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## Evolution of Central European regional mammal assemblages between the late Middle Pleistocene and the Holocene (MIS7–MIS1)

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### ABSTRACT

The evolution of species composition and species richness from the end of the Middle Pleistocene to the Middle Holocene (~200–5 ka, MIS7–MIS1) studied in two Central European bioregional mammal assemblages include 176 chrono-species. The study is based on the list of 745 palaeontological sites and 1604 dated localities. For each region, the descriptive models (non-metric multidimensional scaling technique used) of evolution were obtained for full mammal assemblages as well as particular mammalian “guilds” (carnivorous, large herbivorous, small herbivorous and insectivorous). The models for full assemblages revealed several properties of the evolution process: non-linearity, combination of stationary and nonstationary states, irreversible (evolutionary *per se*) and reversible changes, threshold like effects accompanying transitions between stationary and non-stationary states, and elements of adaptive dynamics in changing environmental conditions. The evolutionary trajectories of mammal “guilds” have the same properties but differ significantly from each other and their relative complexity is no less than the trajectories of full mammal assemblages. Hence, the evolution shows emergent property and irreducibility of complexity at different structural levels of an assemblage. Throughout MIS7–MIS1 the regional faunas responded to global climate changes ( $\delta^{18}\text{O}$  used as temperature variable), but had various contents, directions, consequences mediated by current species composition and geographic positions in relation to the Saale and the Weichsel continental ice sheets. The study shows a time/spatial invariance (scale-invariant property) of species richness for the stationary states of fauna evolution (especially during MIS3), which is described by a power law function. A mammal assemblage evolution is discussed within the framework of concept of open non-linear self-organising complex quasi-deterministic system with an ability of adaptive behaviour. Internal organisation of such systems justifies their existence and evolution in the area at a borderline between order and chaos and thus their evolution is intrinsically unpredictable.

### 1. Introduction

The study of mammalian fauna fossils allows for reconstructions of the evolutionary patterns of their composition, diversity and environmental conditions in the past (Bobrinsky, 1951; Chaline, 1972; FAUN-MAP Working Group, 1996; Hernández Fernández, 2006; Stewart, 2008; Semken et al., 2010; Royer et al., 2013; Kahlke, 2014; Socha, 2014; López-García et al., 2016; Baca et al., 2017; Markova et al., 2019; Axmanová et al., 2020; Wong et al., 2020). By examining the history (evolution) of fossil ecosystems, we hope to gain a better understanding of their modern counterparts and, to some extent, assess possible forecasts for their changes in the future. From a more general point of view, understanding of the evolutionary mechanisms of self-organisation and

responses to environmental changes in living systems underlies the creation of effective technologies for managing natural-socio-economic processes and the prediction of possible effects and consequences of human activities in the future (Puzachenko Yu., 2017). With fast changing Earth environment conditions (including climate), the forecasting of rapid and irreversible changes of modern ecosystems is difficult due to uncertain understanding of the general mechanisms of the ecosystems’ response to such global and regional changes (Barnosky et al., 2012).

The European Quaternary mammal assemblage has received a lot of attention due to the study of evolution at different spatial and temporal scales (Torre et al., 1996; Markova, 1995; Markova et al., 1995, 2002, 2010, 2019; Brugal and Croitor, 2007; Croitor and Brugal, 2010;

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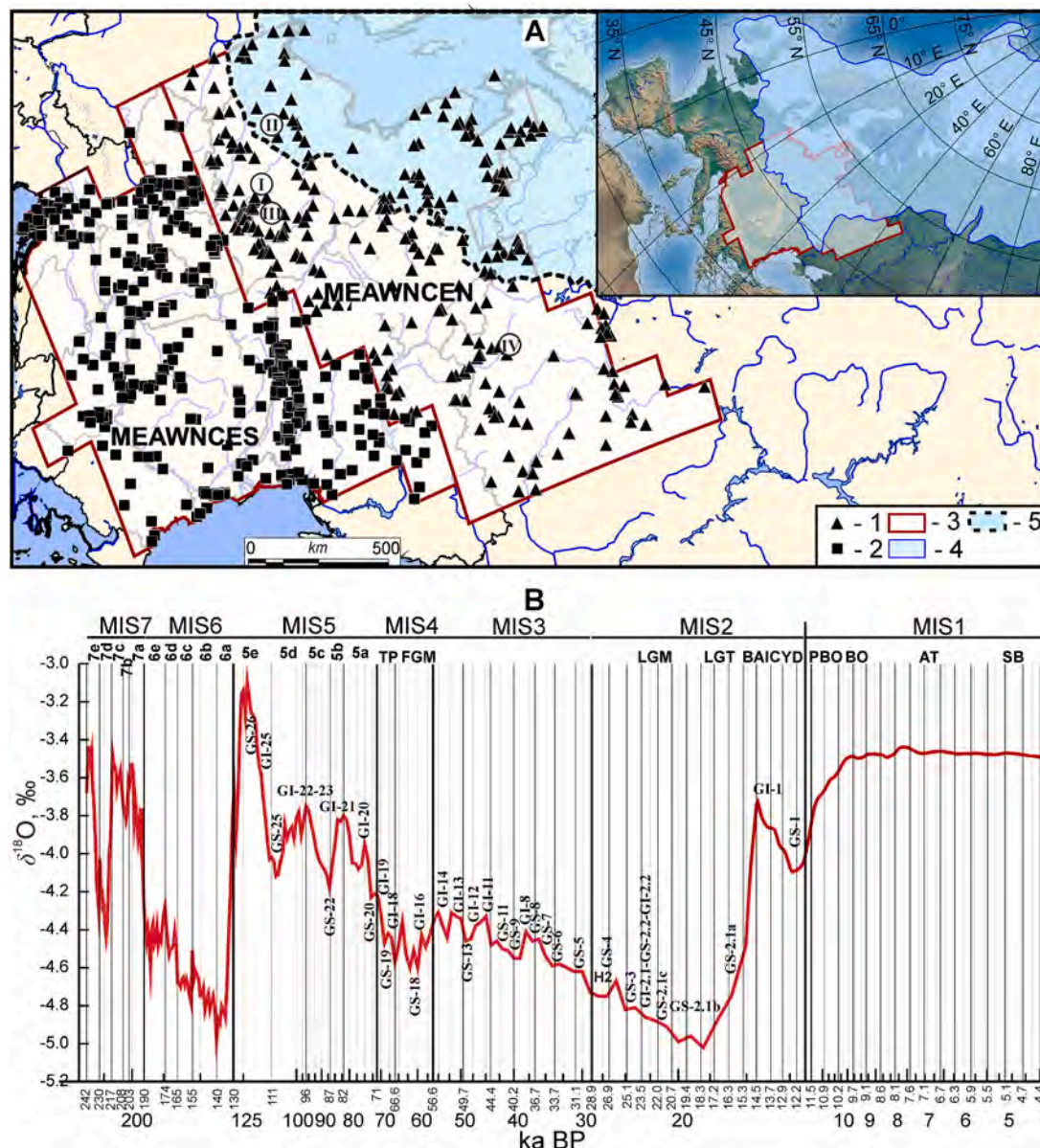
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Pavelková Řičánková et al., 2015; Crees et al., 2016; Álvarez-Lao and Méndez, 2016; Dinnis et al., 2016; Royer et al., 2016; Fernández-García et al., 2016; Discamps and Royer, 2017; Markova and Puzachenko, 2017, 2018, 2021, 2021; Puzachenko and Markova, 2014, 2016, 2019, 2021; Puzachenko, 2019; Puzachenko et al., 2021). It is noteworthy, that most of species from the wide spread orders/superorder (Eulipotyphla, Rodentia, Lagomorph, Carnivora, Cetartiodactyla and Chiroptera) found in numerous Late Middle–Late Pleistocene localities still take part in modern ecosystems of Northern Eurasia. This indicates a high ecological plasticity of the main core of European and North Asian species, which survived relatively abrupt environmental changes during the Late Glacial time and the Pleistocene–Holocene transition. In

Northern Eurasia in the Late Pleistocene the spatial mammal assemblage pattern changes (excluding a relatively small number of “mega-fauna” representatives) were expressed in the reduction/expansion of species ranges because of changes in ecological conditions. At the regional level, these changes manifested themselves not only in changes in areas of the ranges, but also in the temporary or permanent disappearance of some species or the appearance of new species as a result of migration from adjacent regions.

Here we studied irreversible and reversible changes in composition and diversity of the full Central European mammal assemblage (including bats) and then separately groups (“guilds”) of carnivorous, large and medium size herbivores, small herbivores, and representatives



**Fig. 1.** A – the palaeontological sites related to MIS7–MIS1 (240–4 ka BP) used in the study: 1 – bioregion MEAWNCEN (CEN), 2 – bioregion MEAWNCES (CES), 3 – the regional boundaries, I – Belchatów, II – Krosinko. III – Sitkówka, IV – Betovo. The maximum extent of the Saale/Dnieper and Weichsel/Valdai ice sheets are shown schematically after (Svendsen et al., 2004; Velichko et al., 2011; Ehlers et al., 2013): 4 – Saale/Dnieper Glaciation, 5 – Weichsel/Valdai Glaciation. B – The time scale used in the study: MIS7–MIS1 – marine isotope stages, 7e–5a – marine isotope substages according (Railsback et al., 2015; Shackleton et al., 2003; Otvos, 2015);  $\delta^{18}O$ ‰ – climatic time series LR04 (Lisiecki and Raymo, 2005) from ~242 to 15 ka BP and smoothed NGRIP series (Rasmussen et al., 2014) from 15 to 4 ka BP; Eem – the Eemian/Mikulino Interglacial, TP, FGM – SPECMAP Transitional Phase and First Glacial Maximum (Davies and Gollop, 2003), LGM – the Last Glacial Maximum (Clark et al., 2009), LGT – (Denton et al., 2010), BAIC – the Bolling–Allerod interstadial (GI-1) (Hoek, 2009), YD – the Younger Dryas stadial (GS-1) (Carlson, 2013), PBO (Preboreal), BO (Boreal), AT (Atlantic), and SB (Subboreal) – the North European Blytt-Sernander climatic zones (the Holocene) (Khotinski et al., 1991; Schröder et al., 2004). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

of insectivorous mammals. To estimate these changes, a time interval from the Marine Isotope Stage 7 (MIS7) to the Middle Holocene time (MIS1) was selected which included two glacial and two interglacial periods. We hope that the study will provide new information on various aspects of evolution of mammalian fauna and mammalian response to climatic changes at a regional level in Central Europe (Blois and Hadly, 2009).

In this work, several hypotheses about the response of fauna to climatic changes were tested (Grayson, 2007; Graham, 1997, 2014; Lorenzen et al., 2011; Cooper et al., 2015). Firstly, we tested the hypotheses of a uniform, linear, stationary changing of mammal assemblage in time and two hypotheses about scale (time or space) invariance of a species richness. The last two hypotheses, in a broad sense, are based on the hypothesis of an evolutionary process stationarity and hypothesis of self-organising of a mammal assemblage in geographical space and in time (Khaluf et al., 2017). In the next null hypothesis, we hypothesized that the frequency of localities with different mammal species, species composition and parameters of diversity of mammal assemblages changed only because of global climate changing. The last hypothesis suggested species gave collective response to environmental changes and an alternative assumed unique species-specific response.

## 2. Regional setting

The bioregions MEAWNCEN (CEN) and MEAWNCES (CES) used in this study (Fig. 1) are based on cluster analysis of the modern mammal ranges distribution. This approach was generally described in literature (Heikinheimo et al., 2007; Kreft and Jetz, 2010) and, in some specific details, in Puzachenko and Markova (2016), Markova and Puzachenko (2018), and Puzachenko et al. (2021).

Topographically, bioregion CEN is a combination of flat (mainly in the north and northeast) and elevated areas in the south: the Sudetes and Carpathian Mountains separate bioregion CEN from bioregion CES in the south. The central part of CES is occupied by the Pannonian plain (Pannonian Basin). In the west, the bioregion is bounded by the Alps. The southern border of the region roughly runs along the northern spurs of the Balkan Mountains (Balkan–Gebirge). In modern climate for both bioregions, the gradients of temperature and precipitation are traced both from west to east and from north to south. These physical factors determine the regional land cover spatial pattern (Olson and Dinerstein, 2002; Condé et al., 2002; Metzger et al., 2005), which includes: temperate “Sarmatic Mixed Forests”, continental temperate “Central European mixed forests”, “East European Forest Steppe” (in the east) and “Baltic mixed forests” (in the west), the “Central European mixed forests”, south alpine “Carpathian mountain forests”, the “Pannonian mixed forests”, “Balkan mixed forests” and temperate “Pontic steppe”.

In MIS6 (191–130 ka BP) during the Saale Glaciation/Saalian Complex Stage (= Moscow stage of Dnieper Glaciation (Litt et al., 2007), ice sheet covered more than 65% of bioregion CEN (Fig. 1A) (Ehlers et al., 2011, 2013; Velichko et al., 2011) and the Saale ice sheet reached up ~48°N (Svendsen et al., 2004). The next expansion of the ice cover was in the Last Glacial Maximum (MIS2, Greenland Stadials 3 and 2, 27–15 ka BP) of the Weichsel (= Vistula, Valdai) Glaciation. At its maximum extent, the ice covered about 25% of the territory of the region CEN and it reached approximately 52–51°N (Fig. 1A). The bioregion CES was not glaciated during the Last Glaciation.

## 3. Materials and methods

### 3.1. Database

The study was carried out using the PALEOFAUNA palaeontological and bibliographic database (Markova et al., 1995, 2019). The complete list includes 745 sites (Figs. 1A) and 1604 localities (“layers”, “pits”, “trenches”, etc.) (Table 1; Supplement materials, Appendix 1, Tables S1A and S1B), which dated to MIS7–MIS1. The list of ~176

**Table 1**

The volume of raw data.

Bioregion	Number of sites	Number of localities	Sample number (“dates”)	Species number
MEAWNCEN (CEN)	353	657	1421	~138
MEAWNCES (CES)	392	947	2059	~161

species/chronospecies (Supplement materials, Appendix 1, Table S2) includes 32 taxa of Carnivora, 18 – Artiodactyla, 5 – Perissodactyla, 4 – Proboscidea, 18 – Eulipotyphla, 4 – Lagomorpha, 64 – Rodentia, and 28 – Chiroptera. A total taxonomic richness was higher in the southern bioregion CES (Table 1). There were 15 species found in CEN region only, and 37 species found in CES region only. The number of localities was counted for each species/chronospecies. Then, this data was aggregated for each time bin. As a result, we obtained a variation in species frequency in each time bin for each bioregion.

### 3.2. Time scale

The time scale with unequal bins was used to unite within one study the localities dated by various instrumental techniques for which standard deviations of dates differ by an order of magnitude. In addition, in the case of such a scale, it is possible to include in the study information yielded from localities, the age of which was determined indirectly using stratigraphic or biostratigraphic techniques.

The time scale based on radiocarbon dates (up to 50 <sup>14</sup>C ka BP approximately) should take into account the incremental dating “error” to decrease the shifts and statistical uncertainties along the scale with the growing age of localities. Prior to building the scale, all <sup>14</sup>C dates have been calibrated using OxCal 4.4 software and IntCal20 calibration curves (Reimer et al., 2020). We have shown before (Puzachenko and Markova, 2019), that the relation between the standard deviation ( $|\pm\sigma|$ ) and calibrated average date value ( $M$ ) is a complicated and highly nonlinear one. For this study we obtained the following function based on 2811 calibrated dates:  $\ln(|\sigma|) = 3.33 + 0.0011e^{\ln(M)^{0.88}}$ ,  $r = 0.73$ ,  $p < 0.01$  according to  $t$ -test (Supplement materials, Appendix 2).

The scale for MIS7–MIS4 (Fig. 1B) we were guided by the relative content ( $\delta$ , ‰) of the heavy oxygen isotope series (LR04 stack of marine sediments (Lisiecki and Raymo, 2005)). The intervals of the scale for MIS7–MIS6 correspond to nomenclature suggested by Railsback et al. (2015) and MIS5 – by Shackleton et al. (2003) and Otvos (2015). The Marine Isotope Stage 4 was divided by two intervals: 71.0–66.6 ka BP (SPECAM Transitional Phase, TP) and ~66.6–56.6 ka BP (SPECAM First Glacial Maximum, FGM) (Davies and Gollop, 2003).

### 3.3. Descriptive model

The method of constructing a multidimensional descriptive model of the evolutionary dynamics of faunal assemblages was described in detail earlier (Puzachenko and Markova, 2014, 2016, 2019) (for some more details see Supplement materials, Appendix 3). The model system – a “mammal assemblage” – is defined as a logical consolidation of: (1) system’s set of elements (any time interval of the time scale is an element of this set), (2) set of variables (set of taxa) with (3) a metric (Kendall’s tau-b) to assess the relationships (similarity in particular) between any elements of the system under definition. In the general framework of multivariate analysis (James and McCulloch, 1990), we tried to analyse a temporal pattern(-s) along the time scale by reduction of pairwise similarity matrix – “distances” between all pairs of time bins, to a few dimensions and then to map the sequence of bins in a model space. The relative frequencies of localities in which the species were found were “normalized” using the arcsine transformation (Sokal and Rohlf, 1995). Kendall’s tau-b (corrected for ties) rank-order coefficients (Kendall,

1938) among all pairs of time intervals were used as a similarity metric. Then, a matrix of Kendall's coefficients was processed by non-metric multidimensional scaling (NMDS) (Davison, 1983; Hout et al., 2013). The coordinates of this Euclidian modelled space, hereinafter denoted as K1, K2 and so on (the first letter in the name of the metric gives the designation). To interpret coordinates of descriptive model Spearman's rank correlation was calculated between coordinates of descriptive models and explanatory variables:  $\delta^{18}\text{O}$  (‰, mean value for each bin of the time scale) (Lisiecki and Raymo, 2005; Rasmussen et al., 2014), the number of species (SPN, species richness for each bin of the time scale), and the average date for each bin of the time scale (Age).

Five descriptive models were obtained for each bioregion: (1) all mammal taxa, (2) carnivorous species, (3) large herbivorous mammals, (4) small and herbivorous mammals, and (5) insectivorous mammals.

In addition, we have singled out the "dynamic core" of the regional assemblages based on the result of linear multiple correlation analysis. The core includes those species whose variations of occurrence were reproduced not less than 50–60% by the linear combination of a descriptive model' coordinates. In these cases, we can assume the changes in relative spreading of these species in the bioregion are to define the basic evolutionary pattern reproduced by descriptive model.

### 3.4. Biological diversity

Within the framework of perceiving the faunal assemblage as a complex system (Ladyman et al., 2013), the species richness and diversity indices are variables/parameters of its state. Similar to the systems studied in physics, the same values of the system's parameters may correspond to different relationships between its elements or different element compositions.

To evaluate several biodiversity parameters, the frequencies of localities with different species were aggregated into several groups of time intervals corresponding to: MIS7, MIS6, MIS5d, MIS5e, MIS5c, MIS5b, MIS5a, MIS4 (TP), MIS4 (FGM), MIS3 (early part including the SPECAM Stable Warm and Transition Phase: ~57–38 ka BP), MIS3 (late part including SPECAM Early Cold Phase: ~38–29 ka BP), MIS2 (the Late Glacial Maximum: ~29–17 ka BP), MIS2 (the Late Glacial Transition and Bølling–Allerød interstadial: ~17–13 ka BP), MIS2 (the Younger Dryas: ~12.9–11.7 ka BP), MIS1 (the Preboreal and Boreal: ~11.7–9 ka BP), MIS1 (the Atlantic: ~9–5.7 ka BP), and MIS1 (first part of the Subboreal: ~5.7–4 ka BP). It should be noted, the intervals only approximately correlate with SPECAM climatic phases (MIS4–MIS2) or the North European Blytt-Sernander climatic zones (the Holocene) (Khotinski et al., 1991; Schröder et al., 2004). This is because our time intervals' scale does not clearly match with those subdivisions of the Late Pleistocene and the Holocene.

To characterize a variation in biological diversity for each time interval, described above, we estimated (some additional details see in Supplemental materials, Appendix 3): (1) number of taxa or species richness (SPN), (2) Simpson's index of dominance  $-D_{unbiased} = (\sum_i n_i(n_i - 1))/n(n - 1)$  (Simpson, 1949), (3) Shannon's index (entropy)  $-H_{unbiased} = (-\sum_i \frac{n_i}{n} \ln \frac{n_i}{n}) - \frac{(\text{SPN}-1)}{2n}$  (Shannon, 1948), (4) equitability (Pielou's evenness)  $-E = H_{unbiased}/\ln(\text{SPN})$  (Heip and Engels, 1974), and (5) redundancy or "index of order"/"index of self-organisation"  $-(R = 1 - E)$  (Shannon, 1948; Foerster and von, 1960), where  $n_i$  is number of localities with taxon  $i$ ,  $n$  – total number of localities. The  $\beta_t$  Murrelle–Ezcurra species turnover index (Murrelle and Ezcurra, 1997) was used to compare fauna composition between successive bins:  $\beta_t = (g + l)/2\alpha(n-1)$ , where  $g$  is the changes in the number of observed species between successive time interval (-s) (total "gain" of species),  $l$  is the number of undetected species (total "loss" of species), and  $\alpha$  is the average number of species observed in all time intervals, and  $n$  is the number of intervals compared. In case of two intervals, the value of last index is equal to the Whittaker's  $\beta$  diversity index (Whittaker, 1960). The quotient  $\beta_t/\ln(T_i)$ , where  $T_i$  is a timing of a time interval in ka, we

used as estimation of a "species turnover rate" (STR).

It should be specially stressed out, that we use frequencies of localities where species occurred, and does not estimate of abundance of species remains. The diversity indices calculated using standard procedures (D, H, E and R) should be interpreted differently compared to what is usually done in the species ecology or paleoecology. In the case under consideration, the diversity parameters depict adequately the relationship between species in terms of difference in distribution within a region. The index of self-organisation ( $0 \leq R \leq 1$ ) shows how far is the distribution of various taxa localities from equal random continuous uniform distribution ( $R = 0$ ).

Let us assume further on that the number of detected species ( $\text{SPN}_{\text{est}}$ ) in the geographic region with fixed area is proportional to the timing of time interval under study of the fossil record (T). For the both "equilibrium" (strictly) and "stationary" (roughly) system's states it is reasonable to hypothesize  $\text{SPN}_{\text{max}} \approx \text{constant}$ . Then, if complied with *ceteris paribus*, the "species number – time relationship" can write as equation  $\text{SPN}_{\text{est}} = A(T)^b$  (T is expressed in ka), similar to "species number – area relationship" that well-known in ecology (Lomolino, 2001). The parameter A depends on a species richness and b depends on species composition turnovers per time unit (for example, per one thousand years). If SPN and species composition do not change over time or they change very slowly ( $b \rightarrow 0$ ), then A tends to maximum of SPN per time unit. If species composition turnovers rapidly, then A tends to its average value for the entire time interval, and b tends to 1.

If the time interval is fixed, then a similar "equilibrium/stationary" hypothesis – "species number – sample number relationship",  $\text{SPN}_{\text{max}} \approx \text{constant}$  for a selected time interval) – can be written in the form  $\text{SPN}_{\text{est}} = A(N_{\text{samp}})^b$ , where A – average species number per one ("average") regional locality and b – parameter depending on regional specific. The parameter b depends on how the ranges of species are distributed within a bioregion and parameter A depends on species richness: all species ranges overlap completely ( $A > \text{SPN}_{\text{max}} = \text{const}$ ,  $b \rightarrow 0$ ) – all ranges do not overlap ( $A > 1$ ,  $b > 1$ ).

Both models described above assume stable (invariance) dependence of SPN on scales of evolutionary time or geographical space. In both cases, parameter b is a scale constant associated with patterns of fauna composition/SPN changes over time or geographic space, respectively.

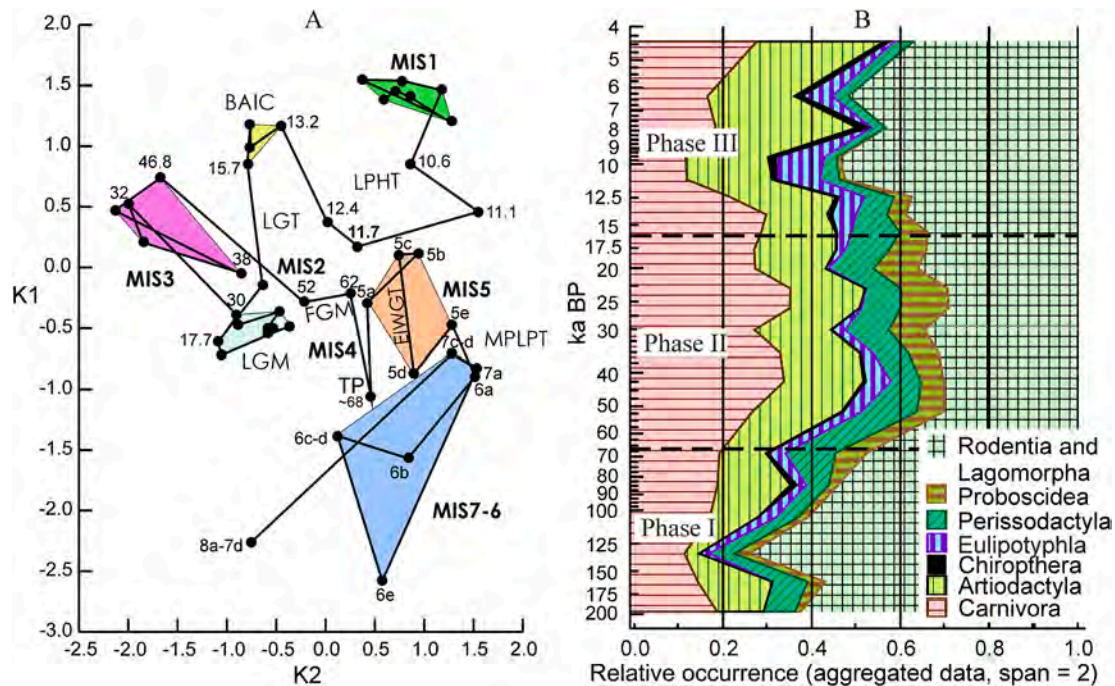
## 4. Results

### 4.1. Evolution of mammal assemblage in the bioregion CEN

Two coordinates of the descriptive model describe the evolution of the mammal assemblage in the region MEAWNCEN. Fig. 2A shows a succession of the model under study along K1 coordinate. This coordinate correlates with the calendar time (Age) (Table 2), which is meaningfully connected with irreversible (evolutionary) changes in fauna composition. The coordinate K2 is not evolutionary in this sense, but reflects the impact of climate changes on the fauna composition.

In this region, the relations of the evolutionary component *per se* in terms of fauna composition, species richness changes and global temperature changes impact are ambiguous. K1 coordinate of the model demonstrates the positive correlation with both SPN and temperature variable. K2, on the other hand, shows a negative correlation with these variables. Since K2 does not correlate with the time variable (Age), the corresponding changes in fauna composition and species richness are most probably reversible. Overall, the linear combination of K1 and K2 coordinates reproduces about 61% of the SPN variance.

One can single out subsets of points (Fig. 2A) that correspond to evolutionary stages when oscillations along K2 coordinate prevail. The MIS7–MIS6 (end of the Middle Pleistocene) is characterized by significant fauna changes. In MIS3, the system underwent major variations prior to transfer to MIS2. An abrupt irreversible, evolutionary transition to the state, which corresponded to the LGT time, was after a relatively stationary phase that correlated with the LGM time.



**Fig. 2.** Descriptive model (K1, K2) of mammal assemblage' evolution (A) and relative occurrences of group of species (guilds) in the bioregion CEN. Marine isotope stages/substages and climatic events are shown according to Fig. 1B. Acronyms: MPLPT – the Middle–Late Pleistocene Transition, LPHT – the Late Pleistocene–Holocene Transition, EIWGT – the transition between the Eem Interglacial and the Weichsel Glaciation. The Phase – designation for the stages of evolution identified by dynamics of occurrence of localities with species included in the regional dynamic core. The numbers on the graph represent the age in ka BP. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

**Table 2**

Spearman rank order correlation coefficients for the coordinates (K1, K2) of descriptive models and explanatory variables (Age, SPN,  $\delta^{18}\text{O}$ ) with proportion of variance explained ( $R^2$ ) of the coordinates associated with all explanatory variables. Statistical significance ( $p < 0.01$ ) is based on  $t$ -criteria; N – sample volume.

Coordinate	Age	SPN	$\delta^{18}\text{O}$	$R^2$
Bioregion CEN, N = 45				
K1	-0.78, $t = -8.2$	0.43, $t = 3.1$	0.54, $t = 4.3$	0.88
K2	0.04, n.s.	-0.56, $t = -4.4$	0.64, $t = -5.4$	0.62
Bioregion CES, N = 52				
K1	-0.91, $t = -15.1$	-0.18, n.s.	0.26, n.s.	0.89
K2	-0.36, $t = -2.8$	-0.74, $t = -7.7$	0.76, $t = 7.7$	0.76

The descriptive model reflects the regional assemblage response to the following climatic events (Fig. 2A, Phases I–III): MLPT – the event that lasted a short time; EILGT – between the 5d and 5c substages of MIS5, approximately; TP/FGM – very significant climatic event for the mammal assemblage (MIS4); the shift from MIS4 to MIS3 (~62–46.8 ka BP) and MIS3–LGM (~32.2–30.1 ka BP); LGM–LGT (~17.7–15.7 ka BP); LPHT – a quick evolution of the assemblage between ~13.2 and 10.6 ka BP from the “Pleistocene state” to the “Holocene state” (~13.2–10.6 ka BP).

The total time interval is divided into three phases for occurrence ratio of localities with rodents, lagomorphs, and carnivores (Fig. 2B). From the MIS7 to ~68–62 ka BP, rodents and lagomorphs predominated over the carnivores. Then, throughout the rest of the Pleistocene up to ~16.7 ka BP, small herbivorous and carnivorous had been practically equally represented in the region. The third phase, including the Holocene, is again characterized by domineering of localities with small herbivorous species. In this bioregion, an extensive spreading of Proboscidea (genus *Mammuthus*) is characteristic for the second phase of mammal assemblage evolution namely ~68 ka BP and ~35–17 ka BP (Fig. 3B).

The most of representatives of various mammal orders occurred in the region irrespectively of each other (no correlation is seen). This gives us the reason to build descriptive models for separate mammalian groups (guilds).

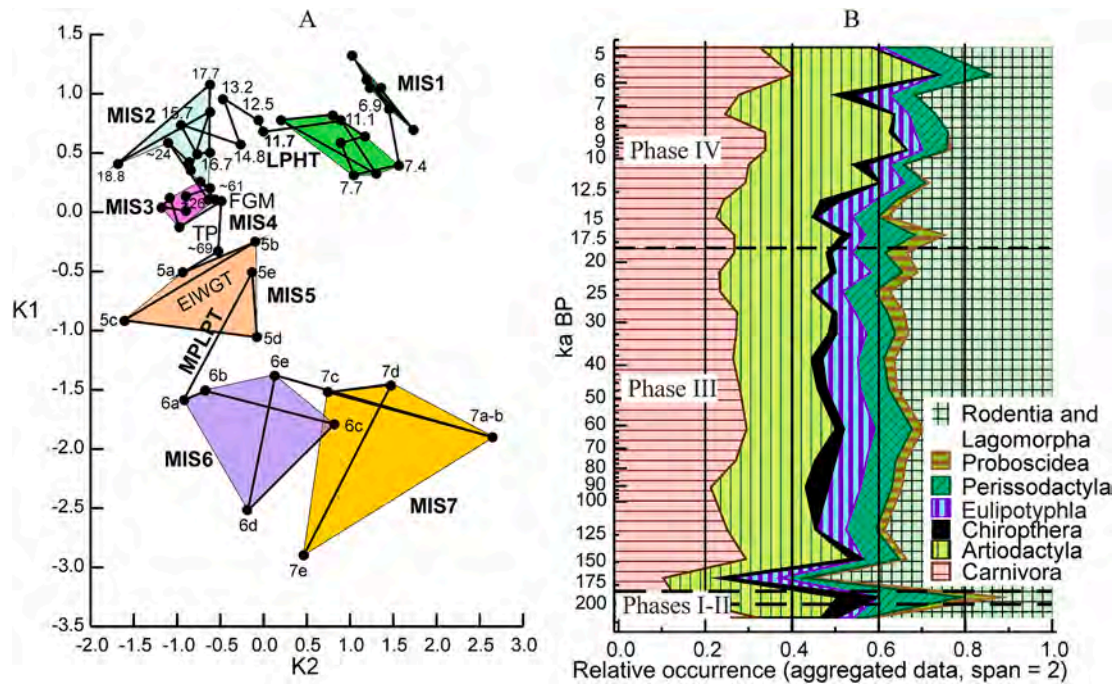
#### 4.2. Evolution of mammal assemblage in the bioregion CES

The two-dimensional descriptive model satisfactorily describes the mammal assemblage evolution in the CES bioregion (Fig. 3A). The stationary states of the assemblage generally correlate with the different MIS stages. The coordinate K1 correlates with time only and reflects the evolutionary component of the regional assemblage history. The coordinate K2 describes the species richness – global temperature negative relationship (Table 2), but, in general, only 57% of SPN variance may be explained by the impact of the global temperature changes.

The differences between MIS7 and MIS6 are explained by the impact of the global temperature fluctuation in the Late Saale Glaciation. The MPLPT event (between MIS6a and MIS5e) has signs of evolutionary transition. The transition between “interglacial” and “glacial” states (EIWGT event, MIS5d–5b) is reflected by consecutive shifts against both coordinates of the descriptive model. After MIS4, evolutionary transition to a very stationary state of the MIS3 stage system took place. A relatively abrupt transition to a less stationary system state in LGM took place between 26 and 24 ka BP.

Unlike the CEN region, the transition between the LGM and LGT states was much weaker pronounced. The LPHT event in itself covers not less than two ka, starting from Greenland stadial GS-1 (Younger Dryas, ~12.9–11.7 ka BP) within the interval ~13.2–1.1 ka BP (Fig. 3A). Aside for the events in the regional complex evolution listed above, one may also stress out the fluctuations inside of the GS-2.1 (~18.8–16.7 ka BP) and within the Atlantic Time of the Holocene – 7.7–6.9 ka BP.

Identification of evolutionary phases in this case is based on occurrences of localities with remains of species from orders Artiodactyla, Rodentia, and Lagomorpha (Fig. 3B, Phases I–IV). The first phase of evolution, when small herbivorous dominated was observed at



**Fig. 3.** Descriptive model (K1, K2) of mammal assemblage' evolution (A) and relative occurrences of different orders in the bioregion CES. The abbreviations/acronyms see in Figs. 1B and 2. The numbers on the graph represent the age in ka BP. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

~235–214 ka BP (MIS7d), and it was characterized by a relatively rough climate (Fig. 1B). Then, in warmer climatic condition (MIS7c–7a) the relative occurrence of artiodactyls was higher than that of small herbivorous. After that and up to the beginning of the LGT (~18.8 ka BP), a significant prevalence of localities with rodents and lagomorphs was marked in the region. Around 17.7 ka BP, an inversion happened for a short period, with rodents and lagomorphs domineering restored. In the Holocene, localities with representatives of the both groups of mammals had similar frequencies. The same as in the CEN region, a positive correlation ( $r = 0.71$ ,  $p < 0.001$ ) was demonstrated between Proboscidea and Perissodactyla in the CES. The peaks of occurrence of species of these orders took place in the MIS7a substage (~190 ka BP), first half of the MIS6b (~150 ka BP), the end of MIS5d (~105 ka BP), the FGM phase (~61 ka BP), and the LGM (MIS2, ~30–26 ka BP).

#### 4.3. Evolution of the mammalian groups (“guilds”)

##### 4.3.1. Carnivorous

The remains of 32 taxa of the Carnivora, belonging to the 14 genera were detected in both bioregions. In the bioregion CEN, number of species and genera (25, 12) was fewer compared to bioregion CES (32, 14) (Supplemental materials, Appendix 1, Table S2).

In both regions, smaller representatives of the order are present (*Mustela*), and species that belong to species of the megafauna group (*Panthera*, *Ursus*). In the CES, very few the Middle Pleistocene relicts were found, *Cyrtaronyx* (MIS6b, MIS5e) and *Canis mosbachensis* (MIS7e) (Spassov et al., 2017; Döppes and Rosendahl, 2009). In the Middle Holocene, the species of the Western Asian fauna complex (*Canis aureus* and *Panthera leo*) invaded the CES steppe ecosystems of lowland parts of the Pannonian Basin (Spassov and Iliev, 1994; Vörös, 2014; Döppes and Rosendahl, 2009; Masseti and Mazza, 2013; Daróczy-Szabó et al., 2020). The finding of the marbled polecat (*Vormela peregusna*) is about the same time dated (Cook et al., 2017).

In the CEN bioregion, two out of three coordinates of the descriptive model correlate with the Age variable (Table 3). K1 coordinate correlates with  $\delta^{18}\text{O}$  more definitely, than with the variable Age. The changes

**Table 3**

Spearman's rank correlation coefficients for the coordinates (K1, K2, and so on) of particular descriptive models (carnivorous, large herbivorous, small herbivorous, and insectivorous) and explanatory variables (Age, SPN,  $\delta^{18}\text{O}$ ) with proportion of variance explained ( $R^2$ ) of the coordinates associated with all explanatory variables. Statistical significance ( $p < 0.01$ , n.s. – not statistically significant) is based on  $t$  criteria; N – sample volume.

Coordinate	Age	SPN	$\delta^{18}\text{O}$	$R^2$
Carnivorous				
Bioregion CEN, N = 40				
K1	-0.49, $t = -3.5$	-0.44, $t = -3.0$	0.80, $t = 8.3$	0.80
K2	-0.68, $t = -5.7$	0.1, n.s.	-0.05, n.s.	0.75
K3	-0.06, n.s.	0.14, n.s.	0.0, n.s.	0.0
Bioregion CES, N = 51				
K1	-0.75, $t = -7.9$	-0.32, n.s.	0.69, $t = 6.5$	0.67
K2	-0.62, $t = -5.5$	-0.02, n.s.	-0.19, n.s.	0.75
Large herbivorous				
Bioregion CEN, N = 45				
K1	-0.22, n.s.	-0.62, $t = -5.1$	0.83, $t = 9.7$	0.79
K2	-0.93, $t = -16.6$	-0.02, n.s.	0.32, n.s.	0.77
K3	-0.21, n.s.	-0.53, $t = -4.1$	-0.24, n.s.	0.63
Bioregion CES, N = 51				
K1	-0.29, n.s.	-0.68, $t = -6.6$	0.80, $t = 9.4$	0.91
K2	-0.84, $t = -11.2$	-0.33, n.s.	0.26, n.s.	0.80
Small herbivores				
Bioregion CEN, N = 44				
K1	-0.29, n.s.	-0.21, n.s.	0.83, $t = 9.9$	0.70
K2	-0.61, $t = -4.9$	0.50, $t = 3.8$	-0.08, n.s.	0.74
K3	0.28, n.s.	0.10, n.s.	0.14, n.s.	0.0
Bioregion CES, N = 50				
K1	-0.82, $t = -4.9$	-0.55, $t = -4.5$	0.66, $t = 6.0$	0.83
K2	-0.24, n.s.	0.20, n.s.	0.21, n.s.	0.30
Insectivorous				
Bioregion CEN, N = 30				
K1	-0.08, n.s.	-0.54, $t = -3.4$	0.1, n.s.	0.35
K2	-0.55, $t = -3.5$	0.31, n.s.	0.54, $t = 3.4$	0.46
Bioregion CES, N = 43				
K1	-0.48, $t = -3.5$	-0.67, $t = -5.8$	0.63, $t = 5.2$	0.71
K2	-0.26, n.s.	0.27, n.s.	-0.08, n.s.	0.33
K3	-0.21, n.s.	0.07, n.s.	-0.02, n.s.	0.4

of the species richness are also partially described by K1 coordinate, which shows the highest correlation with the Age variable. Thus, in this case, the main evolutionary pattern is reproduced by K2 coordinate. Overall, over the entire time interval, the reversible changes in the fauna composition reproduced by K1 coordinate quantitatively prevailed over the evolutionary ones. The coordinate K3 does not correlate with any of explanatory variables.

The dynamic core of the regional carnivorous assemblage includes 9 species (Table 4). The first phase of evolution includes (MIS7, MIS6, and MIS5 stages (Fig. 4A). It is characterized by domineering of *M. erminea* and *P. spelaea* localities and the system fluctuations correspond to the variability of occurrences of *U. arctos*/*P. spelaea* and *M. erminea* (Fig. 4B, Phase I). A transition to the next relatively stationary state of the system (MIS3–MIS2) was within ~85–52 ka BP. During this time, *P. spelaea*, and *U. arctos* occurrence goes down, while *V. lagopus* occurrence goes up (Fig. 4B, Phase II). The period between ~47 and 17 ka BP stand out as the most stable one in the evolution of regional assemblage of carnivores, with *V. lagopus* localities predominate (Fig. 4B, Phase III). The *V. lagopus* is known from MIS6 to the end of MIS2 in the bioregion and on the territory of Poland particular, but between 35 and 16 ka BP it had the most extensive range (Fig. 4B). The range of *U. arctos* – another permanent member of this assemblage – was gradually expanded in the region, especially after ~21 ka BP. A rapid transformation of the carnivorous assemblage was between 17 and 13 ka BP (Fig. 4A). In this phase apparently the *G. gulo*, *P. spelaea* gradually disappeared, and the *V. lagopus* range decreased, but the ranges of *U. arctos* and *F. silvestris* expanded simultaneously (Fig. 4B, Phase IV). The LPHT event for this guild lied within ~13–9.5 ka BP. The event of *V. lagopus* extinction may be considered as a sign of the Last Glaciation ending and the Holocene

**Table 4**

The dynamic cores of the bioregions CEN and CES mammalian assemblages. The proportions of variance of species' relative occurrence explained by the coordinate of the descriptive models are in brackets.

Group of species	Bioregion	
	CEN	CES
Carnivorous	<i>Vulpes lagopus</i> (0.62), <i>Crocuta spelaea</i> (0.55), <i>Felis silvestris</i> (0.63), <i>Panthera spelaea</i> (0.74), <i>Gulo gulo</i> (0.63), <i>Lutra lutra</i> (0.52), <i>Mustela erminea</i> (0.81), <i>Mustela nivalis</i> (0.73), <i>Ursus arctos</i> (0.69)	<i>Vulpes vulpes</i> (0.51), <i>Crocuta spelaea</i> (0.54), <i>Felis silvestris</i> (0.53), <i>Panthera spelaea</i> (0.65), <i>Meles meles</i> (0.70), <i>Ursus ingressus/spelaeus</i> (0.69)
Large herbivorous	<i>Alces alces</i> (0.73), <i>Capreolus capreolus</i> (0.71), <i>Cervus elaphus</i> (0.61), <i>Rangifer tarandus</i> (0.50), <i>Bison priscus</i> (0.56), <i>Bos primigenius</i> (0.63), <i>Rupicapra rupicapra</i> (0.58), <i>Saiga tatarica</i> (0.70), <i>Sus scrofa</i> (0.70), <i>Coelodonta antiquitatis</i> (0.63), <i>Mammuthus primigenius</i> (0.78), <i>Mammuthus intermedius</i> (0.64)	<i>Capreolus capreolus</i> (0.69), <i>Cervus elaphus</i> (0.53), <i>Rangifer tarandus</i> (0.78), <i>Sus scrofa</i> (0.71), <i>Coelodonta antiquitatis</i> (0.66), <i>Mammuthus primigenius</i> (0.66)
Small herbivorous	<i>Lepus timidus</i> (0.73), <i>Eliomys quercinus</i> (0.51), <i>Marmota bobac</i> (0.59), <i>Sciurus vulgaris</i> (0.54), <i>Spermophilus citellus</i> (0.61), <i>S. severskensis</i> (0.50), <i>Micromys minutus</i> (0.58), <i>Apodemus (Sylvaemus) flavicollis</i> (0.59), <i>Cricetus cricetus major</i> (0.51), <i>Arvicola cantianus</i> (0.52), <i>Lasiopodomys gregalis</i> (0.58), <i>M. (Terricola) subterraneus</i> (0.60)	<i>Lepus europaeus</i> (0.74), <i>Castor fiber</i> (0.64), <i>Lasiopodomys gregalis</i> (0.63)
Insectivorous	<i>Crocidura leucodon</i> (0.50), <i>Sorex runtonensis</i> (0.64)	<i>Crocidura leucodon</i> (0.50), <i>Erinaceus</i> sp. (0.90), <i>Neomys fodiens</i> (0.79), <i>Sorex araneus</i> (0.68), <i>Sorex minutissimus</i> (0.52)

beginning in the CEN bioregion (Fig. 4B, Phase V). In addition, a good marker showing the completion of transition from the Pleistocene to the Holocene is a relatively rapid spreading of *L. lutra* (see Fig. 4).

Interpretation of K1 and K2 coordinates of the CES regional descriptive model is the same as in the CEN region (Table 3). The number of species in its dynamic core is fewer, but new species appear – *V. vulpes*, *M. meles* and *U. ingressus/spelaeus* (Table 4). Throughout MIS7–MIS6, the system performed quasi-cyclic movements in the coordinate space (Fig. 5C). By the end of MIS6, the relative representation of cave bear localities went down, but, until ~35 ka BP, it stayed higher than the ones for the other members of the regional dynamic core (Fig. 4D, Phases I, II). From the end of MIS6 stage, the second species in occurrence becomes *V. vulpes*. The MPLPT event took place in the region between ~135 and 121 ka BP. Then, from the end of MIS5e up to mid of the MIS2, the system was in a non-stationary state (Fig. 4C). The system achieved the most stationary state between ~51 and 38 ka BP (MIS3). The LGM–LGT transition happened around 20.5 ka BP. It was marked by the cave bear extinction and the general decrease of locality frequencies in all other species from the regional dynamic core. The event of LPHT was marked by sharp rise in occurrence of forest species (*M. meles* and *F. silvestris*), and before that by extinction of *P. spelaea* and *C. spelaea* (Fig. 4C and D, Phase III).

#### 4.3.2. Large and medium size herbivorous

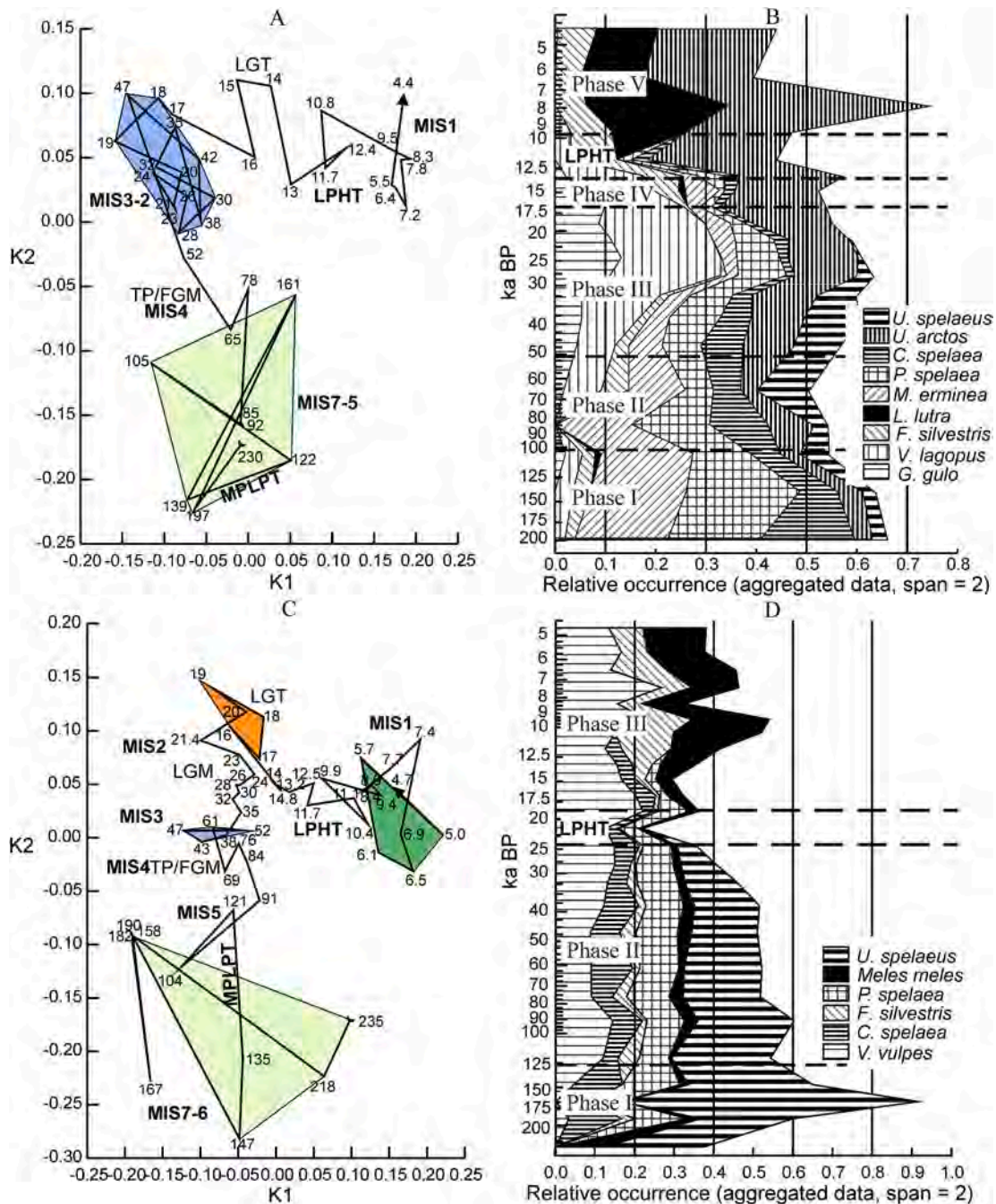
In both bioregions the remains of 19 taxa from the order Artiodactyla (15 genera), 5 taxa from the order Perissodactyla (3 genera) and 4 taxa of Proboscidea (2 genera) were found (Supplemental materials, Appendix 1, Table S2).

In the CEN region, the number of this guild was 22 (17 genera), while in the CES – 27 species (19 genera). The large herbivorous of the CES bioregion include more thermophiles, which is explained by its southern location. Remains of *Bison schoetensacki*, *Dama mesopotamica*, *Ovis orientalis musimon*, and *Stephanorhinus hemitoechus* were found only in the CES region (Guadelli and Delpech, 2000; Jánosy, 2001; Döppes and Rosendahl, 2009; Pazonyi et al., 2014; Gyurova et al., 2015). Among large herbivorous, 17 genera (genus *Alces*, *Dama*, *Megaloceros*, *Rangifer*, *Cervus*, *Capreolus*, *Bos*, *Bison*, *Capra*, *Ovis*, *Ovibos*, *Rupicapra*, and *Saiga*) belong to ruminants and 10 taxa belong to non-ruminant animals (*Sus*, *Coelodonta*, *Stephanorhinus*, *Equus*, *Mammuthus*, and *Palaeoloxodon*) (Pawłowska et al., 2014a, 2014b; Stefaniak et al., 2014; Pawłowska, 2015).

The large herbivorous descriptive model has three coordinates. The second one (K2) correlates with the age of localities and reproduces the evolutionary pattern (Table 3, Fig. 5A). The main coordinate K1 correlates with  $\delta^{18}\text{O}$  and with SPN. Throughout the time interval under consideration the increasing of temperature had a negative impact on the species diversity of this group of mammals. The contribution of the K1t coordinate in the evolution description is limited by two parts of the system's trajectory from MIS5 to MIS4 and short transition between the Pleistocene and the Holocene. K3 coordinate correlates with SPN.

The regional dynamic core consists of 12 species (Table 4); out of 8 are ruminants' species and 4 of them belong to Cervidae family, and the rest – to Bovidae. The non-ruminants also are part of the dynamic core: *S. scrofa*, *C. antiquitatis* and *Mammuthus* sp. (Labe and Guérin, 2005; Titov and Golovachev, 2017; Baigusheva and Titov, 2021).

At the end of the Middle Pleistocene and up to MIS5c substage, the system underwent large amplitude fluctuations against K1 and K2 coordinates (Fig. 5A). In ~ MIS6a, the regional environmental conditions became unfavourable for the majority of large herbivorous and its species richness was shrinking (Fig. 5B). With that, the Phase I (Fig. 5B) of the herbivorous assemblage was over. The species richness level restored in the Eem (= Mikulino) Interglacial. At the same time, the *Palaeoloxodon antiquus* was also present in the region (Kölschoten, 2000; Motuzko, 2007a, 2007b). The system was in non-stationary state throughout MIS5 (Fig. 5A). Between substages 5d and 5a, the system evolved into a new state against K2 coordinate of the descriptive model.



**Fig. 4.** Descriptive model (K1, K2) of evolution in carnivorous guild (A, C) and relative occurrences of localities of species from the regional dynamic cores (B, D). A, B – bioregion CEN, C, D – bioregion CES. The abbreviations/acronyms see in Figs. 1B and 2. The numbers on the graph represent the age in ka BP. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

The diagram on Fig. 5B (Phase II) shows this movement as a long “wave” from ~130 to 70 ka BP. The beginning of the next evolutionary phase was marked by *M. intermedius* disappearance from the regional assemblage, increase of *C. antiquitatis* and *R. tarandus* ranges. The evolutionary phase of evolving the regional variant of “mammoth fauna” took place around 20 ka, from ~68 ka BP to ~47 ka BP (Fig. 5A and B, Phase III). In the course of this time, *M. primigenius* spread over the major part of the region. In addition, the *S. tatarica* became part of the assemblage; the share of localities with *R. tarandus* remained increased. Between ~47 and 20 ka BP, the system was in a stationary state (Fig. 5A and B, Phase IV). This phase completion coincides approximately with the start of the stadial GS-2. Then, the system came out of the stationary area at ~20–18 ka BP (stadial GS-2.1b). After ~21.3 ka BP, gradual, but non-uniform

decrease of the *M. primigenius* range began (Fig. 5B, Phase V) (for more details see (Nadachowski et al., 2011, 2018)). Fast and irreversible transformation of the assemblage and transition to the Holocene took place after interstadial GI-1 (BAIC) between ~14 and 11 ka BP (Fig. 5B, Phase VI). For the species under consideration here, this transition was accompanied by the disappearance of cold-adapted representatives of the mammoth fauna and the expansion of ranges of *A. alces*, *C. capreolus*, *C. elaphus*, *B. primigenius* and *S. scrofa* especially.

In the CES region, a two-dimensional descriptive model coincides in structure with the model for the CEN region. K1 coordinate mainly describes the impact of climate changes onto the both faunal composition and species richness, while K2 coordinate reproduces the evolutionary pattern (Table 3, Fig. 5C). The dynamic core of the assemblage includes



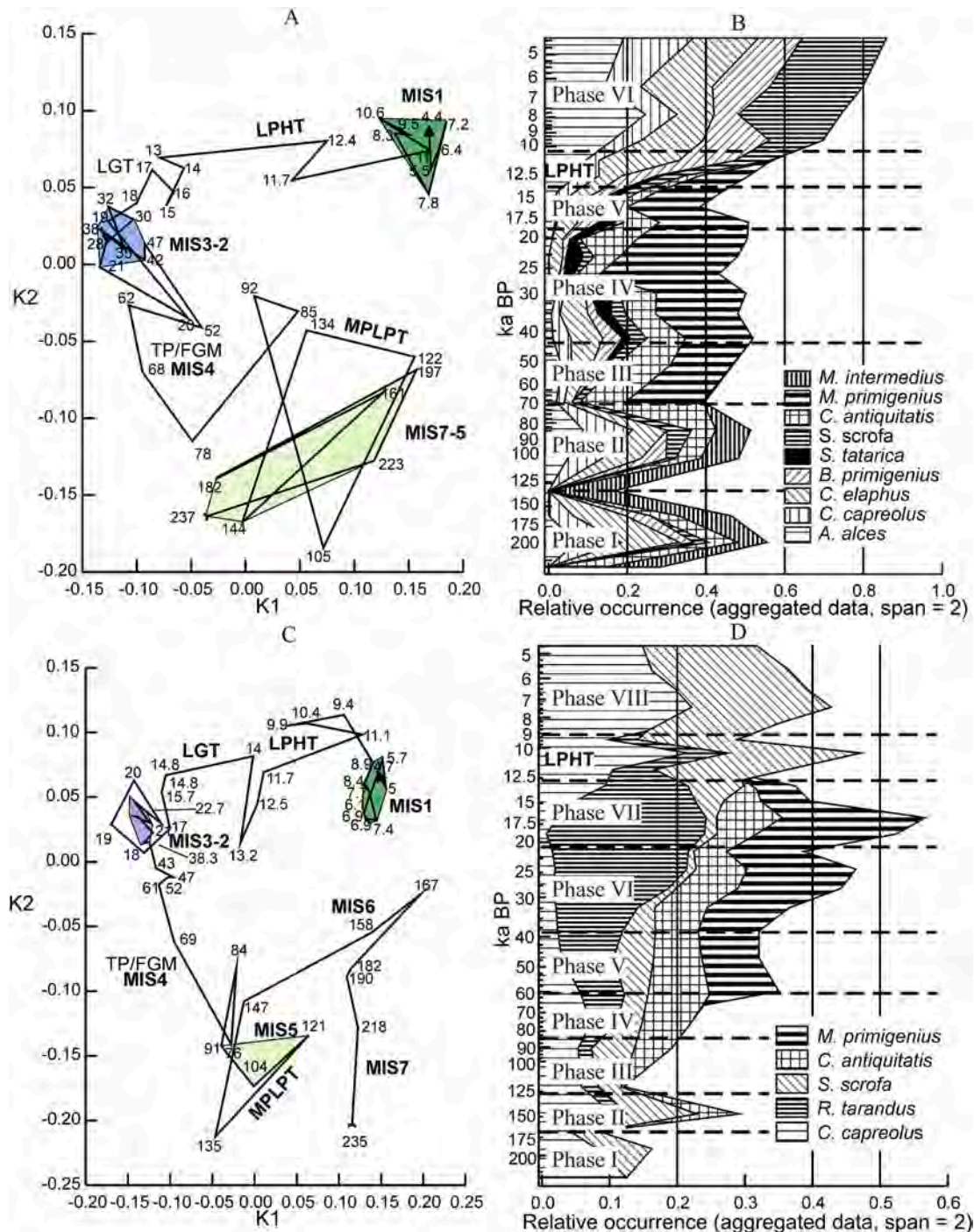


Fig. 5. Descriptive model (K1, K2) of evolution in large herbivorous guild (A, C) and relative occurrences of localities of species from the regional dynamic cores (B, D). A, B – bioregion CEN, C, D – bioregion CES. The abbreviations/acronyms see in Figs. 1B and 2. The numbers on the graph represent the age in ka BP. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

only six species (Table 4).

The trajectory of evolutionary changes (Fig. 5B) indicates an almost non-stationary mode of the dynamics throughout the entire time interval. Against this background, one may single out three periods of time, when the system was in stationary states: MIS5 (between ~120 and 90 ka BP, approximately up to the middle of 5c substage), MIS3–MIS2 (~38–22 ka BP, from the GI-8 to beginning of the GS-2), and MIS1 (<~9 ka BP, after the Boreal time). The first phase of evolution corresponds to the interval MIS7–MIS6e substage (Fig. 5D, Phase I). It was characterized by the temperate species domineering (*C. capreolus* and *B. primigenius*, or *S. kirchbergensis* and *M. intermedius*). The second phase

includes the remaining part of MIS6 (Fig. 5D, Phase II), and in the first half of this phase, a representation of *C. elaphus* was on growing in the region. At the end of the phase, the relative occurrences of *S. kirchbergensis* and *M. intermedius* localities increased. The next phase starts with the transition from MIS6a to the Eem (= Mikulino) Interglacial (Fig. 5D, Phase III). The assemblage composition included thermophilic species, such as *P. antiquus*, *C. elaphus*, and *B. primigenius*. The *C. antiquitatis* localities number grew drastically by the end of the phase at the MIS5c substage approximately (GS-22). The next phase of the evolution with highly non-stationary dynamics is between substage MIS5b and FGM (~84–61 ka BP) (Fig. 5D, Phase IV). The indicators

pointed to evolutionary transformations were an emergence of *M. primigenius* and *S. tatarica*, wide spreading of *C. antiquitatis* and *R. tarandus* and disappearance of *P. antiquus*. The transition (~52–38 ka BP) to the stationary state was characterized by higher presence of cold-adapted species (Fig. 5D, Phase V). In addition, during this phase, *S. kirchbergensis* practically dropped out from the regional assemblage. The stationary phase of evolution (~38–22 ka BP, Fig. 5D, Phase VI) is marked by a relatively abrupt growth of *R. tarandus* and *M. primigenius* relative occurrence. In the coldest and most dry stadial GS-2.1b, the relative occurrence of these species' localities reached its historical high. After the GS-2.1, the guild entered into non-stationary state (Fig. 5C and

D, Phase VII). The megaherbivores *C. antiquitatis* and *M. primigenius* disappeared from the regional assemblage at this time, while the relative occurrence of the temperate species such as *S. scrofa* and *C. capreolus* increased significantly. In accordance with the trajectory of the system, LPHT event, however, happened quite late, after the Preboreal and Boreal temperature fluctuations (Fig. 5C) and the transition to the Phase VIII is marked by the disappearance of localities with *R. tarandus* between 9.5 and 8.9 ka BP (Fig. 5D).

4.3.3. Small herbivorous

Small herbivorous guild (rodents and lagomorphs) is the most

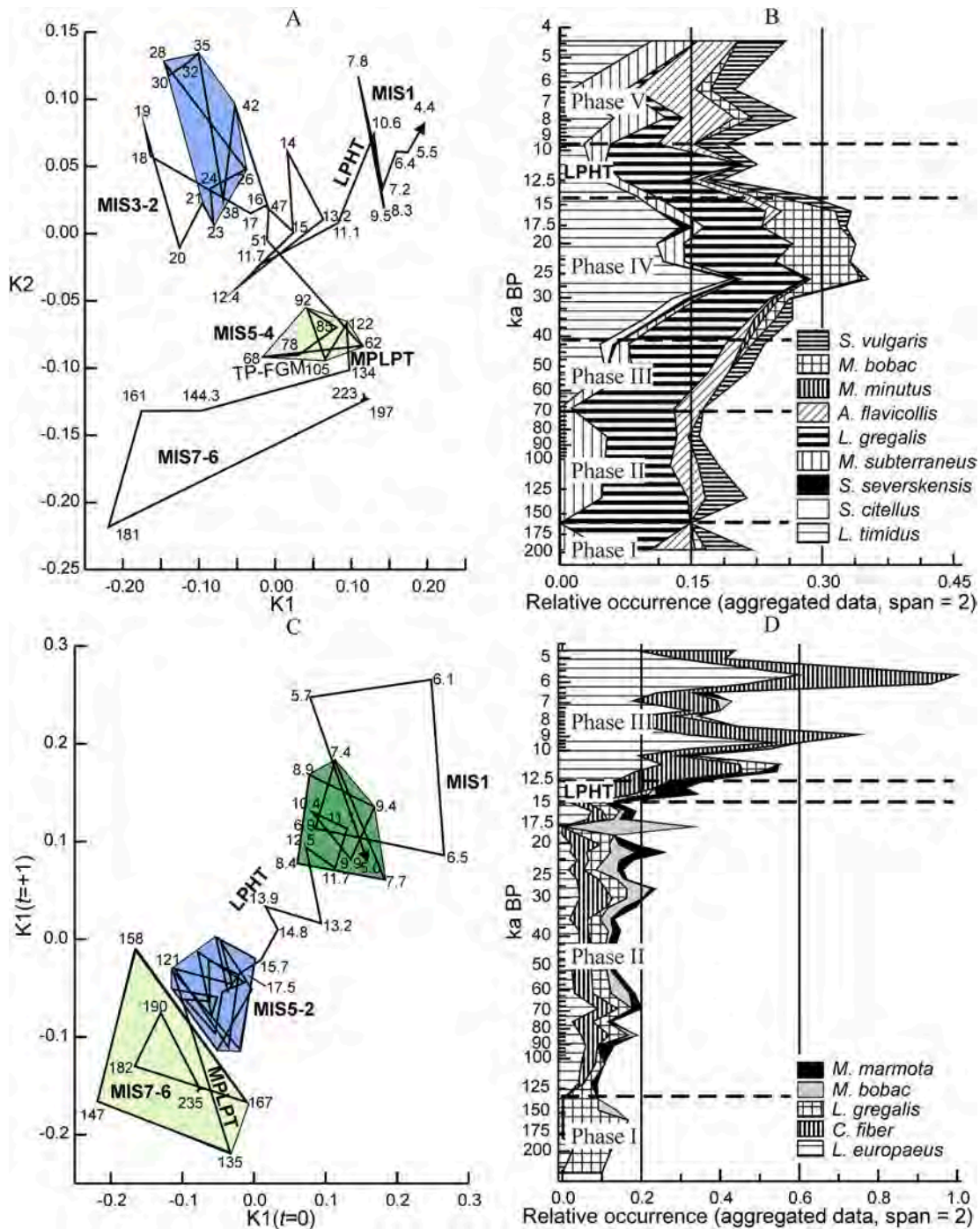


Fig. 6. Descriptive model (K1, K2) of evolution in small herbivorous guild (A, C) and relative occurrences of localities of species from the regional dynamic cores (B, D). A, B – bioregion CEN, C, D – bioregion CES. The abbreviations/acronyms see in Figs. 1B and 2. The numbers on the graph represent the age in ka BP. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

numerous ecological group (53 species, 35 genera) which forms the basis of the taxonomic mammalian diversity of both bioregions (Supplemental materials, Appendix 1, Table S2). In the CEN bioregion, the remains of 48 rodents from 24 genera and 4 lagomorphs from 3 genera were found. The assemblage in the CES bioregion includes 63 rodents belonged to 32 genera and 4 lagomorph's species. Remains of only four taxa were found in the CEN bioregion: *Dicrostonyx simplicior*, *Microtus (Alexandromys) middendorffi*, and *Spermophilus severskensis* (Agadjanian and Erbaeva, 1983; Rekovets, 1994; Markova, 2006; Motuzko, 2007b; Agadjanian, 2009; Nadachowski et al., 2009; Voskresenskaya and Markova, 1995). The small herbivorous guild of the CES bioregion included 17 species, which were not found in the CEN bioregion: *Hystrix brachyura vinogradovi*, *H. cristata*, *S. fulvus*, *Spalax leucodon*, *S. graecus*, *S. zemni*, *Mus spicilegus*, *Allocrietus bursae*, *Mesocricetus newtoni*, *Dinaromys bogdanovi*, *Pliomys coronensis* and some others (Opravil, 1976; Kozłowski and Ginter, 1982; Jánosy, 1986; Kaminská, 1999; Cărciumaru, 2000; Popov and Marinska, 2007; Toškan and Kryštufek, 2007; Paunescu, 2009; Chirica and Bodi, 2011; Lenardić, 2013; Kavacik-Graumann et al., 2016; Majkić et al., 2018; Lenardić et al., 2018).

The structure of descriptive model for the CEN region is similar to the regional models described above (Table 3). Its specificity lies in the fact that the explanatory variable SPN correlates with the coordinate K2, while the first and main coordinate K1 correlates with the climatic variable only. The non-stationary dynamics dominated (Fig. 6A), but there are two areas in the plot with relatively stationary states: (1) MIS5–MIS4 and (2) ~42–~23 ka BP. The MPLPT event was expressionless. The significant transformation of the assemblage most probably happened between ~62 and 42 ka BP. The response of the system on the LGM environmental condition (~21–19 ka BP) expressed in escape out of the stationary area (Fig. 6A). The LPHT event was about at 11.3 ka BP. Then, this assemblage of the CEN bioregion continued its evolutionary transform throughout the Early and Middle Holocene.

The dynamic core of the regional assemblage includes 12 species (Table 4). The sequences of some of their relative occurrences (Fig. 6B) show the main stages of evolution described above. Evidently, the most unfavourable conditions for small herbivores were established not during the coldest period of MIS6, but in its first half (substages 6e, 6d) (Fig. 6B, Phase I). During this period, *L. ex. gr. gregalis* was fully dominating (we use this species name following the current tradition, but see (Baca et al., 2019)). The MPLP event and transition to Phase II is marked by *M. (T.) subterraneus*, *S. vulgaris*, and *A. flavicollis* expansion. TP/FGM (MIS4) event is marked by *L. timidus* emergence in the assemblage composition and a restoration of *L. (S.) gregalis* range. Further evolution up to ~42 ka BP is characterised by wide distribution of *L. timidus*, *Spermophilus* sp. and *M. bobac* apparently maintained expansion of their ranges up to ~28–25 ka BP (Fig. 6B, Phase III). In the LGM, *A. flavicollis* practically disappeared from the assemblage, and the relative share of *L. gregalis* localities increased. The LGT stands out for gradual decrease the ranges of *L. timidus* and *M. bobac*, and the increase of the *A. flavicollis* and *E. quercinus* occurrences (Fig. 6B, Phase IV). During transition to the Preboreal time, the occurrence of *L. gregalis* was higher but *M. bobac* disappeared. The evolution of this guild in the Holocene (Fig. 6B, Phase V) is characterized by gradual decrease of cold-adapted species ranges and expansion of temperate and forest species.

The descriptive model of the evolution for the CES bioregion is utmost simple (Table 3). The coordinate K1 contains information about the evolution *per se*, the species richness changes and the responses to global temperature changes. We used the Lameray diagram of K1 for demonstration of this evolutionary pattern (Fig. 6C). The first stationary area corresponds with the MIS7 and MIS6 stages (Fig. 6D, Phase I). The graph shows how the assemblage gradually loses stability, and then it rapidly moves into a new stationary state (MIS5–MIS2) – a relatively small area, which includes long time intervals from ~121 ka BP up to the beginning of LGT (Fig. 6D, Phase II). The LPHT event took place around ~13.2–12.5 ka BP. The state of the system was approximating

the stationary one in the Holocene (Fig. 6D, Phase III), but a fluctuation was seen with transition to non-stationary state between ~6.9 and ~5.7 ka BP and further return of trajectory back to the stationary area.

Only three species are indicators of the evolution described (Table 4, Fig. 6D). The species from the dynamic core for the first stage of evolution (MIS7–MIS6) is *L. ex. gr. gregalis*. In the second half of MIS6, localities with remains of *M. bobac* emerged. The transition to the next evolutionary stage is marked by the increase of *L. europaeus*, share of localities with *C. fiber*, emergence of *M. marmota*. In the second half of GS-2.1b, especially around 17.7 ka BP, all three species as if disappeared for a short period. This period is marked by a maximum relative occurrence of *M. bobac* in the region. After this event, occurrence of *L. europaeus*, *C. fiber* increased linearly, and with transition to the Holocene, marmots and *L. (M.) gregalis* dropped out of the regional fauna (Fig. 6D).

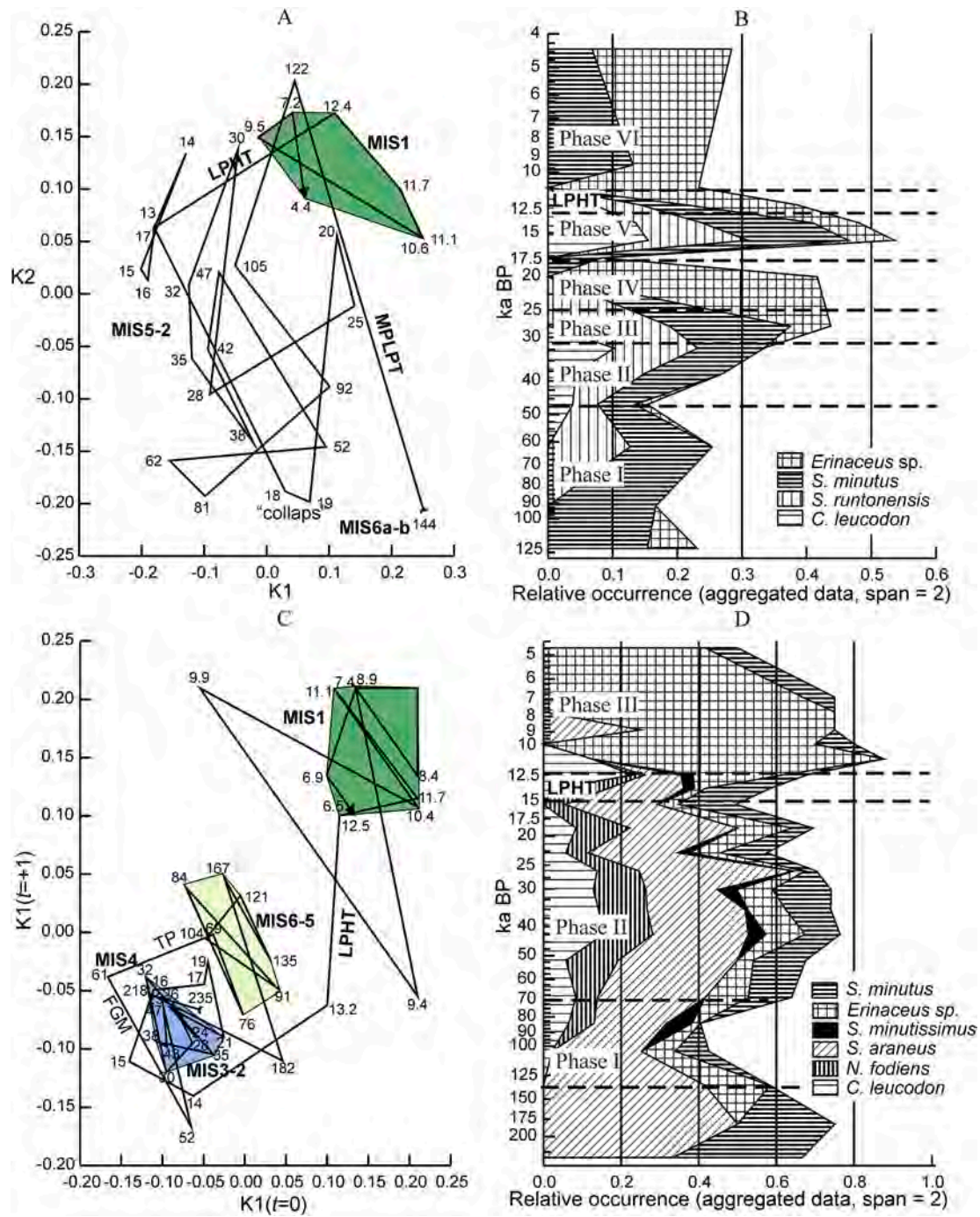
#### 4.3.4. Insectivorous

The list of insectivorous common for the both regions includes 18 species from 6 genera (*Crociodura*, *Sorex*, *Neomys*, *Desmana*, *Talpa*, *Erinaceus*) (Supplemental materials, Appendix 1, Table S2). In the CEN region, 16 species were detected. Five taxa were spotted only in this region: *Sorex caecutiens*, *S. tundrensis*, *S. isodon*, *S. thaleri* and *Talpa minor* (?) (Kalinovski, 1983; Motuzko, 2007b; Ivanov, 2008; Rzebik-Kowalska, 2008; Socha, 2012). The assemblage of the CES bioregion comprises 14 species. *C. russula* and *S. alpinus* were region-specific species (Jánosy, 1986; Valde-Nowak et al., 2003; Toškan and Kryštufek, 2007; Toškan, 2009; Sabol et al., 2017; Lemanik et al., 2020). In addition, we should note, a palaeontological data on insectivorous, probably, is not representative for the Holocene and for the end of the Middle Pleistocene due to insufficient knowledge of the fauna.

For the CEN bioregion, two-dimensional descriptive model was obtained for this group of mammals. K2 coordinate correlates with the variable Age and  $\delta^{18}\text{O}$ , while K1 – with SPN only (Table 3). The dynamics (Fig. 7A) looks like a chaotic “random walk”. Only MPLPT and LPHT events may be pointed out on the plot. The regional dynamic core includes two species (Table 4), that are present in the regional record on the intervals ~46–13 ka BP (*C. leucodon*) and ~80–13 ka BP (*S. runtonensis*) (Fig. 7B). Relative occurrences of *Erinaceus* sp. and *S. minutus* correlate with both coordinates K1 and K2. Several phases of evolution can be selected: ~120–52(47) ka BP (*S. minutus* and *S. runtonensis* predominated, Fig. 7B, Phase I), ~47–32 ka BP (*S. minutus*, *S. runtonensis*, and *C. leucodon* predominated, Fig. 7B, Phase II), ~32–25 ka BP (*S. runtonensis* and *Erinaceus* sp. Predominated, Fig. 7B, Phase III), ~25–18 ka BP (“collapse”, GS-2.1b stadial, Fig. 7B, Phase IV), 18–13 ka BP (*C. leucodon*, *S. minutus* and *S. runtonensis* predominated, Fig. 7B, Phase V), and <13 ka BP (*S. minutus* and *Erinaceus* sp. Predominated, Fig. 7B, Phase VI).

A three-dimensional descriptive model was obtained for the CES region. The only K1 coordinate correlates with all three explanatory variables (Table 3). The regional dynamic core comprises five species (Table 4). A non-stationary transformation at the end of the Middle Pleistocene with the transition to a relatively stationary dynamics mode started from the substage MIS6d approximately (Fig. 7C). The Middle – Late Pleistocene transition was not pronounced. In the beginning of MIS4, the system exited from the stationary state and, after the GS-13 stadial, it transitioned to a new stationary mode between ~47 and 21 ka BP (until the GS-2.1b stadial) (Fig. 8C). In the LGM, the system lost stationary state and, after a quasi-cycle movement (~19–14 ka BP), shifted to the state characteristic for the Holocene. Thus, the LPHT event was well pronounced in this case at the ~13.2–12.5 ka BP interval. In the bioregion *S. araneus*, *S. minutus* and *Erinaceus* sp. definitely presented among the species under consideration at the end of Middle Pleistocene.

Three periods of evolution are singled out in the first approximation on the Fig. 7D (Phases I– III). Starting from the Eem (= Mikulino) Interglacial the species diversity of insectivorous grew due to *C. leucodon*, *S. minutissimus*, and *N. fodiens*. Non-stationary mode



**Fig. 7.** Descriptive model ( $K1$ ,  $K2$ ) of evolution in insectivorous guild (A, C) and relative occurrences of localities of species from the regional dynamic cores (B, D). A, B – bioregion CEN, C, D – bioregion CES. The abbreviations/acronyms see in Figs. 1B and 2. The numbers on the graph represent the age in ka BP. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

described above for the MIS4 stage is marked by an abrupt growth of *S. alpinus* relative occurrence and simultaneous dropping out of *S. minutissimus* from the species list. In the GS-2.1b stadial, a diversity decreases due to extinction of *C. leucodon* and *S. minutissimus*. The third phase starts from the GS-1 stadial (YD) and further includes the whole Holocene.

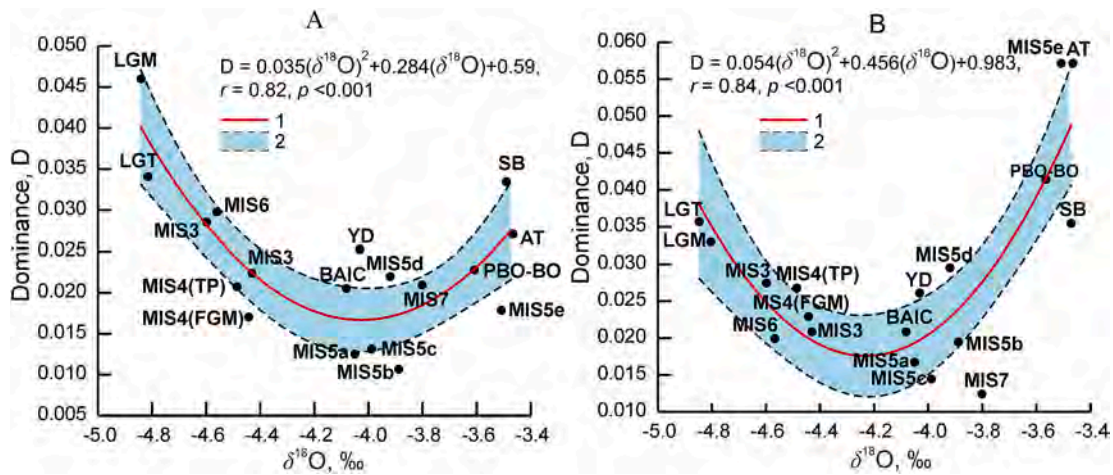
We did not include in the descriptive model the data on bats due to their specific ecology. A special evolutionary model for this group of mammals cannot be built because of large gaps in the data for the cold time intervals. The bats provide not very significant contribution in the total species richness for the Interglacials and in the mega-interstadial of

MIS3 in the both bioregions.

#### 4.4. Mammal assemblage diversity

##### 4.4.1. Dominance index ( $D$ ), Shannon index (entropy, $H$ ), and index of self-organisation ( $R$ )

The dominance and Shannon indexes are different variables of relative occurrence of localities with different species. In the CEN bioregion both parameters change independent of each other, while in the CES bioregion they show a negative correlation ( $r = -0.61$ ,  $p < 0.01$ ). Entropy does not correlate with the index of self-organisation ( $R$ ).



**Fig. 8.**  $\delta^{18}\text{O}$  – dominance index (D) parabolic relationship: A – bioregion CEN; B – bioregion CES. 1 – regression line, 2 – 95% confidence interval. The abbreviations see in Fig. 1B. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

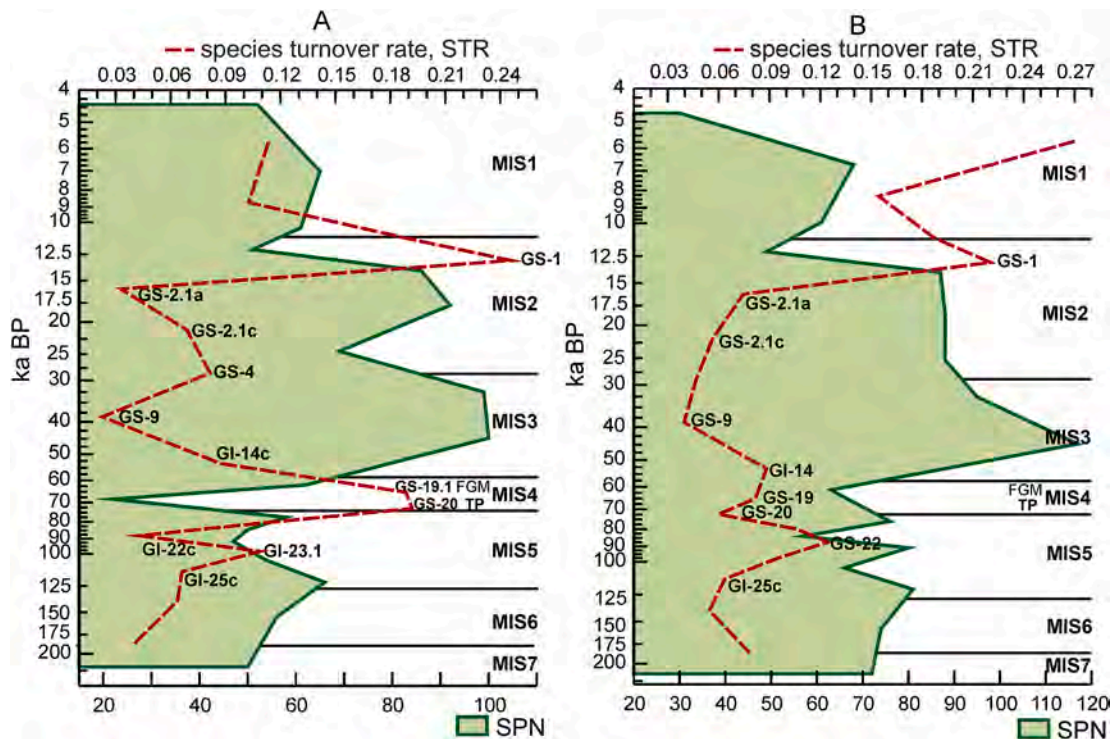
This means that having close values of diversity the systems may have different levels of self-organisation (spatial order of species ranges). In the CEN bioregion, maximum H values are seen in the Eem (= Mikulino) Interglacial, MIS3, and BAIC, while minimal values are in the MIS5b-c, LGM, YD and Subboreal time, and the absolute low of the parameter is matched with MIS4 (Supplemental materials, Appendix 4, Table S4.1).

The correlation between H and SPN is rather high ( $r = 0.82, p < 0.01$ ), but the minimal values of H (for the TP of MIS4 and the LGM) are lower than expected out of this relationship. In the CES region, the local highs of H match with the MIS5c, MIS5a, MIS3, and the BAIC warming. Starting from the YD and further on throughout the Holocene, the entropy values are very low (Fig. 11B). The H dynamics in CES also reflects the SPN dynamics ( $r = 0.81, p < 0.01$ ).

High values of R for the CEN region are seen in cold climatic periods (MIS6, TP of MIS4, and the LGM), but also at the end of MIS3 and the

LGT. Low R values characterize MIS7, MIS5, and the Holocene. Overall, R has a negative correlation with  $-\delta^{18}\text{O}$  ( $r = -0.78, p < 0.01$ ). In the case of CES region, R has a non-linear relationship with  $\delta^{18}\text{O}$  in accordance with parabolic law ( $r = 0.82, p < 0.01$ ). When  $\delta^{18}\text{O}$  value is low (-5 to -4.2), R goes down with the increase of the climatic variable; if  $\delta^{18}\text{O}$  grows further, it grows too. The highest R values correspond to the Eem (= Mikulino) Interglacial, LGT, Preboreal, Boreal and the Atlantic time, while the lowest – to MIS7, MIS5b-d, MIS4, BAIC, YD and the Subboreal time.

The dominance index (D) non-linearly correlates with  $\delta^{18}\text{O}$  in both regions (Fig. 8A and B). Both relationships prove a comprehensive impact of climate onto the number of species that have wide ranges in the regions and domineer due to this fact in the palaeontological record. Both very low and high temperatures reinforce domineering of some species alike, while precipitation amount acts as an additional potential



**Fig. 9.** Species turnover rate (STR, dashed line): A – bioregion CEN; B – bioregion CES. The abbreviations see in Fig. 1B. SPN – species number. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

factor.

#### 4.4.2. Species turnover index ( $\beta t$ ) and species turnover rate (STR)

In this study, Mourelle-Ezcurra species turnover index ( $\beta t$ ) reflects variability of fauna composition between the adjacent time intervals (Section 3.4). The “average” value of the index, produced for the whole-time interval under consideration, have little difference in case of both bioregions (CEN – 0.234, CES – 0.243), as well as corresponding STR values (CEN – 0.0428, CES – 0.0444).

The STR values calculated for separate time intervals are far more informative (Supplemental materials, Appendix 4, Table S4.2). In the CEN region (Fig. 9A), maximal STR values are matched with two events followed by drastic decrease of species richness, that took place in MIS4 and on the borderline between the Pleistocene and the Holocene (YD, GS-1). In addition, relatively high STR values approximately correspond to climatic events of interstadial GI-23.1, and stadials GS-4 and GS-2.1c. During the periods with stationary state of the assemblage in terms of the species richness value the STR is relatively lower. The maximal STR values in the CES region are during transition from the end of the Late Pleistocene to the Holocene (GS-1) and in the Holocene (Fig. 9B). A relatively high value of the parameter matches with the GS-22 stadial (MIS5c–MIS5b). A relatively small increase of STR corresponds to the interval between GS-19–GI-14 (MIS4). Low STR values, including the minimal one, are characteristic for the stationary states of the assemblage existence. One should note a minor increases of fauna transformation rate at the MPLPT and between 5e and 5d substages (~GI-25c) that was pronounced in the CEN region as well. Thus, the main differences between the bioregions in terms of the STR are the response of the southern mammal assemblage to GS-22 stadial and it is a weaker response to climatic events of MIS4 stage. Overall, the correlation between the regions in terms of the STR is low ( $r = 0.49$ ,  $p = 0.04$ ), and this is proof of the specifics of evolution in the different regions.

Judging by the plots in Fig. 9, reversible/irreversible changes of the regional fauna compositions were irregular. However, we have not succeeded in identifying a common rule for the change of STR response to stadial/interstadial conditions of the Late Pleistocene. Fauna transformations in GS-1, accompanied by abrupt depletion of its composition in both bioregions may be interpreted more definitely. In addition, the STR dynamics in both regions corresponds to the modelling results for the “equilibrium/stationary” SPN dynamics (Section 4.4.4).

#### 4.4.3. Species number – timing of a time interval relationship

In this study, for the first time, as far as we know, the zero hypothesis of the temporal invariance of SPN for a fossil record was tested. In theory, in “equilibrium/stationary” state, a species richness (SPNest)

must be “accumulating” over time according to a certain rule, proportional to timing of a time interval. We limited ourselves to the analysis of this model at interval from the Eem (= Mikulino) Interglacial (MIS5e) to the Boreal time (MIS1). The result showed (Fig. 10), that for both bioregions the relationship  $SPN_{est} = AT^b$  is obtainable at a high statistical significance (Supplemental materials, Appendix 4, Table S4.3 and Table S4.4). On average one may find around 60 species per time unit (1 ka) in the CEN bioregion ( $SPN_{est} = 59.9 T^{0.162}$ ,  $r = 0.81$ ,  $r^2 = 0.65$ ) and 66–67 species per time unit in the CES bioregion ( $SPN_{est} = 66.5 T^{0.158}$ ,  $r = 0.88$ ,  $r^2 = 0.76$ ). The difference of these “equilibrium/stationary” of SPNest in various regions is envisaged by the difference of their position against the geographical latitude.

The parameter b (scale-invariance constant) reflects the average rate of transformation of regional fauna composition (see Section 3.4) in the Late Pleistocene. Based on the simulation results, this rate was slightly higher in the northern bioregion. This is in good agreement with the assumption of the direct influence of the ice sheet on the ecological condition in the CEN bioregion during the Last Glacial. It is very likely; parameter b can characterize ecological elasticity (stability) or ecological resilience of a particular mammal assemblage in relation to external factors, such as climate changes. Lower values of b should be matched to a higher elasticity or capacity to recover (resilience). However, further comparative studies are required to obtain more reliable data for such an interpretation of the parameter b.

#### 4.4.4. Species number dynamics

The species number (SPN) or species richness is a basic parameter that characterizes the complexity of the faunal assemblage organisation. We have studied the dynamics of this parameter on two levels: the level of the system’s elements (i.e. for each bin of the time scale) and the level of groups of elements (several jointed time scale intervals) (Section 3.4).

Fig. 11A and B shows SPN dynamics in the CEN and CES bioregions set against  $\delta^{18}O$  timeseries. In the first bioregion no correlations between the temperature variable and SPN were found, while in the second one the correlation was low (Spearman  $r = -0.43$ ,  $p < 0.01$ ). Indeed, both high and low values of SPN may coincide with different climatic events. Hence, the global temperature dynamics cannot make bids for the main control variable for SPN at least over the entire time interval considered here. At the same time, the separate events in the SPN dynamics may be well linked to the several climatic events. The stages MIS7 and MIS6 are characteristic by relatively low SPN. In MIS7, SPN in general was higher than during the maximum extent of the Saale (= Dnieper) Glaciation (MIS6). The transition to the Eem (= Mikulino) Interglacial was accompanied by SPN increase, but the SPN did not reach historic highs in these times. The stage MIS4 had been an important milestone in the

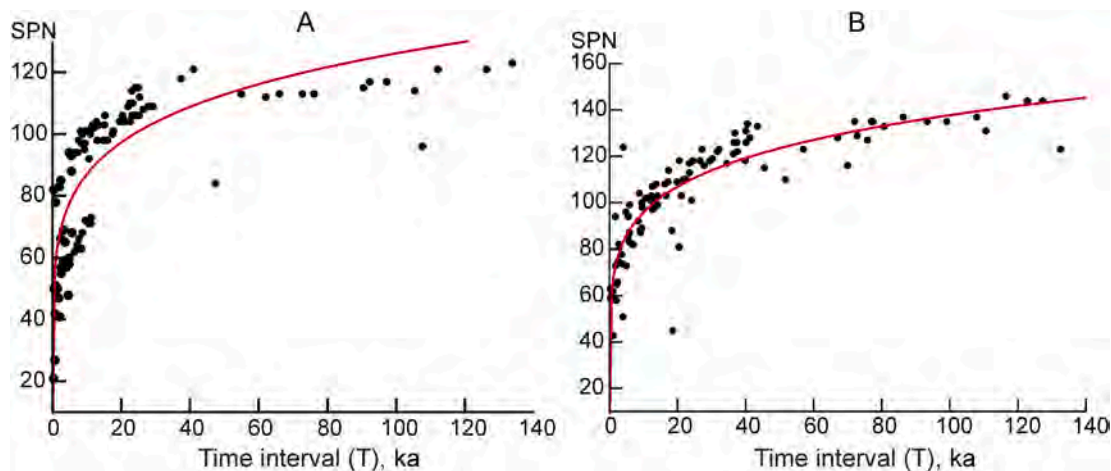
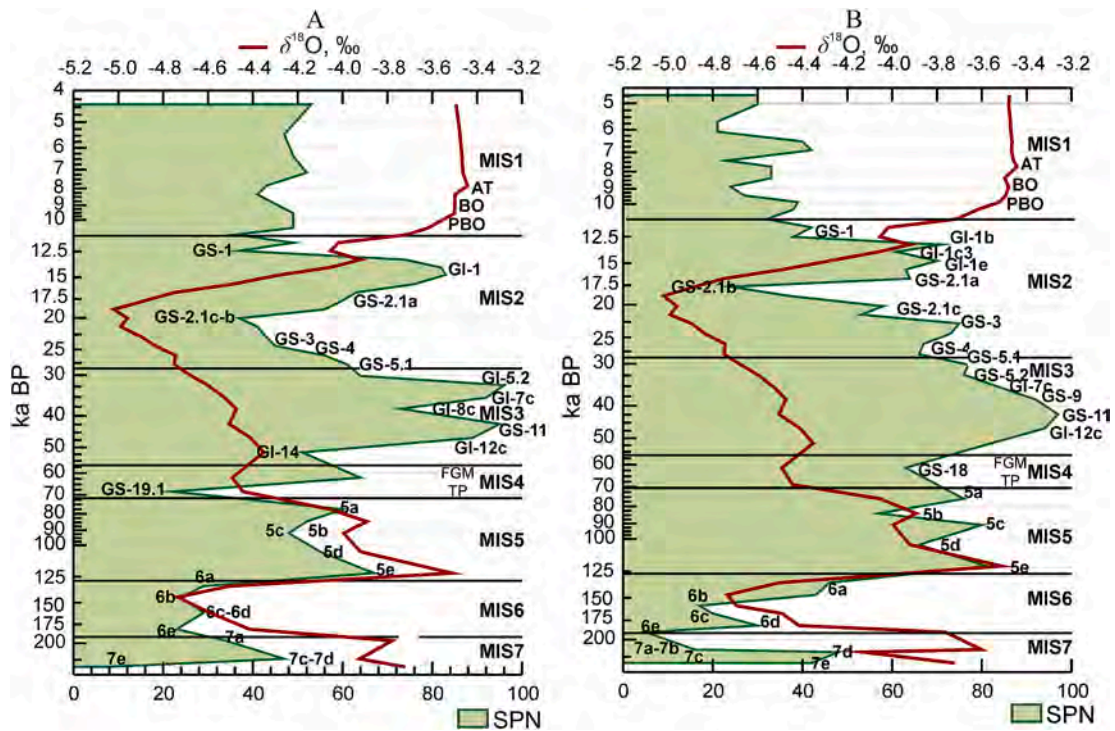


Fig. 10. The “species number (SPN) – timing of a time interval (T) relationship” in palaeontological record: A – bioregion CEN; B – bioregion CES. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)



**Fig. 11.** The species number (SPN) dynamics: A – bioregion CEN; B – bioregion CES. The abbreviations see in Fig. 1B. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

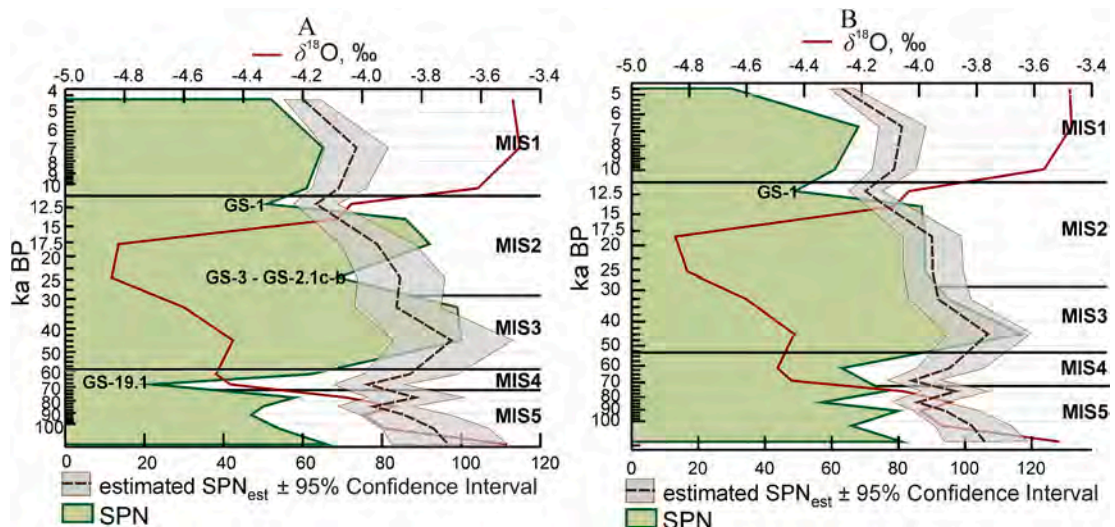
history of species diversity for both regional assemblages, but, naturally, SPN dropped down to a larger degree in the northern bioregion. The maximum SPN is characteristic for the MIS3 (the “golden age” of the *Mammuthus-Coelodonta* Faunal Complex”). Then, SPN started to decrease and reached its minimum in the GS-2.1c-b stadial (LGM) and then it grew up for the last time in the warming of GI-1 interstadial. The Younger Dryas (GS-1) cold event was accompanied in both regions by a drastic dropdown of SPN.

We used  $SPN_{est}$  (Section 4.4.3) as reference values with clear semantics for comparison with the observed SPN values (Fig. 12A and B). The states of mammal assemblages in MIS5e–MIS4 and MIS1 are interpreted as non-stationary ones for both bioregions. In the CEN bioregion, the assemblage was close to stationary state throughout MIS3 stage, and

then – after LGM with the exception of YD cooling (GS-1). The assemblage of CES bioregion was close to stationary state in the course of stages MIS3 and MIS2 except for the Younger Dryas cooling.

4.5. Species number – sample number relationship

We selected several localities of the northern bioregion in order to use them when testing the hypothesis of spatial invariance of SPN (“species number - sample number relationship”) (Section 4.5.2). Mainly, these are recently investigated localities from Poland (data provided by KP). It was especially important for us that these sites differ in terms of taphonomy and details of their current explorations. The Middle Palaeolithic site Betovo (data provided by AM) was also chosen



**Fig. 12.** Estimated species number ( $SPN_{est}$ ) and observed species number (SPN): A – bioregion CEN; B – bioregion CES. The abbreviations see in Fig. 1B. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

because its dates cover a relatively large time interval of Palaeolithic human stable habitation in Eastern Europe and its fauna (large and small mammals) was well studied.

**Bełchatów** (51°15'24.3"N, 19°16'57.1"E, Fig. 1A) is an outcrop situated in the southern part of Poland. Faunal research revealed the presence of steppe mammoth (*M. trogontherii*) and reindeer (*R. tarandus*) (Czyżewska and Wiszniowska, 1982; Pawłowska et al., 2014a). The studies conducted so far show that steppe mammoth remains in Poland are extremely rare (Pawłowska, 2015). The faunal remains from Bełchatów were found within sediments which are connected with the Mazovian (= Holsteinian, MIS11) or Zbojnian (= Reinsdorf, MIS9) Interglacial (Pawłowska et al., 2014a). A rib of *M. trogontherii* with evidence of filleting marks represents the oldest evidence of human-induced marks on mammal bones in Poland (Pawłowska, 2017). The site not only manifested the earliest evidence of mammoth exploitation in Poland but also provides the oldest *R. tarandus* remains known from Polish sites (Pawłowska et al., 2014a). The *M. primigenius* remains from the Bełchatów site belonged to MIS3 stage of the Late Pleistocene.

The **Sitkówka** site (from the north –50°48'21.5"N; from the south –50°48'15.9" N; from the west– 20°33'19.7" E; from the east –20°33'35.9" E, Fig. 1A) is located in the Świętokrzyskie Mountains (Pawłowska, unpublished results). Faunal assemblages comprise of remains of members of the subfamily Bovinae (*Bos/Bison*), rhinoceros, *E. ferus*, *C. latifrons*, *R. tarandus*, carnivores, including *Ursus* sp., *Crocitua spelaea*, and *Meles meles*. Rodents are represented by the *C. fiber*. The presence of the species *C. latifrons*, from which the mandible with teeth (P3-M3) originates, suggests that at least some of the material comes from the Middle Pleistocene (Stefaniak et al., 2014), while the other part of the assemblage is younger (the Late Pleistocene), that is Weichsel (= Vistula) Glaciation (Woroncowa-Marcinowska et al., 2017).

**Krosinko** site (52°13'05.9"N, 16°49'16.5"E, Fig. 1A) is a gravel pit located in the central part of Poland, which was discovered in 2003 by K. Pawłowska (Pawłowska, 2009, 2010). Over 100 animal remains were found there, mainly of *M. primigenius* and *C. antiquitatis*, but also *E. ferus*, *B. primigenius*, *B. priscus*, *R. tarandus*, *M. giganteus*, *P. spelaea*, and *Ursus* sp. (Pawłowska, 2010, 2015, this volume). Any others data on the fauna from Krosinko used in others publications were not verified. The faunal diversity, dominated by the *M. primigenius* along with the *C. antiquitatis* among all identified so far taxa (Pawłowska, 2010, 2015, 2017, this volume) (more details in Supplemental materials, Appendix 4). This site, along with 25 other new sites with mostly *M. primigenius* remains, attest much more potential places in the central part of Poland than previously thought, thus developing our knowledge of its geographical variability. Because for most of the Pleistocene assemblages from open-air sites of Poland, stratigraphy is unknown, the Krosinko site is an exception by recognized lithological and stratigraphic profile. Animal remains are the subject of ongoing research due to the continuous recovery of faunal remains during gravel and sand extraction. Those so far studied should be stratigraphically linked to the Middle and Late Weichsel Glaciation (= Vistula/Valdai), which corresponds to MIS3–MIS2 (Pawłowska, 2009, 2010, 2015, 2017, this volume; Lorenc and Pawłowska, 2010; Croitor et al., 2014; Marciszak et al., 2021).

The **Betovo** Middle Palaeolithic site is situated near the Betovo village (53° 20'56"N, 34° 0'30"E, Bryansk province, Fig. 1A) on the right coast of the Desna R. (Upper Dnieper R. basin). The site was discovered by Tarasov (1989, 1991) and the complex studies began in 2007 (Ocherednoi and Voskresenskaya, 2009; Ocherednoi et al., 2014). According to calibrated <sup>14</sup>C dates for the cultural layers, it was elucidated that the ancient man inhabited this site between 36,000 and 28,500 BP (Ocherednoi et al., 2014) during the Valdai (= Bryansk) interstadial (Markova et al., 2002) and to the end of MIS3. The received archaeological data indicate that the Mousterian tradition survived in the Desna R. basin until the end of MIS3. After E.V. Voskresenskaya, the cultural layer 2 matches to the geological layer 11. The rich small mammal fauna including only tundra and steppe species was yielded from this layer of the site (Voskresenskaya and Markova, 2019). The list of species

includes at least 10 species: *O. pusilla*, *Lepus* sp., *M. bobac*, *Spermophilus* sp., *D. guiljelmi*, *L. sibiricus*, *E. luteus*, *L. lagurus*, *L. (Stenocranius) gregalis* and *Microtus* sp. The remains of large mammals were studied by N.D. Burova. The list of large mammals include *C. antiquitatis*, *E. ferus*, *M. primigenius*, *B. priscus*, *R. tarandus*, and one wole – *M. nivalis*. The Betovo fauna reflects the whole disappearance of the forest zone in the centre of the Russian Plain and the spreading of cold tundra-steppe. The similar reconstructions were received earlier from the other Palaeolithic sites of the Upper Dnieper basin, and for the Russian Plain on the whole (Markova, 1982, 1997; Markova et al., 2019; Velichko et al., 1977).

The hypothesis (Section 3.4) was tested for the time interval of the Betovo site – 36–28.5 ka BP. For the CEN bioregion (465 localities), the relationship between SPN (accumulated) and sample (number of localities, N) is well described by equation  $SPN_{est} = 12.93N_{smp}^{0.47}$  ( $r = 0.61$ ,  $p < 0.01$ , Fig. 13A). Thus, the “average” number of species per one locality for this region is about 13. SPN of the Betovo (cultural layer 2) site is close to this value but SPN of Krosinko, Sitkówka, and Bełchatów sites are lower significantly. Such result is due to specific taphonomy, the lack of information on remains of small mammals and the lack of more detailed knowledge of these new localities etc. In the CEN bioregion, the richest fauna was described from the Komarowa Cave (layers C and D, Poland) (Rzebik-Kowalska, 2008; Nadachowski et al., 2009).

The “SPN – sample number relationship” in the CES (169 localities) is described by the equation  $SPN_{est} = 12.58N_{smp}^{0.58}$  ( $r = 0.77$ ,  $p < 0.01$ , Fig. 13B). The value of A is a little lower in comparison to this parameter in CEN and value of b, however, is noticeably higher. The richest fauna was described from Cioarei à Borosțeni (Romania) (Cărciumaru, 2000, 2007). The statistical significance of relationship between accumulated diversity and the number of localities marks that the regional faunas were in a stationary-like states during the considered time interval. This corresponds to the conclusion about the stationarity of the regional faunas in the MIS3 stage obtained in the “species number – time interval relationship” model (Section 4.4.3).

We interpret the differences between the parameters A and b for regional faunas as following. There were relatively more species with wide ranges in the northern bioregion at the end of MIS3. The SPN of northern and southern bioregions did not differ significantly (80 versus 88) in the considered time interval. The value of the parameter b is lower in the northern bioregion compared to the southern one, which indicates a greater overlapping of species ranges and probably ecological niches of species in CEN. In the south, there were more species with relatively small ranges and probably with more “narrow” ecological niches, accordingly. Formally, in accordance with the obtained equations, in order to discover about 50% of the taxonomic diversity of the regions, it is necessary to take “at random” between 10 (CEN) – 9 (CES) localities (Fig. 13). This parameter (we propose the notation for it –  $SPN_{50}$ ) can be considered as an indicator of species richness to compare regional assemblages for the same time windows that are selected.

## 5. Discussion

The descriptive models of evolution (Section 3.3) allow not only to get a generalized view of the process on the whole, but at the same time to single out its independent components, that are associated with various coordinates of the model space (Sections 4.1–4.3). The models of both bioregions have a component (coordinate) that clearly reflects the evolutionary changes of the fauna composition in time. If we consider the whole-time range, there is practically no impact of the global temperature changes onto these processes in the CES region (Table 2). This result may be interpreted as a consequence of a relative remoteness of the bioregion from the borders of ice sheets. At the same time, the temperature changes significantly impacted the evolution of the assemblage composition in the CEN region, though probably not as pronounced as might have been expected from its geographical position in relation to ice sheets. One should not interpret the results of this study



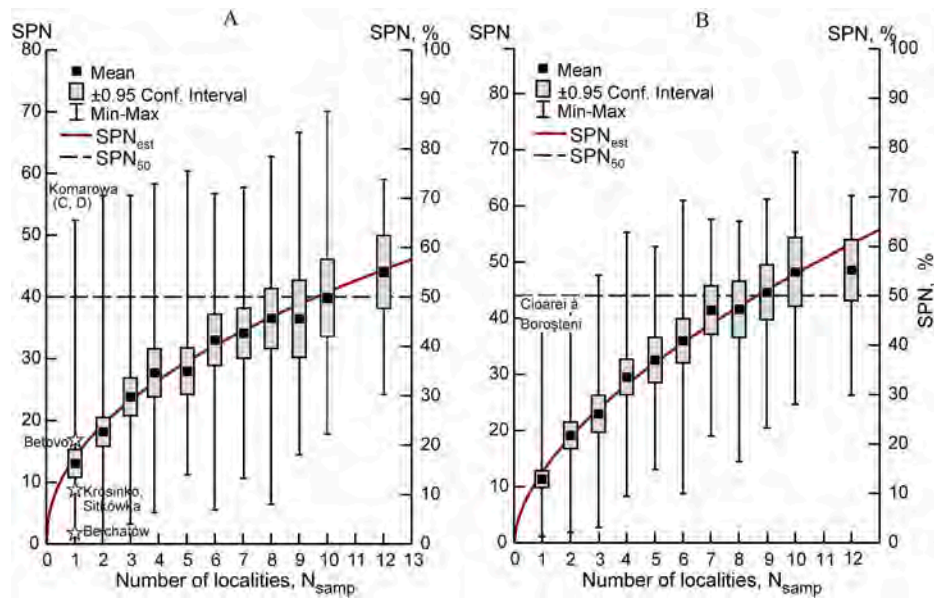


Fig. 13. Species number (SPN) – sample number ( $N_{\text{samp}}$ ) relationship: A – bioregion CEN; B – bioregion CES. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

as proof of fauna evolutions being independent (autonomous) of global climate changes. It is necessary to take into account the length of the time range for which the descriptive models were established. Throughout 200 ka BP the faunas clearly responded to climate changes, but had various contents, directions and consequences. In the north, in CEN bioregion, these processes were a bit more orderly compared to the southern bioregion CES.

Climate changes are usually considered as a driver of mammalian faunas evolution, SPN, and species occurrence variations both in the past and at present (Azanza et al., 2004; Blois et al., 2010; Davies et al., 2011; Brace et al., 2012; Nadachowski et al., 2018; Palombo, 2018; Puzachenko and Markova, 2014, 2019; Morales-Barbero et al., 2021). In our case study, SPN demonstrates a stable link with species composition of mammal assemblage. The maximum of SPN is associated with the Late Pleistocene “mammoth fauna” in both bioregions. This palaeoassemblage fully formed in Central Europe in the MIS3 stage, but reached its greatest prosperity during ~38–28 ka BP (Markova et al., 2010). We have not found an unambiguous correlation between the temperature variable and SPN. In the CES bioregion, SPN correlated negatively with  $\delta^{18}\text{O}$ , while in the CEN bioregion, its dynamics was more complicated and included two independent components. The second coordinates of the models are usually associated with time reversible changes of SPN that correlate with  $\delta^{18}\text{O}$ . A sign of correlation of the

second coordinates with SPN and  $\delta^{18}\text{O}$  are opposite. This means that at least in the Late Pleistocene and the Holocene, SPN was higher in cold periods and lower when climate warmed up. However, this relation is not absolute. In extremely cold periods (MIS6, MIS2), the current species richness decreased. Thus, we proposed the responses of mammal assemblage to global temperature changes were not direct, but mediated by: (1) species composition specifics, which means that previous history of an assemblage is an important factor in itself, (2) geographic positions in relation to the continental ice sheets, the seas/oceans, and (3) a regional orography (Puzachenko and Markova, 2020).

We have previously studied the fauna assemblages of CEN and CES regions on the different time intervals (Puzachenko and Markova, 2019; Markova and Puzachenko, 2021; Puzachenko et al., 2021). The comparison of the data from the Table 5 with the data from the Table 2 shows that diversity of evolution models for the same mammal assemblages and their contents are dependent on the selection of both time range and group of mammals. For example, on the time interval ~50–5 ka BP, climate changes may be considered as the main driver of evolution in both CEN and CES regions. However, a more complex model for the south bioregion CES assumes a factor defining SPN values does not depend on the climate changes. Against the diversity of models described above, a common feature of evolution of mammal assemblages stands out, that becomes noticeable in scale from two and more

Table 5

Spearman rank order correlation coefficients for the coordinates (components: C1, C2, and so on) of descriptive models and explanatory variables (Age,  $\delta^{18}\text{O}$ , SPN) (Puzachenko and Markova, 2019, 2020; Puzachenko et al., 2021). Statistical significance (\* –  $p < 0.01$ ) is based on  $t$ -criteria; N – sample volume.

Region	N	Component of descriptive model								
		C1			C2			C3		
		Age	$\delta^{18}\text{O}$	SPN	Age	$\delta^{18}\text{O}$	SPN	Age	$\delta^{18}\text{O}$	SPN
~50–5 ka BP (all species except bats)										
CEN	31	-0.82*	0.76*	-0.82*	0.07	-0.28	-0.9			
CES	30	-0.77*	0.88*	-0.60*	0.33	0.05	0.55*	0.01	0.04	0.04
~190–60 ka BP (large mammals)										
CEN	10	-0.68*	0.47	0.75*	0.0	-0.1	-0.33			
CES	10	-0.67*	0.13	0.45	0.39	0.32	-0.30			
~190–70 ka BP (small herbivorous mammals)										
CEN	14	-0.03	0.53*	-0.10	0.09	0.60*	-0.32			
CES	14	-0.84*	0.34	0.14	-0.19	-0.10	0.19	-0.34	0.05	0.79*

MIS. Figs. 2–7 illustrate the non-linear nature of the evolutionary process on the whole. This feature reveals in alternate relatively stationary states and non-stationary transitions between them. Thus, evolutionary dynamics of mammal assemblages exhibits a threshold effect, which is characteristic of so-called “non-linear system” (Groffman et al., 2006; Fagre et al., 2009; Seddon et al., 2011).

In context of non-linear dynamics concept, one may interpret stationary areas highlighted in the Figs. 2–7 as fluctuations of a system’s trajectory around some virtual attractor in phase space, which was created by the descriptive model. Then, in general, a self-organisation of a system in time may be described as a motion from one such attractor to the other one. In the beginning, the system abruptly loses stability (threshold effect), and then it shifts, relatively quickly, to a new area of a phase space and forms a new attractor – the rules of adaptation change (Bohórquez Arévalo and Espinosa, 2015). A new attractor corresponds to the changed external (climate or other factors) and/or internal conditions (fauna composition, distribution of species ranges in geographical space, etc.). This evolution is adaptive (a new state of a system is relatively stationary), while such system may be referred to a category of “complex adaptive systems” (Gell-Mann, 1995; Preiser et al., 2018; Phillips and Ritala, 2019).

The descriptive models of separate mammalian guilds, one way or another, differ from those models by the number of coordinates (dimensionality) (Table 3), number of areas with stationary dynamics, duration of intervals with non-stationary dynamics, and contribution of “random walk” into the trajectory of systems in phase spaces (Figs. 4–7). In the both bioregions, the most ordered evolutionary dynamics was found in the guild of carnivorous that situate a top of food chain and then in large herbivorous. The evolutionary pattern of these guilds was most similar to the pattern of full mammal assemblage. We found a significant contribution of “random walk” in the phase space to the dynamics of guilds of small herbivores and especially insectivores. The evolution of small herbivorous, as well as insectivorous is highly specific. Their dynamics include periods of abrupt and “random walk” in the phase space. In the CEN bioregion “chaotic” dynamics type is dominated in both guilds. The guild of insectivorous demonstrates the weakest “evolutionary signal” compared to other mammalian groups. In contrast, SPN of insectivores is higher in the CEN than in the CES. This can be attributed to high sensitivity to dry/humid climate conditions. In accordance with this hypothesis, the drier climate in the south bioregion was less favourable for insectivorous, all other things being equal. We propose, compared to the large mammals, small mammals demonstrate high sensitivity in the environmental changes at relatively short time intervals, but the species composition of this group turned out to be more resilient at long time intervals. These results point out the importance of considering the size of mammals for a forecast of their response to climate changes and environment conditions on the whole (Lyons et al., 2010).

It should be specifically mentioned, that the change of time or space scale of the research might lead to significant change of the descriptive model, including the change of the number of coordinates and their contents. This is not only a particular property of the mammal assemblages under study. Though the inner structure of a living system may be imagined by the form of models in several spatial/temporal scales simultaneously, including the forms of hierarchy, such epistemological reduction does not simplify the system description (Ladyman et al., 2013). Such properties of complex systems as “non-additivity” and practically (i.e. using traditional reductionistic study methods) “irreducibility” of their complexity (= irreducible complexity) are manifested in the impossibility of simply “adding up” particular models for individual guilds of mammals in order to obtain a generalized model for the entire regional assemblage.

This fact that evolutionary models cannot be reduced to each other (uniqueness property) expresses another one property of the complex systems, namely “emergence” (Ladyman et al., 2013). An emergence means that it is impossible to provide adequate description of the

system’s dynamics only at a particular hierarchical level of its organisation, without taking into account how it behaves at “neighbouring” hierarchical levels. In addition, emergence property is manifested in the fact that the number of species in “dynamic cores” (Table 4) is not great compared to the SPN. Hence, the dynamics of the occurrence in majority of species has specific features, which are “hidden” at the level of full assemblage. Probably, in spite of Grayson’s opinion (Grayson, 2007), the “arithmetic” aggregate of knowledge on various species distribution in time does not explain (does not “decipher”) evolutionary trends on the level of mammal assemblages. In the context of understanding of complex systems, the contradiction between hypothesis of “species collectively response” (F.E. Clements’ holistic ecological organicism concept) (Lyons et al., 2010; DeSantis et al., 2012; Cooper et al., 2015; Kirchoff, 2020) and hypothesis of “species-specific responses” (H.A. Gleason’s individualistic concept) (Grayson, 2007; Lorenzen et al., 2011; Graham, 2014; Crees et al., 2016; Palombo, 2018) on a global climate changes may be resolved. We think, both phenomena exist, but they reflect different aspects of evolutionary dynamics in a complex system such as faunal assemblages. These phenomena are not replaced with each other. The emergence, non-additivity and irreducibility properties do not allow a mechanistic extrapolation of the study results between different hierarchical levels of complex systems, or between various spatial/temporal scales, or between various geographical units, etc.

The SPN variable allows to detect another important property for a system in stationary state, namely a scale-invariance (Kwapien and Drozd, 2012). It is described by a power law function:  $AX^b$ , where the exponent,  $b$ , is a scale-invariance constant and it can be related (can change) to the hierarchical structure of a complex system in a general case. On the one hand, it was demonstrated in this study that SPN is non-linearly correlated with time interval length (time scale), but on the other hand, in case when a definite time interval was fixed, it was also non-linearly correlated with a number of localities (a localities number that links with geographical space). Using the relationship between SPN and time interval length, we could evaluate the time interval that characterizes the stationary state of mammal assemblages. It is important because for stationary conditions it is possible to extrapolate carefully the properties of processes or structure in studied system onto other various space/time scales. In addition, parameter  $A$  and scale-invariance parameter  $b$  may be used as biodiversity variables with natural interpretation (Sections 3.4). One may also evaluate representation of particular palaeontological localities in relation to the regional species diversity. In practice, the power laws may not be observed. There may be at least two reasons of it: (1) system’s dynamics is non-stationary, and its trajectory is located far from potential attractor in the modelled phase space, and (2) two or more relatively detached systems are “mixed up” in one study. In the latter case, there is a possibility to search for space/time “borders” of these hypothetical systems. For example, in Fig. 10A, it can be seen that the points form two subsets in the time interval from 0 to ~10 ka. These subsets differ in the average meanings of species richness. It means that in the bioregion CEN at the relatively short time interval, there was a sharp change in species richness accompanied with the change in a rate of fauna composition turnover: a stationary temporal pattern was destroyed. Since that was found in the CEN region only, the phenomenon may be linked with changes of regional fauna in MIS4, if, additionally, take into account information presented in Figs. 9 and 11. In general, a scale invariance property can be used for studying the states of faunal assemblages in both time and space. It is noteworthy, that this approach is close to the method of rarefaction in paleoecology (Tipper, 1979).

As underlined above, the biodiversity parameters (H, D, R) used here depend not on the “real” occurrence of various species in a regional assemblage, but on species distribution in a geographical space. In general sense, this distribution is defined by the sizes of realised ecological niches of species, and not by other factors, such as, for example, the animal size. Hence, the spatial pattern may be interpreted

as a projection of realised ecological niches onto the geographical space, provided all other conditions are equal. Thus, the biodiversity parameters listed above indirectly characterize the ecological structure of regional fauna and its dynamics.

The self-organisation index,  $R$  (Shannon, 1948) is one of the key parameters, which allows to compare not only the states of the same system in time, but also of various ones, including those having different nature. In accordance with a general hypothesis (Foerster and von, 1960), the open system raises the level of internal orderliness ( $R$  increases) in processes so called self-organisation due to consumption of energy and information from environment. Thus, “environment” and “system” should be considered together. In some modern reviews (Marzo Serugendo et al., 2004; Green et al., 2008; Gershenson et al., 2021), the authors pay more attention to internal interactions between system elements. Without entering into the debate, we note several properties of self-organised complex systems: (1) an open system receiving both energy and information about changes in the environment from the environment; (2) functioning without central control, by contextual local interactions; (3) parts and elements of a system achieve a contextual task individually, but a complex collective behaviour emerges from their mutual interactions; (4) ability to change its structure and functionality based on previous experience (evolution) to adapt to changes in internal and environmental conditions; (5) its dynamics is usually nonlinear (some more details see (Bohórquez Arévalo and Espinosa, 2015)). In general, the above list of properties may be well applied to mammal assemblages and their evolution.

In practice, aside for artificial systems created by man to perform the predefined functions, a growth of an internal order in a system may not be observed strictly. Self-organisation systems may both increase or decrease their internal orderliness. In the mammal assemblages under study, high values of  $R$  do not correlate to the periods of stationary states. Overall,  $R$  does not contain information about specific, contextual minor mechanisms that were the cause of system's transition from one state to another. More important for understanding the internal orderliness of a system is variability of  $R$  (in theory,  $R$  may change from 0 to 1). As  $R$  grows, one may expect either stronger impact onto spatial pattern of internal interactions in a system or increasing the impact of ecological factors. Various combinations of this phenomenon may exist. Low  $R$  values mean low level of interactions inside a system, more random, and even chaotic ( $\sim R < 0.1$  (Beer, 1959)) size distribution of ranges. One should specifically stress, that in our case study  $R$  never exceeded the “critical value”  $\sim 0.31\text{--}0.37$ , which equally means that  $R$  did not exceed the value of “internal orderliness”, at which the hypothetical ecological system has lower fitness and low probability of realization (more details see in (Zorach and Ulanowicz, 2003; Ulanowicz, 2009, 2018) and (Puzachenko, 2016)).

Why do complex systems such as biological ones, as a rule, not reach a higher level of internal orderliness (determinism) and why do they limit themselves with  $\sim 30\text{--}40\%$  from what is possible? One of the acceptable phenomenological explanations is as follows: this relatively low level of internal determinism gives them an opportunity (opportunity only!) for adaptation to unpredictable changes in the environment.

## 6. Conclusions

Compared to our previous studies of Central European mammal fauna, the results of this study expand and deepen the understanding of evolution in the regional assemblages, different “guilds” of mammals (carnivorous, large and medium size herbivorous, small herbivorous, and insectivorous) and historical dynamics of biodiversity within the time interval  $\sim 200\text{--}5$  ka BP (MIS7–MIS1). It was discovered that the evolution of mammal assemblages is characterized by the following properties: (1) nonlinearity, (2) combination of two types of non-equilibrium states, alternating in the evolutionary time, – stationary and non-stationary ones, (3) combination of irreversible (evolutionary *per se*) and reversible changes in time, (4) combination of ordered and

chaotic dynamics, (5) threshold like effects, (6) possibility to present at several space/time scales simultaneously, (7) time/space scale-invariance property for stationary states, (7) emergency, and (8) elements of adaptive dynamics as a response to environmental conditions changing.

We suppose, from theoretical and practical points of view, that the results of this study are best interpreted within the framework of broad concept of a “non-linear self-organising complex system” with an ability of adaptive behaviour (Cilliers, 1998; Heylighen, 1999; Holden, 2005; Ladyman et al., 2013; Ma'ayan, 2017). Internal organisation of such non-linear “quasi-deterministic” systems justifies their existence and evolution in an area at a borderline between ordered and chaotic dynamics and thus intrinsically unpredictable.

## Author contributions

AYu proposed the main research idea, contributed the results of data processing and prepared most of the manuscript. AM and KP contributed new data of several Late Pleistocene sites. All authors discussed the data and the results, participated in the preparation and improvement of the manuscript.

## Data availability

The basic data presented in this manuscript is available in Supplemental materials (Appendices 1–4). Any additional data is available on request.

## 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.2021.11.009>.

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