B. priscus*, and *E. ferus,* commonly found ones are *E. hydruntinus, E. sibiricum*, *C. elaphus*, *S. tatarica*, *C. lupus,* and *P. spelaea*. The interglacial features rather low species richness. The list of species attributed to MIS 5e includes *M. t. chosaricus/M. intermedius*, *E. sibiricum*, *S. kirchbergensis*, *C. antiquitatis*, *E. ferus*, *E. hydruntinus*, *B. priscus C. lupus*, *V. vulpes*, and *S. scrofa*.

In MIS 5, after the interglacial, 23 species were recorded, most widespread being *B. priscus*, *E. hydruntinus*, *M. t. chosaricus*, *E. ferus*, *C. lupus*, *C. antiquitatis, M. giganteus, S. tatarica* and *P. spelaea*. Of the common and rare species, *C. alpinus*, *P. antiquus*, *E. sibiricum*, *S. kirchbergensis*, *V. corsac*, *U. spelaeus* and *C. fiber* should be noted. In MIS 4 two rhinoceros species disappear from the list, as well as probably *M. t. chosaricus* and some others. The species attributed to that stadial include remains of *E. hydruntinus*, *C. elaphus*, *S. tatarica*, *C. lupus*, *C. antiquitatis* and *M. giganteus*. Commonly found in localities dated to MIS 4 are *B. priscus, R. tarandus, V. corsac, U. spelaeus* (in Crimea), *E. ferus* and *C. c. spelaea*. It may be safely concluded that the assortment of the most widespread large mammal species changed only slightly in MIS 6–MIS 5, while the principal changes fell on MIS 4 stadial.

A two-dimensional model of evolution was developed for that regional assemblage. Coordinate BC1 correlates with fluctuations of the species richness ($r = 0.87$, $p = <0.01$) and relative frequency of occurrence for localities of *M. t. chosaricus/M. intermedius* (−0.95, <0.01), *M. giganteus* (−0.90, <0.01) (assemblage I) and *C. lupus* (0.89, <0.01). Coordinate BC2 shows a correlation with occurrence of localities of *C. elaphus* (−0.69, at a trend level), *E. sibiricum* (0.72, 0.04), *S. kirchbergensis* (0.84, <0.01), *E. ferus* (0.86, <0.01), and *B. priscus* (0.92, <0.01) (assemblage II). There is a general trend towards a decrease in the relative occurrence frequency of mammoth and giant deer from MIS 6 towards MIS 4 (Fig. 12B). The representatives of assemblage II show (altogether) the relative occurrence maximum in the region in MIS 5e. For *C. elaphus* the frequency of occurrence reached its maximum in the first half of MIS 6. At the end of that stage and in MIS 5e-c it drops out of the regional list. Later on, its presence became more apparent in MIS 4. The wolf is present almost constantly in the region except MIS 6c and MIS 6a intervals.

The dynamics of relative frequency analysed for widespread species not belonging to assemblages I and II is shown in Fig. 12C. All of them are typically decreased in occurrence at the first half of MIS 6. The relative occurrence frequency of one of the most typical regional species – *E. hydruntinus* – increased sharply at the end of MIS 6 – in MIS 5e and persisted at that level up to MIS 4. Unlike the above-mentioned species, *S. tatarica* and *P. spelaea*, made their presence more conspicuous at the end of MIS 6, but disappeared from the regional list of species in the interglacial. Later on, the occurrence frequency of *S. tatarica* localities rose in the middle of MIS 5 and kept relatively high up to MIS 4. Occurrence of *P. spelaea* grew also in the middle of MIS 5, but in MIS 4 it is absent from the palaeontological record. The occurrence of *C. antiquitatis* localities gained in importance in MIS 5e, though it was not recorded in the second half of MIS 6. Later the woolly rhinoceros seemingly occurred widely in the region until MIS 4. The dynamics of *V. vulpes* occurrence resembles that of *C. lupus* (Fig. 12B). *V. corsac* is present occasionally in the list of regional fauna, its maximum of occurrence falls on the middle of MIS 6 and on MIS 4. The presence of *R. tarandus* is recorded in the region early in MIS 6 and in MIS 4, while the greater part of MIS 6 and MIS 5 are devoid of it.

Among species of rare occurrence (single finds) there are *P. antiquus* (Shkurlat), *U. rossicus* (Veshenskaya, Chernyi Yar), *C. knoblochi* (Chernyi Yar), *Alces* sp. (Veshenskaya, Chernyi Yar), and *U. arctos* (Kodak 1). Most part of the species remains (except for *U. arctos*) originated from the east and belong to MIS 6 stage.

As has been noted before, the regional assemblage of large mammals did not experience essential changes at the MIS 6 – MIS 5 boundary. That is clearly seen in the picture of its evolution in the coordinates BC1 and BC2 of the model (Fig. 12D). The interglacial stays aside with reference to BC2 coordinate (that is, it is marked by increase of relative occurrence frequency of species belonging to assemblage II. The stadial MIS 4 is distinguished first of all by relatively high species richness, as well as a low occurrence frequency of the members of assemblage II.

3.1.14. Western Asian Caucasian region

The region lies south of the East-European-Asian Ponto-Caspian region (Fig. 1A (XVII)). We consider it to be a part of European territory mainly following an established tradition. The region includes the Greater and Lesser Caucasus ridges, as well as Transcaucasia (except for its south-eastern part). The Quaternary history of the regional fauna development is distinct for many "geographical sources" of invasion and their heterochrony (Vereshchagin, 1959; Abdurakhmanov and Batkhiev, 2013). Noteworthy is that, in addition to a considerable number of endemic mammal species with very small ranges, the modern fauna of that mountain region displays a well pronounced influence of the

East-Mediterranean, Southwest Asian, and Central Asian (Turanian) faunal complexes.

Palaeontological materials on MIS 6 – MIS 4 interval are rather scarce and were obtained from 11 sites (17 localities). The localities yielded remains identified as belonging to 26 species of large mammals (Tables S13A and S13B). The list of the most informative localities in the region is as follows: Kudaro 1 (Crégut-Bonnoure and Baryshnikov, 2005), Il'skaya 2 (Hoffecker et al., 1991; Baryshnikov and Hoffecker, 1994), Myshtulagty Lagat or Weasel Cave (layer 14) (Hidjrati et al., 2003), Akhshtyrskaya Cave (layer 5/2, 112 ± 22 ka BP) (Baryshnikov, 2012), Ortvale Klde (layers 7, 9, and 10, 75.9–40.5 ka BP) (Bar-Oz and Adler, 2005), Mezmaiskaya Cave (layers 2b3, 2b4 and 3, 70.6–46.5 ka BP) (Baryshnikov et al., 1996; Golovanova et al., 1998; Skinner et al., 2005; Soubrier et al., 2016), Kudaro 3 (layer 3, >41 600 BP, OxA-19611) (Baryshnikov, 2010).

Local faunas of Kudaro 1 and Il'skaya 2 localities characterize the regional assemblage in MIS 6 and include *E. ferus*, *E. hydruntinus*, *S. tatarica*, *B. bonasus* (more likely than the *B. priscus*), *C. elaphus*, *M. giganteus*, *P. pardus*, *C. lupus*, *C. alpinus*, *V. corsac*, and *U. kudarensis*. A scanty fauna recovered from the Weasel Cave is dated to MIS 5 and includes *E. ferus*, *B. bonasus*, *Capra caucasica*, *C. elaphus*, *C. capreolus*, *S. scrofa*, *C. lupus* and *U. kudarensis*. Local faunas from Ortvale Klde, Mezmaiskaya Cave and Kudaro 3 probably dated to MIS 4 stadial. They consist mostly of the following species: *B. primigenius, B. bonasus, C. caucasica, O. orientalis, C. elaphus, C. capreolus, R. tarandus, S. scrofa, C. lupus, C. aureus, V. vulpes, L. lynx, F. silvestris, P. pardus, P. spelaea, U. kudarensis* and *U. arctos.*

The localities dated directly or by implication to MIS 6 yielded

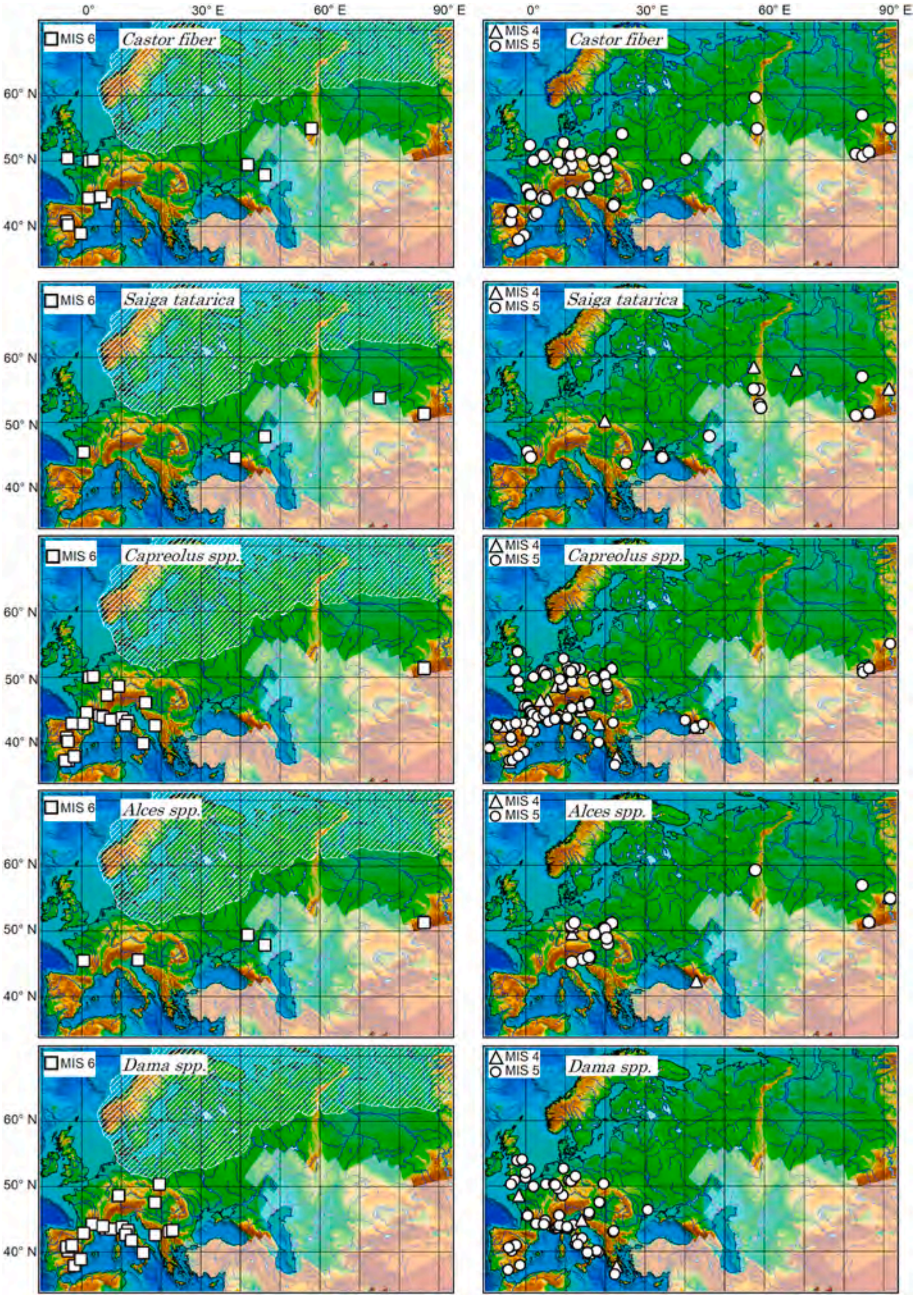

Fig. 13. The localities of the herbivorous large mammal species in MIS 6–MIS 4 stages. This figure is available in colour online. The territory of the Asia which was not included in this study marked by transparent fill. This figure is available in colour online.
Fig. 13. (continuation).

remains of 11 species. Most common of them contain *C. elaphus* and *U. kudarensis*. Apart from them, there are *M. giganteus*, *B. bonasus* (Soubrier et al., 2016; Grange et al., 2018), *S. tatarica*, *E. ferus*, *E. hydruntinus*, *C. lupus, C. alpinus*, *V. corsac*, *P. pardus* in the list. The list of localities attributable to the interglacial includes 8 species only (all of them recovered from single localities): *C. elaphus*, *C. capreolus*, *B. bonasus*, *C. caucasica*, *S. scrofa*, *E. ferus*, *C. lupus*, and *U. kudarensis*. The same number of species was found in the localities dated to MIS 5d-a. Most often found are localities with *U. kudarensis* and *C. elaphus*, then *C. caucasica*, *C. capreolus*, *B. bonasus*, *C. lupus,* and *S. scrofa*. One find was identified as belonging to Rhinocerotidae. The fauna dated to MIS 4 appears to include 19 species. The most often found are localities with remains of *U. kudarensis*, *B. bonasus*, *C. elaphus*, *C. caucasica*, *O. orientalis,* and *V. vulpes*. There are typically forest species, such as *L. lynx*, *F. silvestris*, and *A. alces* present in the fauna. The cold-adapted species (*R. tarandus* and *P. spelaea*) are also recorded. The MIS 4 fauna as a whole reflects the influence of altitudinal zonation and a relatively high diversity. It is to be noted, as well, that many species that inhabited the Caucasus in MIS 6–MIS 4 are present in the regional fauna in the Holocene (Puzachenko and Markova, 2020).

3.2. The ranges of selected species in Europe in MIS 6–MIS 4

Here we give information on the changes in the ranges of some herbivorous mammals indicative of changes in the climate and environments in Europe in MIS 6 – MIS 4.

Narrow-nosed rhinoceros (*S. hemitoechus*) was better adapted to more open habitats. However, its finds in Eastern Europe are rare enough. In the Saale time (MIS 6) its range included the Iberian and Apennine peninsulas, Central Europe, and the south of Eastern Europe (Fig. 13). Since the beginning of the Eemian Interglacial the species is often present in Western, Central, and Southern Europe. During the MIS 4 stadial its range is noticeably reduced to the Apennine Peninsula where the last representatives of the species could persist to MIS 3 (Pushkina, 2007; Puzachenko and Markova, 2019).

Merck's rhinoceros (*S. kirchbergensis*) persisted in the forested landscapes of Western Europe for a long time during the Late and Middle Pleistocene up to and including MIS 3 in the Late Pleistocene. The rhinoceros was much less common in Eastern Europe and Asia because of the widespread steppe biotopes there (Fig. 13). In MIS 5e the species penetrated to the north (Kirillova et al., 2017) and east along river valleys and floodplain forests; it became more common in Eastern Europe and pervaded as far east as Central Asia. In the MIS 4 stadial its range shrank, the species being mostly confined to Western and Central Europe, though a few finds are also known from Asia, including the north and northeast of Siberia (Shpansky and Boeskorov, 2018) and, probably, from the Far East. The latest finds of *S. kirchbergensis* are known from the Mediterranean region (Alexeeva, 1990; Pushkina, 2007).

Straight-tusked or forest elephants (*Palaeoloxodon* spp). It is generally agreed that the straight-tusked or forest elephant *P. antiquus* was a dweller of forested areas with a mild humid and warm climate. During the cold MIS 6 period, the elephants lived predominantly on the Iberian and Apennine peninsulas, in the south of Western Europe, on the Atlantic coast of Western Europe (Fig. 13). Their range enlarged considerably, as the zone of mixed and broadleaf forests expanded its area. Supposedly, it expanded over the entire Western and Central Europe along river valleys. In Eastern Europe *P. antiquus* penetrated as far east as the Volga drainage basin, as far south as the north Caucasian forelands, and northwards up to the upper reaches of the Dnieper River. With the onset of the last glacial period the range of straight-tusked elephants was noticeably reduced, they persisted in the southwest of Europe until MIS 3 (Alexeeva, 1990; Pushkina, 2007; Puzachenko and Markova, 2019), though there is information about individual finds datable to that time in the Middle European Atlantic Region (Mol et al., 2007). The Asian straight-tusked elephant occurred commonly in the same period. The remains of straight-tusked elephant in the deposits of Denisova Cave belong most probably to this species or subspecies.

Mammoths with relatively thick enamel (*M. intermedius*) with lamellar frequency 6.0–8.5 per 10 cm were widespread in Eurasia from Western Europe (except the Iberian Peninsula) to West Siberia since the late Middle Pleistocene. In MIS 5e it expanded still more and included the Iberian Peninsula, Ireland Island (Fig. 13), and even the Kola Peninsula (Molodkov and Yevzerov, 2004). Beginning of the MIS 4 stadial approximately, the typical woolly mammoths *M. primigenius* almost everywhere replaced *M. intermedius*.

The elephant *M. t. chosaricus* that existed at the same time probably occupied forested landscapes in the north-eastern Black Sea region and in the lower reaches of the Volga River. The range of *M. t. chosaricus* was, most likely, relatively wide, but the diagnostics of its remains is insufficiently developed at present. The *M. primigenius* distribution over Eurasia was irregular.

Porcupines (*Hystrix* spp.). In the MIS 6 period they were spread in the southern part of Western Europe and absent from Eastern Europe and West Siberia (Fig. 13). During MIS 5 their ranges were noticeably enlarged and expanded over the middle part of Western Europe, Crimea, Transcaucasian region, the Urals, and the southeast of West Siberia (Weers, 1994; Baryshnikov, 2003a, 2003b; Lopatin, 2019). At the end of MIS 5 and in MIS 4 the porcupines disappeared from Europe and the Urals, and persisted till the middle of MIS 3 in the Caucasus and in the southeast of West Siberia (Kuzmin et al., 2017). The porcupines penetrated into Europe and southeast of West Siberia from southern and south-eastern regions of Asia, and to the Urals – from the southeast of West Siberia.

Beaver (*C. fiber*) occurred on the Iberian Peninsula, in Central and Western Europe, and in the south of Eastern Europe (Fig. 13). Its range expanded considerably during MIS 5–MIS 4 and occupied, apart from the listed regions, the Urals, West Siberia, and the southeast of West Siberia. The range of *C. fiber* was considerably reduced at the time of the Weichsel (= Valday) glaciation, its remnants are recorded in the localities in Central and Southern Europe, and in the south of West Siberia (Puzachenko and Markova, 2019).

At the late Middle Pleistocene *S. tatarica* was widely spread over the Western Palearctic as far west as Western Europe. During MIS 5 *S. tatarica* occurred in the Western, Central, and Eastern Europe, as well as in the Urals and in West Siberia (Fig. 13). The species range reached its maximum expansion in MIS 3–MIS 2.

The roe deer (*Capreolus* spp.) was common in the central and southern regions of Western Europe (*C. capreolus*) and in the southeast of West Siberia (*C. pygargus*) during MIS 6, MIS 5 and MIS 4 (Fig. 13). In MIS 5 it made its appearance in the Caucasus, while in Western Europe its range expands northwards and eastwards. The roe deer was seemingly absent from Eastern Europe, the Urals, and West Siberia through MIS 6–MIS 4.

In the west and south of Western Europe and in the southeast of West Siberia there are occasional findings of the elks (*Alces* spp.) inconsiderable in number and dated to MIS 6 (Fig. 13). In the MIS 5 and MIS 4 its range expanded northwards and eastwards. The moose (*A. alces*) inhabited central and western regions of Europe, as well as the Caucasus (Fig. 13). The remains of moose found in the Urals and southeast of West Siberia and dated to MIS 5–MIS 4 have not been identified to a level of species.

The fallow deer (*Dama* ssp.) occurred in MIS 6 in Southern Europe, in the south of Central Europe, and on the Iberian Peninsula (Fig. 13). In the interglacial time and during the entire MIS 5 the thermophilic deer that inhabited forest biotopes by preference enlarged its range and included almost entire Central and Western Europe together with Great Britain. As the climate became cooler again in MIS 4, its range shrank again, and the deer was confined to the southern regions of Western and Central Europe, the Balkan Mountains, and the Apennine Peninsula.

3.3. Parameters of biological diversity

The estimates of the diversity parameters, and the entropy and redundancy in particular, permit to consider the evolution of the regional faunal assemblages as the evolution of a very "complex system" (Grabowski and Strzałka, 2008; Ross and Arkin, 2009; Ma'ayan, 2017). From here on, we shall use the term "system" to mean a research model of a real object, phenomenon, or process. In our case parameters *H* and *R* are to describe, first of all, a diversity of the spatial pattern in the distribution of species findings within different bioregions. In an effort to obtain better substantiated results of the comparison between the regions in the diversity parameters, we aggregated the data on the time intervals MIS 6, MIS 5e, MIS 5d–a (and for the entire MIS 5 stage), and MIS4.

To save room, we use abbreviations for the bioregions and their roman numbers in this section (Table 1, Fig. 1A).

The calculations of the diversity parameters (Chao-1, *H*, *R*) are performed for 10 bioregions where the starting data were available in sufficient amounts (Table S14). Table 2 summarizes the results relevant to isotope stages MIS 6, MIS 5 and MIS 4. Besides, the table shows values of "species turnover" index (βt) calculated for pairs of intervals: MIS 6 – MIS 5e and MIS 5d-a – MIS 4, as well as the value of that index for the entire sequence of the time intervals under consideration. In the latter case, index βt reflects general "variability" of the taxonomic composition of regional assemblages at the end of the Middle Pleistocene – in the first half of the Late Pleistocene.

3.3.1. Species richness (SPN, Chao-1) and Mourelle – Ezcurra species turnover index

We have demonstrated above that the species number varies essentially both from one region to another and between different time intervals. One of variations recorded almost everywhere was a decrease of the species richness at the end of MIS 6 and its growth early in MIS 5. Less conspicuous is a decrease in species richness in MIS 4 in comparison with the interval MIS 5d–a, which was recorded in all the regions where the data were sufficient for calculations (Fig. 14A). In some regions – MEAWSMIS and MEAWSMIN (I and II), MEAWSMA (VII), and MEAWNEP (XVI) – the number of species identified in MIS 6 is greater than in the interglacial ($\Delta NSP < 0$). Noteworthy is that all three regions are situated in the south of the considered territory. In that case the relatively low species richness MIS 5e in comparison with the young Saalian time may result from one and the same cause in all the three cases. The maximum growth of the species richness at the interglacial was recorded in the MEAWNCEN (X) region located in the north of Central Europe and exposed to the direct impact of the ice sheet. The most pronounced increase in the species richness ($\Delta NSP > 0$) after MIS 5e was recorded in MIS 5d–a interval in the southern regions (MEAWSMIS, MEAWSMIN (I, II), MEAWSMA (VII), and MEAWNEP (XVI)) against the background of the decreasing global temperature. A decrease of the species richness in the MIS 4 stadial (in comparison with MIS 5d–a) is hidden in many cases by a low rate of that process. Nevertheless, the negative ΔNSP value is obtained in all the considered regions, when a comparison is performed between the species number in MIS 4 and their number in the second half of MIS 5 (Fig. 14A). Regions MEAWSMIS, MEAWSMIN (I, II), MEAWNCES (IX) and MEAWNCS (III) are noted for the most considerable decrease in species richness. At the same time, practically no essential drop in species richness was recorded in MIS 4 in the region MEAWNCEN (X), adjacent to MEAWNCES (IX).

The species turnover index is proportional to the changes in the species composition of the assemblage for two or more consecutive time intervals. The lower is the index, the more stable the taxonomic composition of the assemblage. That is why β_t may be used as an indicator of stationarity, or stability, of the regional assemblage within a given time interval.

The index displays a moderately positive correlation with the absolute ΔNSP value for the intervals MIS 6– MIS 5e ($r = 0.78$, $p < 0.01$) and

Table 2
Diversity parameters for the regional faunal assemblages of MIS 6–MIS 4.95% confidence intervals are given for entropy (*H*) and redundancy (*R*).

Region	MIS 6					MIS 5					MIS 4				
	SPN	Chao-1	*H* (nit)	*R*	βt, MIS6–MIS5e	*SPN*	Chao-1	*H* (nit)	*R*	βt, MIS5d–a–MIS4	*SPN*	Chao-1	*H* (nit)	*R*	βt, MIS6–MIS4
MEAWSMI	30	47	2.87	0.16	0.27	36	43	3.18	0.11	0.29	22	22	2.88	0.07	0.28
			2.75–2.99	0.19–0.12				3.11–3.25	0.13–0.09				2.79–2.98	0.1–0.05	
MEAWNCS	41	41	3.40	0.08	0.13	51	57	3.46	0.12	0.13	40	44	3.24	0.12	0.13
			3.36–3.44	0.10–0.07				3.42–3.49	0.13–0.11				3.16–3.33	0.14–0.01	
MEAWNCN	31	33	3.08	0.10	0.12	43	45	3.37	0.11	0.19	34	39	3.11	0.12	0.15
			2.99–3.16	0.13–0.08				3.33–3.42	0.12–0.10				3.02–3.20	0.14–0.09	
MEAWNWEN	19	20	2.61	0.11	0.30	24	26	2.88	0.09	0.18	9	–	1.75	0.20	0.34
			2.51–2.72	0.15–0.08				2.80–2.96	0.12–0.07				1.53–1.98	0.23–0.17	
MEAWSMA	25	30	2.90	0.10	0.39	30	34	3.07	0.10	0.18	22	–	2.6	0.15	0.33
			2.79–3.0	0.13–0.07				2.97–3.18	0.12–0.07				2.45–2.77	0.17–0.14	
MEAWNCES	34	40	3.02	0.13	0.24	45	45	3.39	0.11	0.19	31	36	3.00	0.13	0.18
			2.92–3.13	0.16–0.10				3.33–3.45	0.13–0.09				2.87–3.14	0.15–0.10	
MEAWNCEN	13	22	2.07	0.19	0.56	35	42	3.15	0.11	0.22	26	27	2.96	0.09	0.33
			1.8–2.29	0.25–0.13				3.05–3.26	0.14–0.09				2.84–3.09	0.12–0.06	
NEAWCE	22	26	2.75	0.11	0.31	34	36	3.22	0.09	0.28	23	34	2.73	0.13	0.28
			2.64–2.85	0.14–0.08				3.14–3.29	0.11–0.07				2.61–2.85	0.16–0.10	
NEAWCESE	32	32	3.23	0.07	0.14	41	44	3.45	0.07	0.09	31	31	3.19	0.07	0.11
			3.17–3.30	0.08–0.05				3.40–3.50	0.08–0.06				3.12–3.26	0.09–0.05	
MEAWNEP	23	–	2.70	0.14	0.39	24	30	2.79	0.12	0.33	19	21	2.69	0.09	0.37
			2.55–2.86	0.17–0.10				2.65–2.93	0.16–0.09				2.59–2.79	0.12–0.05	

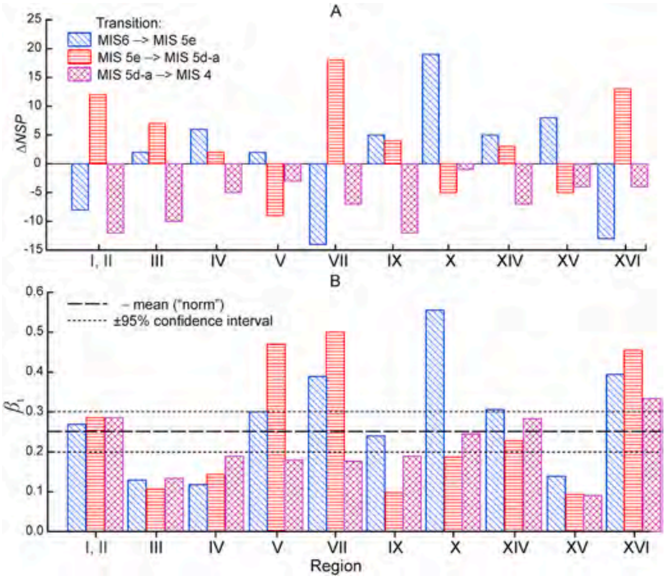

Fig. 14. Changes in species richness (Δ*NSP*) and species turnover index (β_t) in the selected bioregions. A – Δ*NSP* for MIS 6 – MIS 5e, MIS 5e-MIS 5d– a and MIS 5d–a – MIS 4 time interval; B - species turnover index (β_t) for MIS 6 – MIS 5e, MIS 5e-MIS 5d– a and MIS 5d–a – MIS 4 time interval; "norm" (mean value) of the β_t is equal 0.25. Abbreviations and roman numbers of the bioregions see in Table 1. This figure is available in colour online.

MIS 5e–MIS 5d-a (0.81, <0.01). However, no correlation between Δ*NSP* and β_t was found within the interval MIS 5d-a – MIS 4. The mean value of the index is 0.25 ± 0.024, and at 95% confidence interval – 0.20–0.30. Mean β_t value we consider to be "norm" (most probable value) when different regions are compared (Fig. 14B). The group of regions with low β_t values includes: MEAWNCS (III), MEAWNCN (IV), and NEAWCESE (XV). The composition of MEAWNCES (IX) regional assemblage is less stable (for MIS 6 – MIS 5e interval in particular). On the whole, within MIS 6–MIS 4 interval the index is rather low for the listed four regions and varies within 0.11–0.18 (Table 2). The group of regions noted for a very unstable composition of fauna includes MEAWNWEN (V), MEAWSMA (VII), MEAWNCEN (X), and MEAWNEP (XIV).

In the regions MEAWNWEN (V) and MEAWSMA (VII) the maximum value of the species turnover was recorded within the interval MIS 5e–MIS 5d-a. The region MEAWNCEN (X) underwent most conspicuous changes in the species list between MIS 6 and the Eemian interglacial. Essential changes in the faunal assemblage of the MEAWNEP region occurred between MIS 6 and MIS 5d-a. During the entire time interval under consideration the index β_t varied between 0.33 and 0.37. Finally, regions MEAWSMI (I, II) and NEAWCE (XIV) display an "average" level of the species turnover (0.28) over the entire MIS 6–MIS 4 interval (Fig. 14B, Table 2).

We used the estimator of species number Chao-1 in order to estimate a possibility to employ it to evaluating palaeontological data (see also Markova and Puzachenko, this volume). We succeeded in obtaining the index for practically all the time intervals (Tables 2 and S14). When the number of localities was small, the estimate of the predicted number of species was obviously unacceptable in 4 cases out of 50 (extremely overestimated forecast values). If the cases were excluded from consideration, the correlation between the number of species in the palaeontological record and their estimates (Chao-1) was high enough. For MIS 6 $r = 0.82, p < 0.01$, the coefficient of the regression equation is 9.1; for the interglacial the values are 0.91, <0.001, and 12.8, respectively; for MIS 5d-a – 0.88, <0.01, and 10.2, respectively; for MIS 5–0.96, <0.001, and 4.2, respectively; for MIS 4–0.89, <0.01, 1.97, respectively. The results obtained testify that the estimator may be used provided a certain minimum of necessary data is available (in our case – a necessary number of localities). If the hypothesis is true, then the "underestimated" species richness here may be somewhere in the interval between 13 and 2 species (on the average, 7.6 ± 1.99 for MIS 6–MIS 4). It should be kept in mind that it is only speculative estimate of the palaeontological record incompleteness and not a real number of species.

Our earlier work (Puzachenko and Markova, 2019) on the mammal fauna dated to MIS 3 –MIS 2 proved the stable positive correlation between the regional species richness in Europe in the Late Pleistocene on one hand and the modern species richness for the same geographical units on the other. In case of small mammals (Markova and Puzachenko, in press) the correlation between the species richness in MIS 6 and the same at present is 0.66 ($p = 0.02$). In this work we performed similar estimation taking large mammals dated to MIS 6, MIS 5e, MIS 5d-e, all MIS 5 and MIS 4 stages. The correlation coefficients calculated for those intervals are as follows: MIS 6–0.65 ($p = 0.08$, outliers are MEAWNCS and MEAWNCEN), MIS 5e – 0.73 (0.04, outliers are MEAWNCS and MEAWNWEN) (Fig. 15A), MIS 5d–a – 0.78 (0.02, outliers are MEAWNCS and MEAWNCES), MIS 5–0.77 (0.04, outliers are MEAWNCS and MEAWNCES), MIS 4–0.69 (0.03, outlier is MEAWNCS).

As may be seen from the results, in spite of changes in the faunal composition and environments, the spatial pattern in the mammal species richness variations over the European territory persisted over at least the last 200 thousand years. Against that background the Middle European Western region (MEAWNCS) demonstrates a persistent (in all the time intervals under consideration) deviation from the "general rule". At present its territory is inhabited by ~23 species (not counting alien species) belonging to the considered size group of mammals. At the end of Saale, in the interglacial time and during the first part of the Weichsel there was found 40 to 51 mammal species in the region. It follows that the modern species richness is essentially below that in the Pleistocene. For similar reason, the characteristics of some intervals depart appreciably from the general tendency: Middle European Central – Southern region (MEAWNCES, modern *SPN* = 24), Middle European Central –Northern region (MEAWNCEN, modern *SPN* = 23) and West European Atlantic Southern region (MEAWNWEN, modern *SPN* = 9).

3.3.2. *Entropy and index of self-organization*

In the case under consideration, the Shannon entropy (*H*), or information entropy, is an indirect characteristic of the species distribution over the region. The occurrence frequencies of localities with a certain species are assumed to be proportional to their range area within the region. Hypothetically, the entropy reaches its maximum when the species ranges coincide and the occurrence frequencies of localities are approximately equal for all the species. In fact, the entropy value is influenced more essentially by the number of species with relatively small ranges within the region ("rare" species). Beside that explanation, the entropy may be considered from the position of ecology. In the natural environments not quite uniform the species ranges are proportional to species ecological niches. Therefore, the higher is the entropy, the greater (on average) is the potential intersection of ecological niches and the stronger is competition between species similar in their environmental requirements in other things being equal. On the other hand, the presence of a great number of rare and highly specialized species presumes a high diversity of habitats and a complicated organization of regional ecosystems.

Entropy values show linear and positive correlation with species richness (*SPN*). The correlation depends on the influence of the number of rare species found in one or two localities on both variables. In the considered case, the correlation coefficient varied from 0.94 (MIS 4) to 0.97 (MIS 5e) (Fig. 15B). That being so, based on entropy dynamics we can distinguish several groups of regions similar in *H* variations within MIS 6–MIS 4 interval. The first group (southern regions MEAWSMI (I, II), MEAWSMA (VII), and MEAWNEP (XVI)) is distinguished by notable (though not always statistically significant) decrease of *H* and its subsequent rise during MIS 5d-a. The second group of regions (MEAWNCES

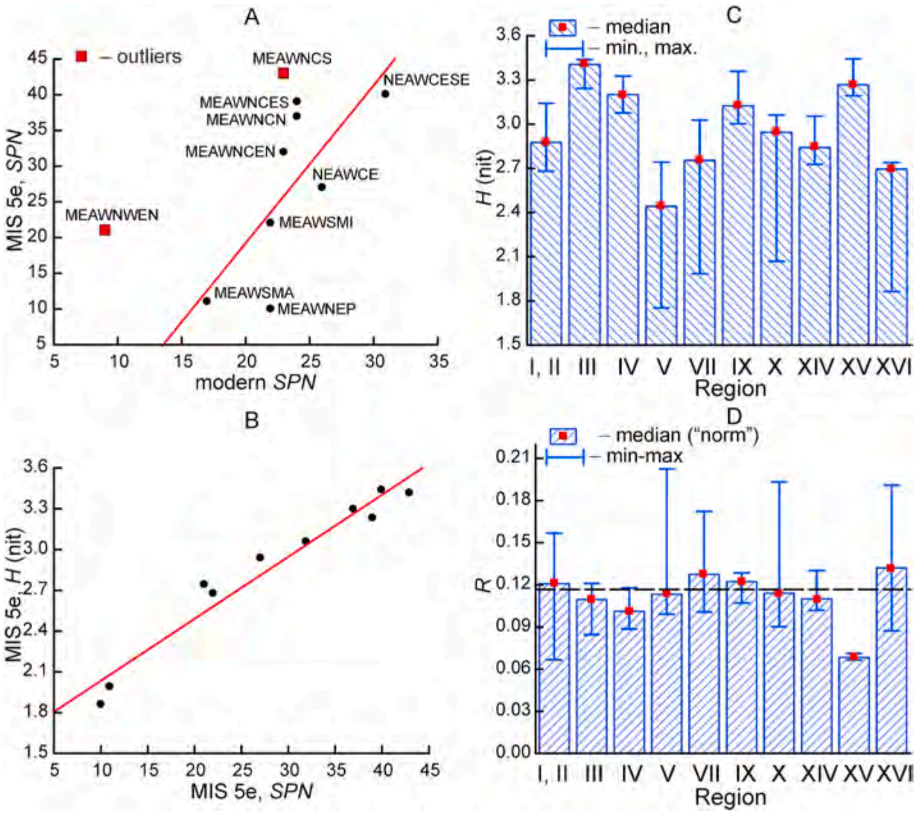

Fig. 15. Diversity parameters in the selected bioregions. A – regression between modern species richness and species richness in MIS 5e; B – correlation between species richness in MIS 5e and entropy (*H*); C, D – variations of entropy (*H*) and index of selforganization or redundancy (*R*). Abbreviations and roman numbers of the bioregions see in Table 1. This figure is available in colour online.

(IX), NEAWCE (XIV)) the entropy rises from MIS 6 towards MIS 5d-a, and then decreases again at MIS 4 stage. In the regions NEAWCESE (XV) and MEAWNCEN (X) the entropy reaches its maximum in the interglacial and then varies insignificantly (MEAWNCEN) or decreases steadily (NEAWCESE). The region MEAWNWEN (V) bears a close similarity in the dynamics, with the difference that a decrease in entropy after MIS 5e is much better pronounced. Finally, the entropy in MEAWNCS (III) region varies insignificantly within the considered time interval. The last Middle European Western region demonstrates a highly stable degree of diversity against the background of climate fluctuations at the boundary between Middle and Late Pleistocene. In other words, during the entire time interval the regional environments were kept diversified and favourable for high and relatively stable level of the species richness.

The regions show considerable differences in their size and variability of *H* (Fig. 15C). The high entropy and its relatively small variability suggest a relatively stable "state of the system". In this context regions MEAWNCS (III), MEAWNCN (IV), MEAWNCES (IX) and NEAWCESE (XV) should be particularly mentioned. During the entire MIS 6–MIS 4 interval the regions were "centres" of a high biological diversity of the considered mammal group in Europe and in the south of West Siberia. Regions MEAWNWEN (V) and MEAWNEP (XVI) display relatively low entropy and a large variation of its values over time. That may be interpreted as an indicator of unstable environments unfavourable for maintaining high diversity.

The index of self-organization or redundancy (*R*) is calculated from the entropy values and often (though not always) shows a negative correlation with the latter. In our case, the negative correlation of *R* and *H* was obtained for MIS 6 (−0.82, <0.01), MIS 5e (−0.92, <0.01) and MIS 4 (−0.73). That result (negative correlation between *R* and *H*) means that at high values of entropy there is a decrease of "orderliness" in the spatial pattern of the distribution of species ranges within the region. That may be interpreted as indicative of a reduced effect of the assumed environmental factors that impose limitations on the species expansion.

The level of self-organization in the biological system dynamics may increase or decrease. The *R* changes of considerable amplitude may be indicative of essential restructuring in the paleo-assemblage structure. That is why we are interested, first, in "standard" (normal), that is, the most probable value of *R* and, second, in amplitude of its changes in the process of the faunal assemblage evolution at the end of the Middle Pleistocene – the first half of the Late Pleistocene, against the background of the climate fluctuations from the glacial environments in MIS 6 to MIS 5e interglacial.

For 10 bioregions considered in the paragraph, the average R values are equal: for MIS 6–0.119 ± 0.0115 (standard deviation = 0.0363, min = 0.067, max = 0.193), for MIS 5e – 0.119 ± 0.0119 (standard deviation = 0.0378, min = 0.066, max = 0.191), for MIS 5d–a – 0.106 ± 0.0048 (standard deviation = 0.0151, min = 0.071, max = 0.126), and for MIS 4–0.116 ± 0.013 (standard deviation = 0.0412, min = 0.067, max = 0.202). The results suggest some standard mean value of the parameter common for MIS 6 and MIS 5e, with the coefficient of variation equal to 30.4% and 31.7%, respectively. After the interglacial the standard value decreases, and the coefficient of variation drops to 14.2% (in this time interval no correlation is found between H and *R*). In MIS 4 the standard (norm) increases together with the coefficient of variation (35.4%).

It should be noted that the difference in "standards" of different time intervals differ insignificantly (except for MIS 5d-a). So, if the value *R* is found to be close to 0.118 in a particular region and particular time interval, it may be safely supposed that the relations between different species and those between the species and environments give rise to a stationary "spatial pattern" in the geographical space. The state of the "system" after MIS 5e and up to MIS 4 is characterized with, on one hand, a lesser degree of spatial organization and, on the other – with a relative homogeneity over the entire territory of Europe (on average), indicated by a lower standard deviation of *R*. It may be safely suggested that the most favourable ecological conditions for the European large mammal assemblage existed during that period.

Further we applied the above obtained standard for estimating the *R* variability in individual regions taking into consideration the amplitude of the minimum and maximum *R* values (Fig. 15D). The Asian West-Siberian South-Eastern (XV) region departs widely from the standard towards lower values; similar tendency was displayed (though to a lesser extent) by two West European regions – Middle European Atlantic (IV) and Middle European Western (III). Another region – East European-–Asian West-Siberian Central region (XIV) is rather close to that group. Quite probably, the named regions presented most stable and favourable conditions for large mammals on the background of a high species richness.

The East-European-Asian Ponto-Caspian (XVI) and South European Mediterranean Apennine regions (VII) are noted for *R* deviations upwards (above the standard) and relatively high amplitude of fluctuations in time. The environmental conditions may be reconstructed as harsh and changeable over time (not necessary controlled by climate changes only) and imposing limitations on the species distribution within regions.

The Iberian Peninsula (I, II) may be also attributed to the two above mentioned regions, considering the significant amplitude of fluctuations *R*. The West European Atlantic Southern (V) and Middle European Central–Northern (X) regions are distinct for large amplitude of *R* fluctuations at median values close to normal. In those cases, we take into consideration the essential influence of external factors (first of all, climate changes and glaciation) on the evolution of regional assemblages.

4. Discussion

The paper presents the first attempt at the analysis of the evolution of the European regional faunal assemblages of mammals at the transition from the Middle Pleistocene to the Late Pleistocene (MIS 6–MIS4) (MLPT: Middle–Late Pleistocene Transition). We succeeded in constructing descriptive models of the evolution and finding general regularities in variations of relative frequency of occurrence of localities of species and species richness, reflecting changes in the European environments within the time interval under consideration. The regularities were differently manifested in different parts of the subcontinent depending on geographic position of the considered region.

Here we arrive at formulating several provisions concerning the nature of the faunal assemblage evolution in the MLPT process (MIS 6 – MIS 5). We will compare the newly obtained results with results of similar investigations of the event of Pleistocene–Holocene Transition (PHT: MIS 3–MIS 1, ~50000–5000 yr BP).

At the end of the Saale glaciation (MIS 6b–a) most of the regions display a notably diminished species richness (*SPN*), which gives way to a relatively sharp increase of its value in the Eemian interglacial (MIS 5e). It follows that the MLPT is typically characterized by that fluctuation of biological diversity, resulting in an increase of species number in the palaeontological records and – occasionally – in the increase of information entropy (*H*). It should be noted that we described a similar evolution earlier in the case of small mammals, though only in the assemblage from the Middle European Central Southern region (Markova and Puzachenko, this volume). The first coordinate of the evolution models (denoted here as BC1) shows a close correlation with *SPN* practically always. The number of taxa was not included into the original (source) data. Therefore, the correlation of the first (principal in its content) coordinate of the model with *SPN* is actually its own emergent effect.

When investigating analogous models of the evolution of the European regional mammal assemblages (the complete species list being analysed) for the PHT event, we got (as would be expected) an inverse relationship between the *SPN* and *H* in the Last Glaciation and the Holocene (Puzachenko, 2019). The exception presented only the bioregions where the land surface was directly covered by the ice sheet. In those cases the maximum decrease of both indexes fell, on average, on the transition between the Pleistocene and Holocene. The species richness of the European mammal fauna was diminished by factor of two in the Holocene as compared with the second half of the Late Pleistocene. The decrease in entropy was not so considerable, though its values varied considerably from one region to another. It may be concluded therefore that changes in the mammal species richness that resulted from LMPT event were fundamentally different from those in case of PHT.

A general “picture” of large mammal faunal complex evolution in Europe may be obtained taking 10 BC1 coordinates of the models as variables that characterize evolution in regions. In this case we applied the common principal component analysis to the model development (Fig. 16A). There are two states of the assemblage corresponding to MIS 6 and MIS 5 distinctly seen on the scatterplot of PC 1 and PC 2. They are separated by a gap relative to PC1. The model thus obtained is in

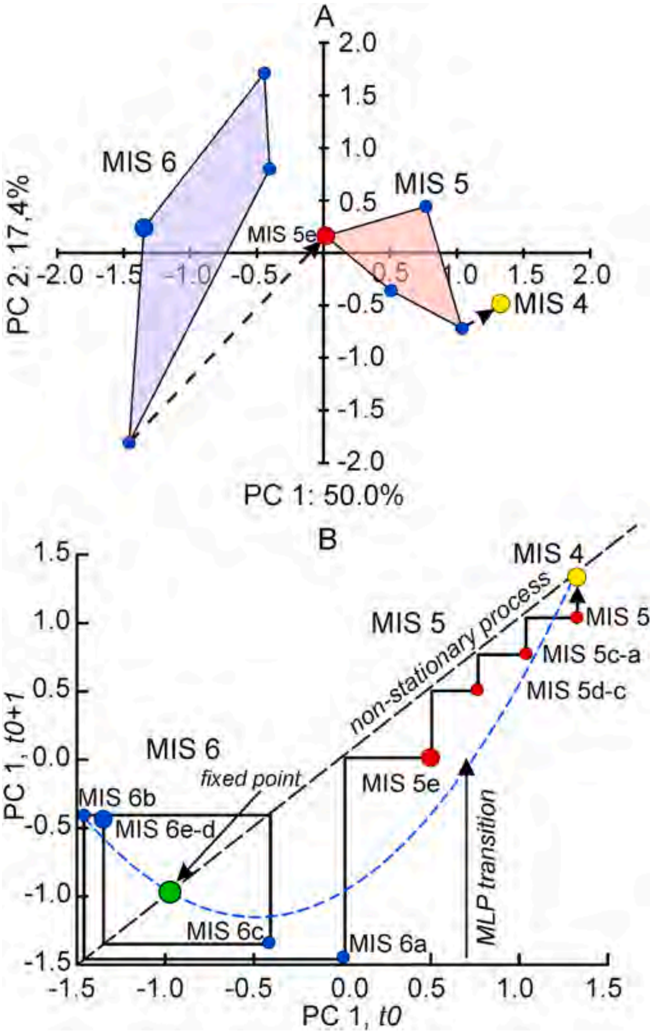

Fig. 16. The generalized image of the evolution of European large mammals complex between MIS 6 and MIS 4 isotope stages. A – the “portrait“ of evolution in projection on two first principal components (PC 1, PC 2; % – explained variance); B – Lamerey diagram of the time sequence shows the main nonlinear pattern of evolution described the first principal component (PC 1). The fixed point indicates stationary evolutionary phase (“quasi–cyclic fluctuations”) in MIS 6, but the fixed point itself is unstable. This figure is available in colour online.

reasonable agreement with evolution models for most regions. Considerably more may be found out about various states of the European large mammal assemblage from the Lamerey diagram of the time sequence which shows the main pattern of evolution described by the first principal components (PC 1) (Fig. 16B). First, MIS 6interval may be interpreted as the period of a relative stability of the assemblage as suggests the so-called "fixed point" shown in the diagram. Under conditions of a glacial time the studied system shows "quasi-cyclic fluctuations" (the cycles of fairly regular periods but varied amplitudes (Coulson et al., 2004)) around the "fixed point". Then the system drops abruptly from the area of the stationary dynamics mode. That transition occurs quickly (considering time scale) between the stages MIS 6a and MIS 5e and corresponds to MLPT properly. As follows from the diagram, the complex does not show any signs of being stationary in MIS 5. That may be interpreted as a reflection of its continuous restructuring in a certain direction. On the whole, it shows changes towards the development of a new glacial mammal assemblage that would reach its maximum in Europe as early as the second half of the Late Pleistocene (MIS 3–MIS 2).

The Lamerey diagram shown in Fig. 16B is essentially the same as that obtained earlier for the PHT of joint assemblage large- and medium-sized mammals on the East European Plain (Puzachenko and Markova, 2016: Fig. 5). In other words, in both cases the transition from glacial to interglacial conditions occurred in the same way – from a relatively stationary evolution regime at the glacial time to unsteady regime in the interglacial resulting from an abrupt jump. The described system response to the global warming was similar in both cases.

The "transition" from the Pleistocene mammal assemblages to those of the Holocene was abrupt, practically jump-like in some region (for more details see Ponomarev et al. (2013); Puzachenko and Markova (2016) and Puzachenko (2019)). It was also irreversible due to an extinction of some species and a destruction of Eurasian "*Mammuthus–Coelodonta*" faunal complex (Kahlke, 2014) which included "disharmonious" or "non-analogue" faunas (Semken et al., 2010). In various regions the time of the transition from one state of the faunal complex to another could differ notably from the presently accepted stratigraphic boundary between the Pleistocene and Holocene (Walker et al., 2009; Puzachenko, 2019). On the whole, in most cases in the second half of the Late Pleistocene there was recorded a negative correlation between *SPN* and δ^{18}O. Therefore, the local temperature rises at the end of the Late Pleistocene affected adversely the species diversity in most bioregions.

In such a manner, considering the changes of global temperature between MIS 6 and MIS 5e and between MIS 2 and MIS 1(Lisiecki and Raymo, 2005; Svensson et al., 2008), both approximately the same in speed and relative amplitude, the regional fauna response is qualitatively different, which is reflected in changes of *SPN* and – in some cases – of informational entropy (*H*) and self-organization index (*R*). Those differences may be traced even against a highly diversified background of the faunal assemblage evolution in different regions. Most probably, they were due to differences in the composition of faunal assemblages at the end of Middle and the end of Late Pleistocene. The assemblages differed in the diversity of ecological groups, in particular in the proportion of thermophilic-hydrophilic/cryophilic-xerophilic groups of species. This issue calls for further investigation and quantitative assessment.

At present the results obtained from the comparison between the models of evolution of regional faunal assemblages in the MLPT and PHT offer us a clearer view of the differences between the modern and Late Pleistocene faunas. Quite possibly, the disparity of the glacial time faunas in MIS 3–MIS 2 relative to the modern ones, and probably faunas of the Last Interglacial time relative to MIS 6, provided a necessary condition of their stability to temperature fluctuations typical for even-numbered isotope stages. It follows that the present-day interglacial "harmonic" mammal assemblages in Europe, in common with the whole regional assemblages at the Late Pleistocene beginning, are unstable to the impact of global climate change. Thus, the modern anthropogenic press contributes locally to that instability (for example, by creating uniform agro-landscapes), or increases the stability (by a development of mosaic cultural landscapes).

The next important conclusion we have come to consists in that the global temperature change in MLPT (δ^{18}O variable) and further on, up to MIS 4, cannot be considered as a "direct action" factor, when interpreting not only species richness, but the species composition in the regional assemblages. We have not found a correlation between (at least) the first significant coordinates of the evolutionary models (BC1 and BC2) and δ^{18}O. The direct "positive" impact of the climate changes may be considered in a few trivial cases – for example, the regions covered with the ice sheet completely or partly in the MIS 6 stage (Middle European Central Northern (X) or East-European-Asian West-Siberian Central (XIV) (Fig. 1A). It should be noted that we have found a poor correlation (at a level of tendency) or its complete absence between coordinates of similar evolutionary models and δ^{18}O when studying regional assemblages of small mammals within MIS 6–MIS 5 interval (Markova and Puzachenko, in press). That specific feature makes the MLPT event fundamentally different from the PHT event. Our previous investigation into the dynamics of European regional mammal assemblages in the second half of the Late Pleistocene and in middle Holocene (Puzachenko and Markova, 2019) revealed the climate changes (i.e. global temperatures) to be of primary importance controlling the species richness variations; the dependence appears to be correct in most cases, though not in all the regions. Thus, of 19 models of evolution of the regional assemblages, the first coordinate (BC1) demonstrated the statistically significant correlation in 16 cases with δ^{18}O and in 15 cases – with *SPN* (see also Puzachenko and Markova, 2020)). The second coordinate (BC2) correlated also with δ^{18}O in many cases, which suggests a complex influence of the climate on the evolution of regional assemblages at the PHT. On the whole, it is valid to say that the climate fluctuations exert a much greater direct influence on the mammal species richness (and the composition of faunal assemblages, accordingly) in Europe in the second half of the Late Pleistocene and at the Pleistocene – Holocene transition (PHT) as compared with the end of the Middle Pleistocene and the transition to the MIS 5e interglacial.

At the same time, the scale of changes in the ranges of different species varied widely within the considered time interval. A few species did not change their ranges at all. For example, the range of *S. hemitoechus* was confined to Western Europe all the time, while *Palaeoloxodon* spp., *Mammuthus* spp., *S. tatarica* and many others inhabited continuously Western Europe, Eastern Europe, the Urals, West Siberia and the south-eastern part of the latter. Some species changed their ranges insignificantly. At the interglacial time (MIS 5e) all the thermophilic species dispersed from the refugia that existed in MIS 6 in the south and/or in the southwest of Europe. Rhinoceros *S. kirchbergensis* came probably into the Urals from the south of Eastern Europe. Porcupine appeared in the southwest of West Siberia from southern and/or south-eastern regions of Asia, while he came to the Urals, in all probability, from the southeast of West Siberia. Beaver penetrated to the Urals and West Siberia, most probably, from the south of Eastern Europe, and the moose settled the Urals from West Siberia. The Caucasus was populated by roe deer and elk having come, in all probability, from the European territory, though the roe could appear from the southern West Asian refugia. The rate of the range enlargement could be rather high. Porcupines, for example, appeared in the Urals as early as the MIS 5e interglacial (Fadeeva et al., 2020).

The last subject to be discussed here is the correlation between the modern species richness of the bioregions and the species richness of the same regions written in palaeontological records. A positive and statistically significant correlation has been obtained for all three isotope stages – MIS 6, MIS 5, and MIS 4. For small mammals the correlation between the species richness in MIS 6 and the modern species richness was equal to 0.66 ($p = 0.02$) (Markova and Puzachenko, this volume). Our earlier work (Puzachenko and Markova, 2019: Fig. 1) on the mammal fauna dated to MIS 3 and MIS 2 proved a positive correlation between the regional species richness in the second part of the Late Pleistocene on one hand and the modern species richness for the same geographical units on the other ($r = 0.83$, $p < 0.001$). That steady result provides a basis for the hypothesis about a stable geographical pattern controlling variations of the biological diversity over the Europe for at least the last 200 thousand years. Noteworthy is that the hypothetical pattern is invariant to global climate changes at the glacial–interglacial cycles.

One of possible consequences of that hypothesis is our earlier conjecture about a relative historical stability of the boundaries of bioregions and of natural zones in Europe in the second half of the Late Pleistocene (Markova et al., 2019). That being so, the inner meaning of the units (and first of all, the fauna and flora composition) changed dramatically. Noteworthy is that, in the opinion of the American palaeontologists, the boundaries of faunal provinces of North America might persist through long periods, since the Oligocene (Hagmeier, 1966; Tedford et al., 1987; Graham et al., 1996; Janis et al., 1998). We have no similar hypotheses that would deduce about biogeographic provinces of the past from the present-day pattern of the species distribution ("from the present to the past") in reference to Eurasia. However, attempts have been undertaken more than once at substantiating the "objective" boundaries of the modern faunal assemblages based on the specific features of their prolonged development (that is, "from the past to the present"). In this context, the method put forward by Mekaev (1987) which is focused at properly "historical biogeographic groups – faunal assemblages", deserves further development. In our opinion, both variants of the province boundary substantiation, though fundamentally different, would give similar results only if the boundaries themselves are really stable in time; it should be pointed out that we mean the geographical position of the boundaries, not faunal complexes within them at any historical interval.

In the considered case, the formal method for drawing boundaries between the modern bioregions (here we carefully correlate them with the rank of biogeographic provinces/subprovinces, approximately) is the comparison between the standard spatial units (grid cells) which have the same area. The list of species of any grid cell was compared with the list obtained from any other cell. As the result of that hierarchic classification, clusters were formed, each of them including cells with similar species lists. In other words, the assemblages within regions are relatively homogenous, though different from assemblages in other regions. Similarity/dissimilarity relationships between the compositions of the regional assemblages were calculated much in the same way as the similarity/dissimilarity between individual grid cells. The species lists of the fossil assemblages are essentially differed in different time intervals of the Pleistocene for one and the same region. Practically the only consistent criterion to be directly used in testing hypotheses about the stability of biogeographic units in time and the preservation of spatial geographic pattern is a quantitative assessment of persistence in the similarity/dissimilarity relationships between the units. If the relationships are held constant, the hypothesis may be considered correct. Otherwise, we have only random combinations of regions in groups, characteristic only for the current state of the European faunal assemblage, without tracing it in time. The null hypothesis assumes that the regions are combined randomly, their relationships aren't kept constant over time.

To test the hypothesis we calculated the similarity matrix for the regions based on comparison between their large mammal fauna composition in MIS 6, MIS 5, MIS 4 and the modern fauna using the Jaccard coefficient as the metric. Further on, in order to estimate the similarity between the matrixes, they were compared in pairs using the permutation ($n = 9999$) Mantel test. The results of the test are given in Table 3. In every case, statistically significant positive correlation coefficients were obtained in the range from 0.73 to 0.46. These results permit, at least, to reject the null hypothesis. The present-day spatial pattern appears to be most similar to the analogous pattern in MIS 5 and most definitely different from the MIS 6 pattern. Actually, the strongest time continuity is obtained for the MIS 6 and MIS 5 patterns. Therefore, against the background of historical continuity of inter-regional relations, there are some quantitative variations, which probably reflect the specifics of a particular time interval.

Table 3
Correlation coefficients (above diagonal) between matrixes of Jaccard coefficients and their statistical significances (*p*, under diagonal) according to results of permutation Mantel test.

Assemblage	Assemblage			
	Modern	MIS 4	MIS 5	MIS 6
Modern		0.59	0.66	0.46
MIS 4	0.0001		0.65	0.49
MIS 5	0.0001	0.001		0.73
MIS 6	0.004	0.0037	0.0001	

As an example, Fig. 17 shows three unrooted trees illustrating the variability in the similarity relations of the same regions in MIS 6, MIS 5 and at nowadays. It should be noted, first, the continuously detached position of the Western Asia Caucasian region (XVII in the Fig. 1A). That attests to the validity of suppose that the mammal fauna of that region doesn't belong to European faunas in the strict sense, as implies the name of the region. Second, the modern pattern differs essentially from the Pleistocene ones by a different position of the East-European-Asian Ponto-Caspian region (XVI; Fig. 1A). At present the region occupies a detached position and demonstrates the resemblance to Caucasian region, which agrees well with the geographical position of the two regions and the lack of dividing barrier between them (in the past the regions were repeatedly disconnected through the Kuma–Manych Depression at the periods of the Caspian Sea transgressions). During MIS 6, MIS 5 (Fig. 17) and in MIS 4 the faunal assemblage of the region was heavily influenced by assemblages of East European – Asian West-Siberian Central subregions (XIV, XV; Fig. 1A). The last group of regions demonstrates a similarity in all the studied time slices in the Pleistocene and at present. A similar group is formed by two regions of the Iberian Peninsula – South European Mediterranean Iberian divided into Southern and Northern regions (I and II in Fig. 1A) and South European Mediterranean Apennine region (VII; Fig. 1A). In MIS 4 the latter becomes close to South European Mediterranean Balkan region (VII; Fig. 1A). Two Middle European regions, Western and Atlantic (III, IV; Fig. 1A) display also a persistent similarity that was somewhat distorted only in MIS 5. In the Pleistocene, regions III and IV belonged to the geographical regional cluster, which included also Middle European Central – Southern region (IX; Fig. 1A), and in MIS 5 and MIS 4 – Middle European Central – Northern region. In the nowadays, the geographical patterns of last regions also demonstrate a similarity in their faunal compositions. The Balkan region as a whole does not show any steady relationships with other regions. It may be partly attributed to the deficit of the palaeontological data (Fig. 1B). In the modern pattern it is associated with the Middle European Central region.

Finally, the "insular" West European Atlantic Southern region (V; Fig. 1A) formed an individual branch of the tree, which is mostly similar to the cluster of regions III, IV, IX, X, or (as in case of MIS 4) differentiates from all the other regions. The latter may be due to the scarcity of data on that stadial.

On the whole, the above analysis strengthens the idea of the continuity of the biogeographical boundaries since the end of the Middle Pleistocene against the background of changing composition of regional faunas and major climatic fluctuations through the first half of the Late Pleistocene and further up to the present days. The reasons for that continuity should be investigated separately; it may be supposed, however, that in any case they should be highly invariant with respect to variable climate characteristics within the time scale of the evolution. It can be said with confidence that the geographical pattern would impose restrictions on the evolution paths and on the amplitude of fluctuations in the diversity parameters *SPN*, *H* and *R* of the modern regional faunal

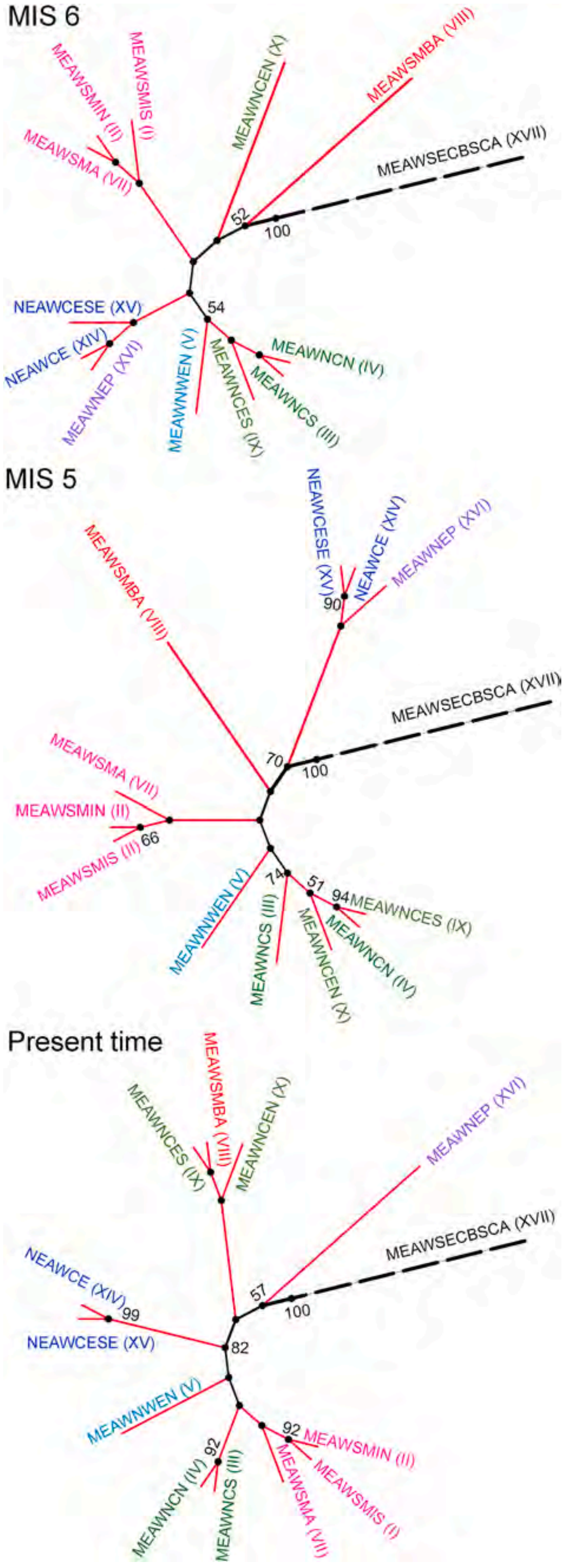

Fig. 17. Unrooted trees of the bioregions based on the Jaccardian distances matrixes for MIS 6, MIS 5 and the modern time (recent species ranges). The numbers near nodes of tree are bootstrapping values (%) of branches for a resampled set (1000) of species list. This figure is available in colour online.

assemblages in Europe under conditions of both the global warming and the global cooling (at the transition to the next glacial epoch).

5. Conclusions

For the first time, we examined a big array of palaeontological data on large mammals from a numerous number of sites and localities for the whole of Europe dated by the Dnieper (= Saale, Wolston, Riss, Pechora) glaciation (MIS 6), Mikulino (= Eem, Ipswich) interglacial (MIS 5e) and Early – Middle Valdai (= Weichsel, Würm, Devens) glaciation MIS 5d–MIS 4). Despite the different methods of dating and possible errors in dating of some sites and localities as well as differences in their taphonomy, this research shows usefulness of the meta-analyses of "not very accurate" palaeontological raw data applying multivariate technique.

Equable approach to studying of evolution of glacial and interglacial faunas at the end of the Middle Pleistocene – beginning and end of the Late Pleistocene – first half of the Holocene (our previous studies) let us discover their common nonlinear time pattern, reflected in descriptive models of evolution in both cases. This pattern shows the transition from relatively steady state conditions of European faunal assemblages during ice ages (MIS 6, MIS 4–MIS 2) to unsteady state conditions in interglacials (MIS 5e and MIS 1). We especially indicate, that it revealed against background of quite different trends both in changing of species richness and influence of global temperature changing on the processes of transition in the MLPT and PHT events.

The result of comparison of modern species richness of large mammals' regional faunas with the richness of fossil faunas of MIS 6, MIS 5 and MIS 4 for the same regions became an additional grounding hypothesis, to the previous ones, of relative stability of "provincial" biogeographical borders in Europe for mammals.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.quaint.2020.08.038.

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