



## Mammal fauna during the Late Pleistocene and Holocene in the far northeast of Europe

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The paper summarises materials on the mammal remains in northeastern Europe, dated by radiocarbon. Altogether, 23 local faunas of small mammals and 47 local faunas of large mammals were analysed. Multidimensional statistical analysis shows a strong correlation between changes in small mammal fauna composition and climate changes throughout time. The correlations with the spatial gradients, however, are less pronounced. The faunas are classified into three groups: (1) faunas of Holocene age; (2) Late Pleistocene 'stadial' assemblages; and (3) Late Pleistocene 'interstadial' assemblages. In some cases, changes in species abundance are better understood in terms of biotic interrelations rather than of climatic effects. The most pronounced change in small mammal fauna composition and structure occurred at the Preboreal/Boreal boundary, and a less conspicuous alteration took place at the LGM/Lateglacial transition. The most noticeable transformation in the large mammal fauna composition is dated to the early Holocene. Less significant changes are observed at the Middle Weichselian/LGM transition and at the LGM/Lateglacial transition. It is safely concluded that variations in the faunas of small and large mammals recorded in NE Europe during the last 35 000 years occurred synchronously and unidirectionally.

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A vast area of northeastern Europe is of particular interest to palaeozoologists because of its location near the centres of Pleistocene glaciations. From north to south, the region stretches over several biomes. Moreover, this area consists of two distinct parts: the western plain and the eastern, mountainous area. Because of this there is a considerable diversity of animals in different parts of the region, so that the faunal history of several contacting biomes can be studied here in detail. A large volume of data has been obtained from the Polar Urals (Smirnov *et al.* 1999; Smirnov & Golovachov 1999; Golovachov & Smirnov 2009; Svendsen *et al.* 2010), the SubPolar Urals (Ponomarev 2005), the Northern Urals (Kuzmina 1971; Guslitser *et al.* 1990; Kosintsev 1991, 2007a; Kochev 1993; Smirnov 1996; Ponomarev 2001; Bachura & Kosintsev 2007), the West Uralian (Permian) forelands (Kuzmina 1975; Fadeeva & Smirnov 2008) and the Timan Ridge (Ponomarev *et al.* 2005; Kryazheva & Ponomarev 2008). The descriptions of either the local faunas or the faunal changes in the various regions are presented in these publications. However, many of the local faunas analysed in these publications have not been radiocarbon-dated.

Recently, new local faunas have been described, and new radiocarbon dates have been obtained for previ-

ously recovered material. This has resulted in a large volume of data, forming part of the COMSEC ('Collapse of the Mammoth Steppe Ecosystem') project (<http://www.mammothsteppe.com>). These materials enable the investigation of both large and small mammal faunas during the Late Pleistocene and the Holocene across the entire territory of northeastern European.

Another recent extensive data set on palaeovegetation was gathered within the framework of the project 'The evolution of the mammalian fauna and flora in Western, Central and Eastern Europe during the Pleistocene–Holocene transition (25–10 kyr B.P.)' (Markova *et al.* 2008). These data were used to compare faunal history with environmental and climatic changes.

Although there are palaeozoological data on certain areas and time-slices, the generalized history of fauna of the entire region still needs to be investigated. In particular, the development of small and of large mammal faunas needs to be compared in order to find specific features and changes. Here we analyse these groups using different approaches: a quantitative method is used for the small mammals, and a more qualitative method for the large mammals. Statistical

methods are applied to identify parameters describing the composition of the small mammal fauna for various locations of NE Europe. They reveal trends in these faunal compositions, which are correlated with changes in climate and geographical location. We compare the results obtained using principal component analysis with those obtained by non-metric multidimensional scaling. Each technique is assessed for its effectiveness in describing the spatio-temporal evolution of the fossil assemblages on the basis of palaeontological data.

## Regional settings

It is customary to define the northeast of Europe as a vast region extending from south to north for ~1000 km (from the Severnye Uvaly Ridge, at 60°N, to the coasts of the Barents Sea), and from the Mezen River in the west to the Urals in the east. In our analysis, we include the northern part of the Permian region, as far south as 58°N.

The region is usually divided into two parts (Isachenko 1964a; Obedkov 1995), each with a distinct relief and geological structure: the eastern (mountainous) part belongs to the Urals, while the rest is part of the Russian Plain.

The modern climate of this region is controlled by the near Arctic Ocean, remote from the Atlantic; it is strongly influenced by arctic air masses and by cyclones. A cold-temperate (boreal) climate is typical of the major part of the region; the climate is known for its long and rather severe winters and for its short, relatively warm summers (Ovchinnikova 1964; <http://meteo.infospace.ru/climate/html>).

The climatic parameters change gradually with latitude, but changes are large enough to be used for analysis. The climate of the region is excessively wet, with annual precipitation exceeding evaporation.

The northernmost part of the region lies in the tundra and forest-tundra zones. The rest belongs to the taiga, and all the taiga subzones (northern, middle and southern) are present here. In addition to the observed changes in landscape with latitude, certain trends in environmental characteristics can be traced from west to east: the climate continentality increases and the Siberian elements become increasingly significant in the biota (Isachenko 1964b).

Together with brief descriptions of the ecology of modern species, the present-day mammal populations of the various biomes in the European Northeast are given in Tables S1 and S2 in the Supporting Information (Ognev 1950; Kulik 1972; Estaf'ev 1994, 1998; Gromov & Erbaeva 1995; Petrov 2002). Not all modern species are included in Table S2 – only those that were also found in the studied localities. In the tundra zone, riparian (intrazonal) species are present in addition to the tundra animals, with some species of the taiga

faunal assemblage in the south (*Sicista betulina*, *Microtus agrestis*, *Clethrionomys rutilus*, *Clethrionomys glareolus*, *Ursus arctos*, *Gulo gulo*, *Lutra lutra*). Various investigations, such as the trapping of wild animals, the analysis of pellets of rough-legged buzzards (*Buteo lagopus*) and the faeces of polar foxes, have shown that the most abundant mammals in this zone are *Dicrostonyx torquatus*, *Lemmus sibiricus* and *Microtus gregalis* (Kulik 1972; Estaf'ev 1994, 1998; Voronin 1995; Polezhaev 1998; Petrov 2002). *Arvicola terrestris* and *Clethrionomys rutilus* are also common here.

Mammals of the forest-tundra usually belong to the taiga faunal assemblage; there are also some intrazonal species, including one tundra rodent, *Lemmus sibiricus*. The taiga zone is inhabited by representatives of the taiga faunal assemblage and some intrazonal species (Turyeva *et al.* 1977; Turyeva & Balibasov 1982; Bobretsov *et al.* 2005; Petrov & Poroshin 2005).

## Material and methods

Our study includes 23 local faunas of small mammals and 47 local faunas of large mammals. They are listed in Tables 1 and 2. Figure 1 shows a map of the region, with all localities indicated. The material for the larger mammals includes local faunas from cave localities (Table 2) (Kuzmina 1971, 1975; Ponomarev 2001), dated single finds (Pacher & Stuart 2009; Svendsen *et al.* 2010; Campos *et al.* 2010a, b) and remains recovered from archaeological sites (16 localities) (Kosintsev 1991; Ponomarev 2001). Only the localities with numerous remains of larger mammals are listed in Table 2. The dates obtained for the faunal assemblages and the individual bones are listed in Table S3. By the term local fauna, we mean that the taxa are recovered from one layer (or several conventional horizons) (Smirnov 2003). With one exception (Kur'yador), all local faunas of micromammals have been recovered from localities of a single taphonomic type, namely, the zoogenic deposits in karst caverns.

For comparison purposes, some data from the literature on modern small mammal remains recovered from predatory bird pellets and polar fox faeces in the tundra zone were included in the analysis (Voronin 1995; Polezhaev 1998). In addition, recent material obtained from breeding places of avian predators in the taiga zone (Smirnov 2003) was included.

The following categories were used to describe small mammal assemblages: (1) very abundant species (30% or more); (2) abundant (10–29.9%); (3) common (1–9.9%); (4) rare (0.2–0.9%); and (5) very rare (less than 0.2%) (Smirnov *et al.* 1990).

The term 'small mammals' is used here for animals up to hare-size, with the exception of marmots and species of the *Mustela* and *Martes* genera.

The data on small mammals were analysed using a multidimensional statistical approach. We assumed

Table 1. Frequencies (%) of micromammalian remains from localities in the European Northeast. 1 = Shezhim, modern (Smirnov & Sadykova 2003); 2 = Pikhtovka, modern (Smirnov & Sadykova 2003); 3 = Polar fox 1 (Polezhaev 1998); 4 = Polar fox 2 (Polezhaev 1998); 5 = Rough-legged buzzard pellets, modern (Voronin 1995); 6 = Bolshaya Makhnevskaya (Fadeeva & Smirnov 2008); 7 = Pymvashor, layer 3 (Smirnov *et al.* 1999); 8 = Kamen' Koziy (Fadeeva & Smirnov 2008); 9 = Pymvashor, layer 4 (Smirnov *et al.* 1999); 10 = Pizhma 1, layer 5 (Ponomarev *et al.* 2005); 11 = Sokoliny, layer 2 (Ponomarev 2005); 12 = Pymvashor, layer 5 (Smirnov *et al.* 1999); 13 = Makhnevskaya 2, horizon 6 (Fadeeva & Smirnov 2008); 14 = Medvezhaya, brown loam A (Smirnov 1996); 15 = Sedyu 1 (Kryazheva & Ponomarev 2008); 16 = Rasik, horizon 21 (Fadeeva & Smirnov 2008); 17 = Pymvashor, layer 6, upper part (Smirnov *et al.* 1999); 18 = Rasik, horizon 24 (Fadeeva & Smirnov 2008); 19 = Rasik, horizon 27 (Fadeeva & Smirnov 2008); 20 = Medvezhaya, brown loam B (Smirnov 1996); 21 = Pymvashor, layer 6, lower part (Smirnov *et al.* 1999); 22 = Makhnevskaya 2, horizon 9 (Fadeeva & Smirnov 2008); 23 = Kur'yador (Kochev 1993).

Species	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23
<i>Desmana moschata</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Talpa europae</i>	-	-	-	-	-	2.35	-	-	-	-	-	-	-	-	0.06	-	-	-	-	-	-	-	-
<i>Ochotona pusilla</i>	-	-	-	-	-	-	-	3.3	-	0.1	-	-	-	-	2.31	1	-	0.3	-	-	-	1	-
<i>Sciurus vulgaris</i>	29.3	16.5	-	-	-	0.7	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Sicista</i> sp.	-	-	-	-	-	0.4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Cricetulus migratorius</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	0.1	-	2.4	-	1.5	1.7	-	-	-	0.7
<i>Cricetus cricetus</i>	-	-	-	-	-	-	-	-	-	-	-	-	0.1	-	-	-	-	-	-	-	-	-	-
<i>Spermophilus</i> sp.	-	-	-	-	-	-	-	0.2	-	-	-	-	0.1	-	-	-	-	-	-	-	-	-	-
<i>Clethrionomys rufocanus</i>	8	10.3	-	-	-	27.2	17.7	3.3	0.6	0.6	9.9	-	0.9	1.32	1.16	-	-	-	-	0.3	-	-	0.3
<i>Clethrionomys</i> ex gr.	12	5.2	-	-	-	40.3	15.6	10.0	0.6	0.2	10.4	-	2	1.99	5.07	0.3	-	-	-	0.5	-	-	0.7
<i>rutilus-glaucolus</i>	-	-	-	-	-	-	0	-	-	-	-	-	0.2	-	-	2	-	1.7	2.3	-	-	-	0.3
<i>Lagurus lagurus</i>	-	-	27.03	22.36	46.51	-	4.1	0.1	56.4	43.1	5.4	45.6	25.6	17.88	2.25	42.1	89.5	48.4	57.4	73.9	93.5	33.9	62.5
<i>Dicrostonyx</i> sp.	-	-	52.7	46.58	9.3	-	4.1	-	21.2	17.3	14.6	35.9	19.4	27.81	55.65	4	9.3	2.2	2.4	10.4	6.5	25.7	29.17
<i>Lemmus sibiricus</i>	13.3	8.2	-	-	-	20.8	8.8	5.3	6.7	2.1	3.8	-	-	3.97	0.51	-	-	-	-	1	-	-	-
<i>Myopus schisticolor</i>	10.7	46.4	10.8	9.94	25.28	5.9	12.9	2.0	1.7	0.2	0.1	-	4.5	1.0	8.92	0.3	-	-	-	-	-	0.6	-
<i>Arvicola terrestris</i>	-	-	5.4	20.49	13.95	-	2	41.1	10.6	35.6	33.9	18.5	26.5	32.5	9.11	45.9	1.1	45.9	35.6	13.7	-	26.2	8.3
<i>Microtus gregalis</i>	14.7	8.2	2.7	-	-	2.3	32	15.0	1	0.4	10.4	-	13.6	6.5	9.82	2	-	-	-	-	-	5	-
<i>Microtus oeconomus</i>	10.7	2.1	1.35	0.6	-	1.8	2.0	19.6	0.6	0.4	7.5	-	1.0	7.0	3.4	-	-	-	-	-	-	0.2	-
<i>Microtus agrestis-arvalis</i>	-	-	-	-	-	-	0.7	-	0.6	-	3.8	-	2.9	-	1.67	-	-	-	-	0.3	-	4.2	-
<i>Microtus middendorffii</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Number of remains	75 <sup>1</sup>	97 <sup>1</sup>	-	-	554	170	841	177	3294	704	195	1992	1557	1065	354	1750	1018	198	77	1340	120	-	-

<sup>1</sup> Maximum number of the same molar.

Table 2. Number of megamammalian remains from localities in the European Northeast. 1 = Medvezh'ya cave, inside gallery; 2 = Bysovaya; 3 = Bliznetsov; 4 = Zaozer'e; 5 = Mamontova Kur'ya; 6 = Medvezh'ya cave (brown loam 'B'); 7 = Ladeyniy; 8 = Tchernie Kosty; 9 = Surya IV; 10 = Surya III; 11 = Rasik (horizon 27); 12 = Rasik (horizon 24); 13 = Rasik (horizon 21); 14 = Medvezh'ya cave (brown loam 'A' and grey loam); 15 = Drovatnitskiy (layer 3). SA = Subatlantic.

Species	Middle Valdai					Late Valdai 1 (LGM)		Late Valdai 2 (LGT)							SA
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	
<i>Lepus timidus</i>			55	1		4343	+	1		+	208	345	558	411	89
<i>Castor fiber</i>															19
<i>Marmota bobak</i>			5												
<i>Canis lupus</i>		2	2		1	208	+				1	5	5	103	
<i>Alopex lagopus</i>		1	33			1003	+			+	31	66	36	103	
<i>Vulpes vulpes</i>						10								1	
<i>Ursus arctos</i>			1				+				2		2	3	
<i>Ursus spelaeus</i>	1														
<i>Martes zibellina</i>						9							1	6	
<i>Gulo gulo</i>			1			11									
<i>Mustela eversmannii</i>			7			21								2	
<i>Mustela erminea</i>			1			32	+				6	28	48	2	
<i>Mustela nivalis</i>						18	+				15	54	131	2	
<i>Meles meles</i>															1
<i>Lynx lynx</i>													1		
<i>Panthera spelaea</i>						6						1		7	
<i>Equus sp.</i>		1	79		1	337	+	80	4		4	4	13	606	
<i>Coelodonta antiquitatis</i>		3	17	1		77	+	2	4	+			1	1344	
<i>Alces alces</i>			1					2						2	
<i>Rangifer tarandus</i>		30	211	1	7	3198	+	20	6	+	64	110	155	86	
<i>Bison priscus</i>			2	1		28	+	10		+	1		5	11	
<i>Saiga tatarica</i>	1			15		40	+			+	4	1	2	1	
<i>Ovibos moschatus</i>			1	6		181								18	
<i>Mammuthus primigenius</i>		2447	1	1	7	109	+	2						42	

that the mammal assemblages are complex, and that their composition and ecological structure are affected by a large number of natural factors. It is often difficult to identify the dominating factors, in particular when dealing with past ecosystems that have no modern natural analogues – such as the Pleistocene mammoth steppe. The local assemblages can be described using variations in the frequency of occurrence of the individual species belonging to a particular assemblage.

The input data are the taxon distributions per locality studied. For every locality, the data were processed using the so-called Fisher transformation (Plokhinsky 1970). This takes into account the fact that rare and occasional species are less likely to be recovered from the excavated deposits, under otherwise equal conditions. This formalism is used to approach a normal distribution as closely as possible.

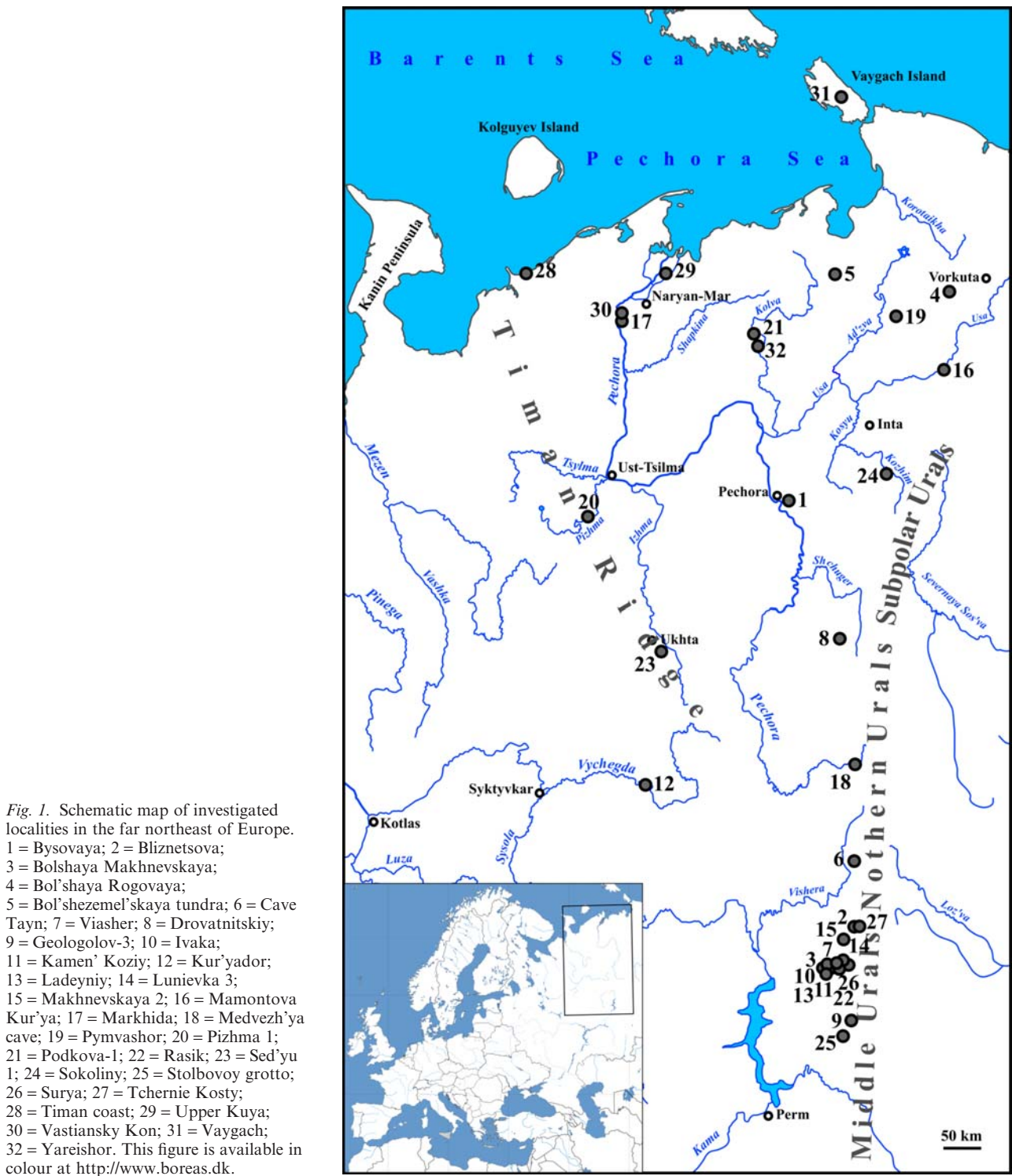
Subsequently, the data were processed using (i) principal component analysis (PC) and (ii) non-metric multidimensional scaling (MDS) (Kruskal 1964; Davison & Jones 1983; James & McCulloch 1990). We calculated two matrices with the geometric distance and the so-called Kendall rank correlation between each pair of localities. These matrices were then processed using MDS. In this paper, we denote the principal components as PC. The MDS parameters obtained using geometric (Euclidean) distances are denoted as E, and

those of the Kendall rank correlations as K. Both methods describe relationships between the studied objects; the optimum number of virtual factors is determined by applying the technique developed by Puzachenko (2001).

The large mammal fauna compositions were analysed by another approach, in which only qualitative methods were applied. Various chronological intervals were analysed, determined by the taphonomic heterogeneity of the large mammal localities. The large mammal sites include zoological deposits in small caves (rockshelters), alluvial localities and archaeological sites. All locations in rockshelters and the Upper Palaeolithic archaeological and alluvial sites are dated by radiocarbon. The younger archaeological sites (from the Mesolithic to the Medieval period) are dated by radiocarbon and/or by artefacts. For northeastern Europe, a detailed archaeological periodization has been developed (Ashikhmina *et al.* 1997), which allows faunas to be dated by means of archaeological material with reasonable accuracy. For the Younger Dryas, Preboreal and Boreal periods, isolated large mammal bones are sparse, and therefore it is not possible to perform a thorough analysis for these time intervals.

The climatic data used in our analysis are based on the  $^{18}\text{O}$  isotope records from the Greenland ice sheet NGRIP (Andersen *et al.* 2006; Rasmussen *et al.* 2006;





Svensson *et al.* 2006; Vinther *et al.* 2006). Part of this record is used as shown in Fig. 2. Note that the ice-core chronologies for NGRIP are published in b2k, defined as calendar years relative to AD 2000 ('before 2000').

Time scales are denoted in different units, depending on dating techniques and conventions. Radiocarbon

dates are published in defined BP units, based on internationally agreed conventions on half-life value, standardization and isotopic fractionation correction (e.g. Mook & van der Plicht 1999). Radiocarbon dates are calibrated into calendar years using the presently recommended calibration curve IntCal09 (Reimer *et al.*

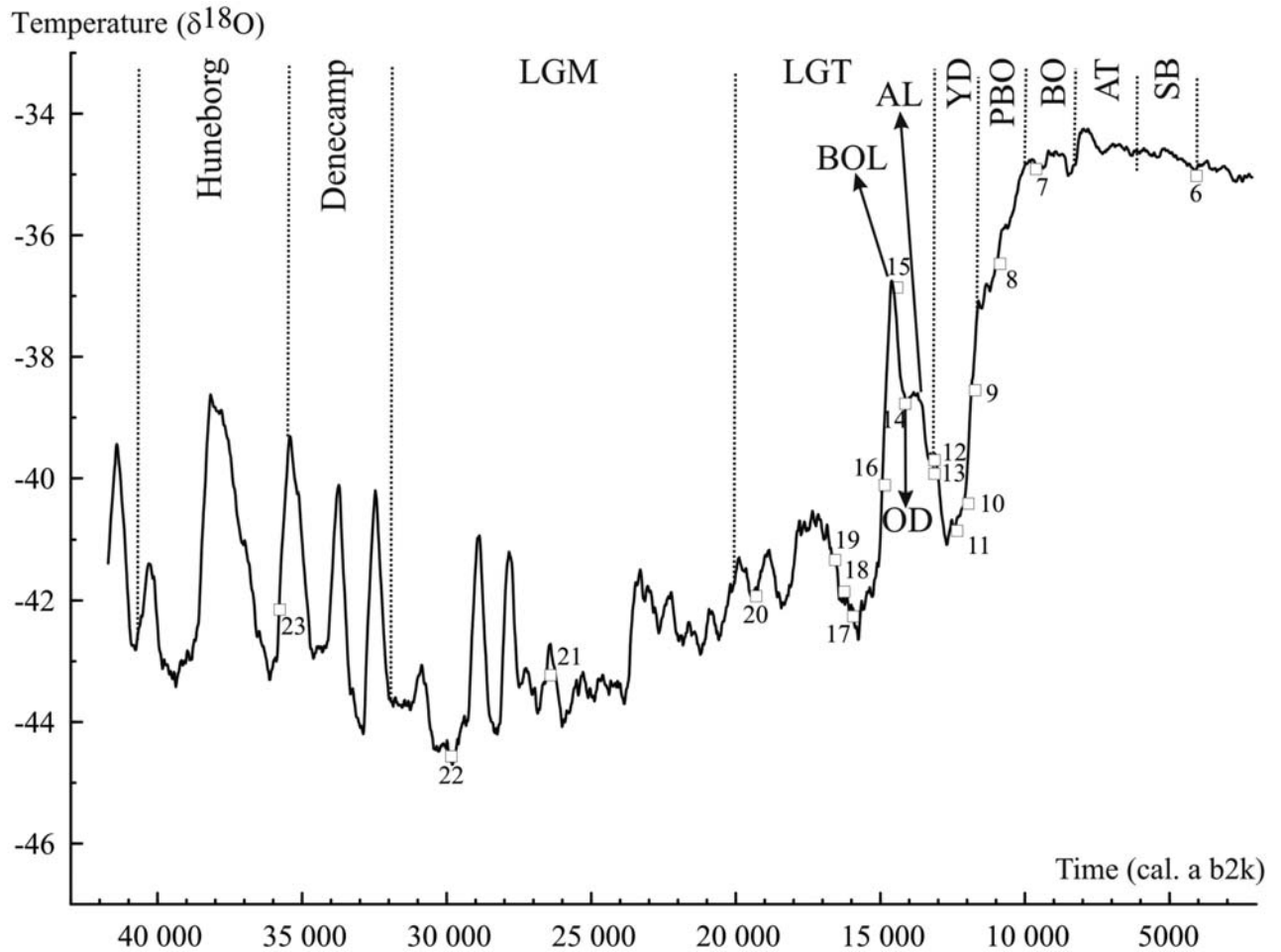


Fig. 2. Position of localities on time and temperature (NGRIP1) scales. cal. a b2k = absolute time scale (AD 2000) after Rasmussen *et al.* (2006). Indications of climate stages see in the text; localities numbers as in Table 1.

2009). Calibrated  $^{14}\text{C}$  dates are denoted in cal. a BP, that is, calendar years relative to AD 1950. Thus, cal. a BP = cal. a BC + 1950 (Mook 1986).

In this work, we have chosen the same time intervals as those in the COMSEC project (numbers in  $^{14}\text{C}$  years BP): (i) the late part of the Middle Valday, 35 000–24 000; (ii) the Last Glacial Maximum (LGM), 24 000–17 000; (iii) the Lateglacial Transition (LGT), 17 000–12 700; (iv) the Bølling–Allerød Interstadial Complex (BAIC), 12 700–10 950; (v) the Younger Dryas (YD), 10 950–10 150; (vi) the Preboreal period of the early Holocene (PB), 10 150–9000; (vii) the Boreal period of the early Holocene (BO), 9000–8000; (viii) the Atlantic and Subboreal periods of the middle Holocene (AT–SB), 8000–2500; and (ix) the Subatlantic period of the late Holocene (2500–200) (SA).

## Results

We found that for the matrix of the Euclidean distances, the optimum number of MDS parameters is 4,

while for the distance matrix based on the Kendall rank correlation this number is 5. The combinations of these parameters describe most (up to 98%) of the variations in locality occurrence for most species (Table 3: square of the coefficients of multiple regression). In addition, they describe the radiocarbon age of the localities well, as well as the geographical location (latitude and longitude), and the temperature (via  $\delta^{18}\text{O}$ ). When applying principal component analysis, five parameters were again used, which describe 55–94% of the species occurrence frequency, 69% and 62% of the latitude and longitude (respectively) variation, 39–40% of the radiocarbon age variation and 79% of the temperature variation (Table 3).

According to data shown in Table 3, for abundant taxa (such as *Dicrostonyx* sp., *Microtus gregalis*, *Arvicola terrestris*, *Lemmus sibiricus*), the Euclidean distance parameters reproduce the input frequencies better than the MDS parameters based on rank correlation and principal components. In the case of rare species (average occurrence frequency less than 1%),

Table 3. Correlation between frequencies of main taxa, geographic coordinates of the locality, dates, temperature, axes of MDS and principal components. E = MDS axes for Euclidean matrix; K = for Kendall distances matrix; PC = principal components.

Taxa	Average frequency of taxa in locality (%)	Coefficient of multiple correlation			Pearson correlation coefficient		
		E (4 axes)	K (5 axes)	PC (5 components)	E1	K1	PC1
<i>Dicrostonyx</i> sp.	32.9	0.99	0.92	0.87	-0.90	-0.78	-0.77
<i>Microtus gregalis</i>	18.4	0.96	0.83	0.87	-0.24	-0.29	-0.42
<i>Lemmus sibiricus</i>	15.7	0.97	0.76	0.74	-0.24	-0.30	-0.30
<i>Arvicola terrestris</i>	6.7	0.92	0.82	0.91	0.52	0.41	0.57
<i>Microtus oeconomus</i>	5.6	0.71	0.77	0.80	0.68	0.63	0.62
<i>Clethrionomys</i> ex gr. <i>rutilus-glareolus</i>	4.8	0.92	0.80	0.97	0.74	0.74	0.74
<i>Clethrionomys rufocanus</i>	4.2	0.93	0.86	0.96	0.77	0.76	0.80
<i>Sciurus vulgaris</i>	3.6	0.81	0.78	0.73	0.57	0.55	0.59
<i>Myopus</i> sp.	3.4	0.95	0.92	0.98	0.81	0.86	0.85
<i>Microtus agrestis-arvalis</i>	2.6	0.73	0.87	0.92	0.58	0.60	0.53
<i>Microtus middendorffii</i>	0.6	0.42	0.83	0.75	0.10	0.03	0.03
<i>Ochotona pusilla</i>	0.3	0.58	0.78	0.86	0.22	0.22	0.10
<i>Cricetulus migratorius</i>	0.3	0.69	0.88	0.95	-0.28	-0.38	-0.44
<i>Lagurus lagurus</i>	0.3	0.70	0.84	0.95	-0.29	-0.39	-0.44
Latitude		0.71	0.81	0.83	-0.19	0.02	0.03
Longitude		0.67	0.77	0.79	0.28	0.13	0.14
<sup>14</sup> C date		0.63	0.62	0.63	-0.59	-0.60	-0.56
<sup>14</sup> C calibrated date		0.64	0.64	0.64	-0.61	-0.63	-0.58
T, d <sup>18</sup> O (‰) <sup>1</sup>		0.86	0.91	0.89	0.84	-0.63	-0.58

<sup>1</sup>Average for confidence interval of calibrated date.

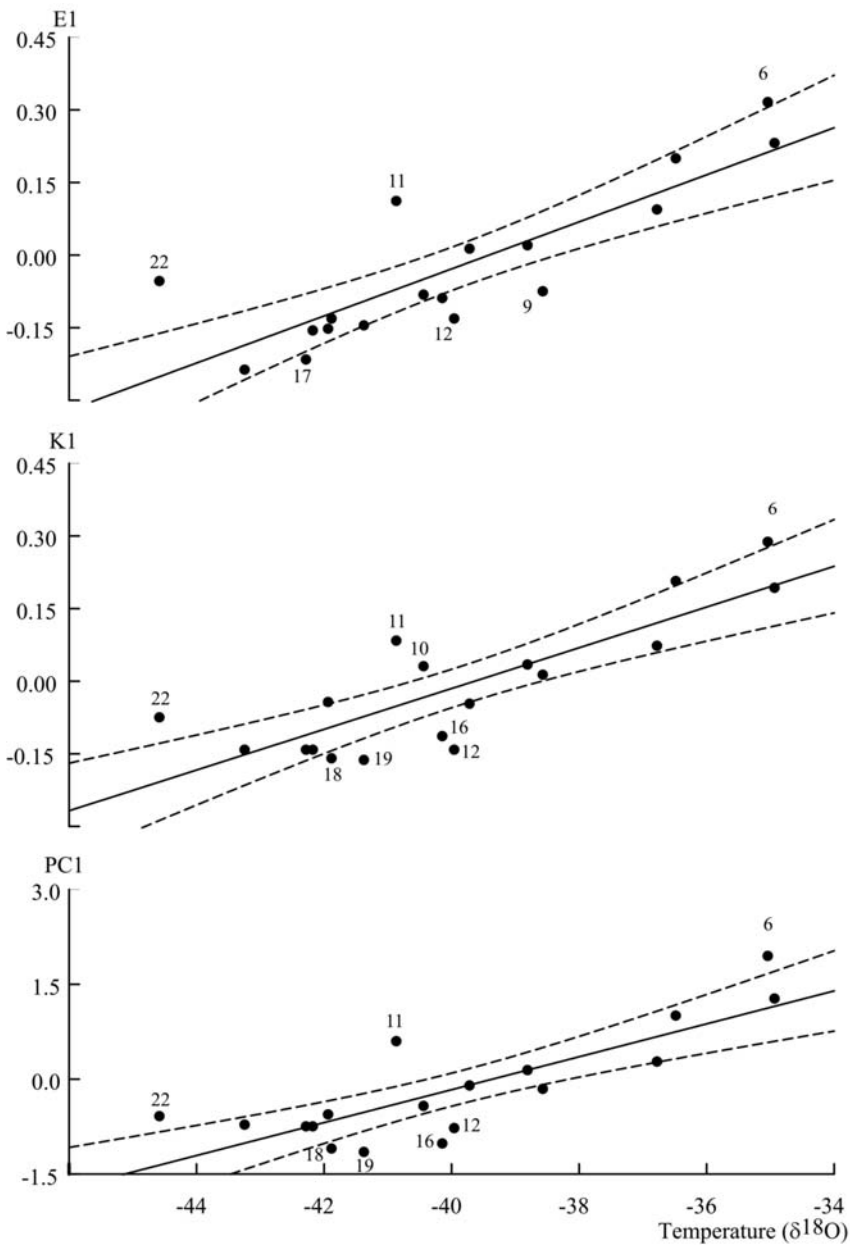
the second method (i.e. the MDS-based Kendall correlation, as well as the principal components) turned out to be preferable.

Table 4 shows the virtual parameters containing information on the evolution of faunal assemblages as related to changes in global climate (Fig. 3). All statistical variables indicate that the first component (E1, K1, PC1) is the most significant (Table 4). This component reveals a correlation between the composition and the structure of the local small mammal faunas, as well as between the temperature and latitudinal location.

Analysis of data from Table 4 shows that several parameters can describe the spatial variations of the mammal assemblage composition independently of the global climate changes; these parameters are E2, E4, K2, K3, K4, PC2 and PC3. The other parameters (K5, PC4 and PC5) do not correlate either with climate change or with the geographical position of the sites. Parameter K5 shows a partial correlation with the occurrence frequency of Middendorff's vole, PC4 with that of the water vole and the Siberian lemming, and PC5 with that of Middendorff's vole.

Table 4. Spearman's rank correlation coefficients for trend factors (MDS axes, principal components), geographic coordinates of the locality and <sup>14</sup>C dates.  $r/r^2$  = multiple coefficient of linear correlation/determination of the factor with geographic location and global temperature. Main variables are shown in descending order of their significance.

Factor	Latitude	Longitude	<sup>14</sup> C, cal.	T, d <sup>18</sup> O	$r/r^2$	Main variables
E1	-0.09	0.34	-0.78	0.80	0.91/0.82	Temperature, longitude
E2	0.70	-0.49	0.17	-0.10	0.69/0.47	Latitude, longitude
E3	0.06	0.24	-0.21	0.31	0/0	-
E4	-0.56	0.16	0.14	0.08	0.41/0.16	Latitude
K1	0.14	0.27	-0.76	0.73	0.85/0.72	Temperature, longitude
K2	-0.39	-0.18	0.38	-0.35	0.49/0.24	Latitude, longitude
						temperature
K3	-0.61	0.41	-0.03	0.19	0.63/0.39	Latitude
K4	0.26	-0.47	0.00	0.24	0.41/0.17	Longitude
K5	-0.29	-0.15	0.10	-0.07	0/0	-
PC1	0.25	0.25	-0.72	0.68	0.86/0.75	Temperature, longitude
PC2	0.46	-0.50	0.34	-0.41	0.67/0.46	Temperature, longitude, latitude
PC3	0.67	-0.13	-0.24	0.14	0.65/0.42	Latitude
PC4	0.18	0.07	-0.08	0.15	0/0	-
PC5	0.0	-0.26	0.06	0.08	0/0	-



*Fig. 3.* Correlation between temperature and main factors (E1, K1, PC1), describing changes of small mammal communities. The local faunas above the 95% confidence interval show warmer appearance; below – colder. Indications as in Fig. 2.

The generalized linear model (GLM), which includes both the temperature and the geographical coordinates, accounts for 72 to 82% of the variations in parameters describing the principal pattern in variability of the composition of the local fauna in the region (Table 3,  $r^2$ ). Here, we focus on those aspects of the faunal assemblage evolution that are common to all localities.

Figure 4 shows the successive changes of the composition of small mammal assemblages in the European northeast during the Late Pleistocene–Holocene, which are reproduced by the first MDS parameter (E1) and the first principal component factor (PC1). As discussed above, these factors reflect the faunal changes

that correlate with the changes in temperature (bottom graph in Fig. 4). The assemblages resembling that of recent tundra in composition and structure are distributed during the Late Pleistocene up to 15 ka BP and are correlated with the most severe climatic conditions. The palaeo-assemblage composition, however, was essentially different from the modern one because of the presence of species dwelling in the steppe and forest-steppe, such as the steppe pika, an inhabitant of the dry shrub steppe and forest-steppe, the grey hamster, and the steppe lemming, a dweller of the herb steppe and semi-desert.

The modern taiga mammal faunas coincide with those of the Holocene mammal faunas after *c.* 5 ka BP.



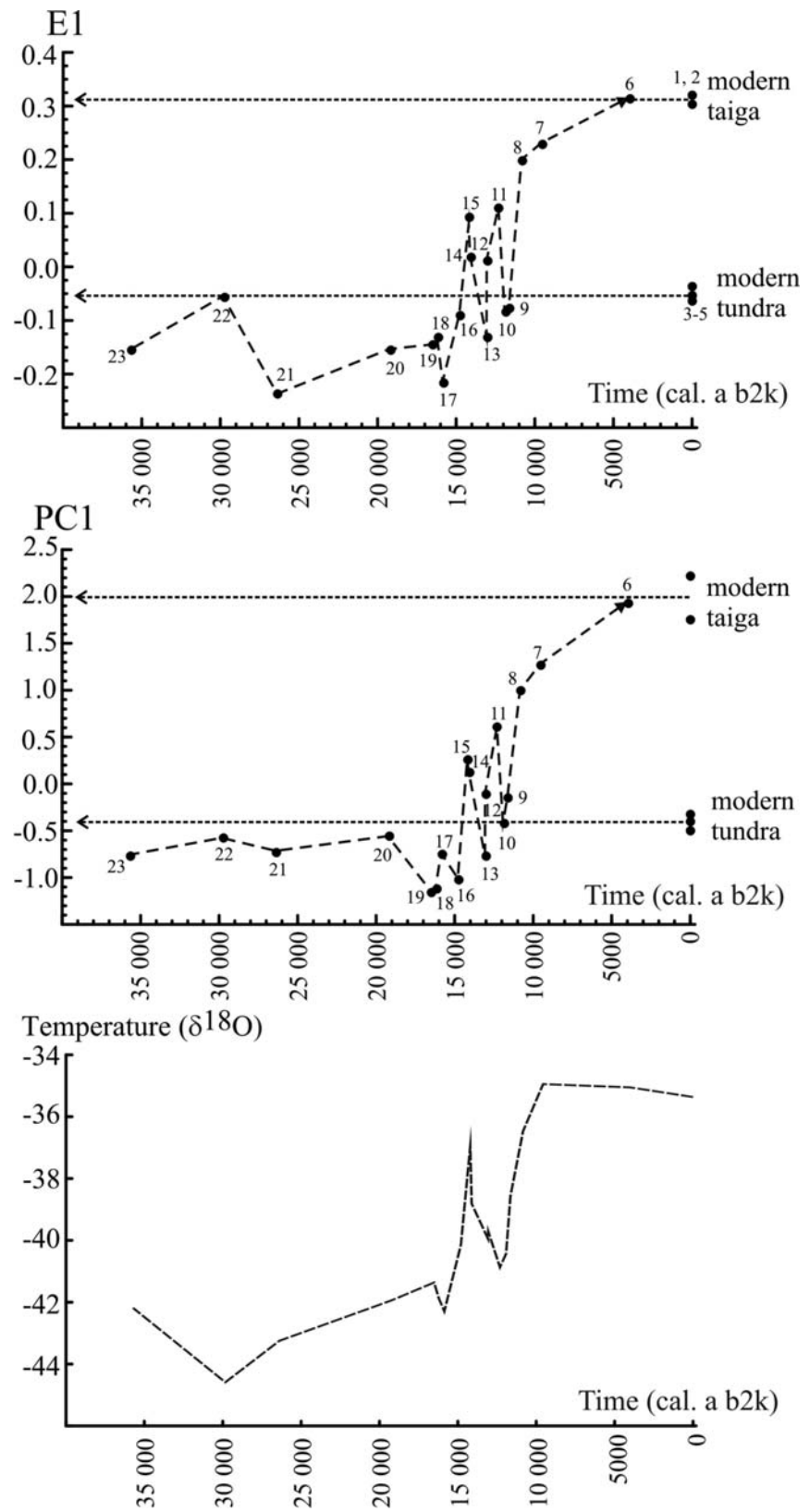


Fig. 4. Changes in composition of the small mammal assemblages reproduced by the first MDS axes (E1) and first principal component factor (PC1) on the temperature and time scales used in NGRIP1. Indications as in Fig. 2.

In this case, the species composition and the ecological structure of the small mammal communities are almost identical. The graphs in Fig. 4 show a general trend: the faunas of open landscapes have a tendency to be gradually replaced by forest faunas from the early Holocene against the background of climate warming.

There are occasional deviations from this trend, sometimes rather conspicuous, that can be attributed to the specific geographical position of the locality in question. This is illustrated by the response of the fauna to the Younger Dryas cooling. Despite the general cooling trend, the mammal community in the SubPolar Urals (Sokoliny locality; number 11 in Fig. 4) was still 'temperate' in its characteristics, which is normally associated with forest-tundra assemblages. In contrast, in the north of the region (Pymvashor locality, layer 5; number 13 in Fig. 4) the small mammal faunas retained their characteristics in composition and structure from the maximum Pleistocene cooling through the warming of the Bølling–Allerød. Only the later Holocene warming (Pymvashor, layer 3; number 7 in Fig. 4) resulted in the spread of taiga forests over the area; later, the taiga degraded in response to cooling.

Thus, the local geographical conditions mean that the response of the mammal communities to global climatic changes are not synchronous, and form the basis of the natural zonal structure. This first appears as a gradient from west to east, followed later by one from north to south as well. The Ural Mountains evidently have a profound impact on the region; their presence permitted the persistence of relatively rich faunas through the extremely cold intervals owing to the presence of numerous local micro-biotopes.

The history of the small mammal assemblages (Fig. 4) can be divided into three chronological stages. The first stage, which spanned the coldest period of the Late Pleistocene, ended at *c.* 15 ka BP. The second stage covers the Pleistocene–Holocene transition and is characterized by sharp and opposing changes in the assemblage composition; the changes correspond to drastic short-term fluctuations of the global climate (Older and Younger Dryas cool intervals, Bølling and Allerød warm intervals). However, a trend can be recognized through the fluctuations. The mammal assemblages were changing their composition from 'tundra-steppe' type to 'forest-tundra' and then further to 'taiga' type. The third stage, the Holocene, is characterized by dominant forest and intrazonal (mostly riparian) species in the assemblages. The peak in the 'taiga' assemblages in the region coincides with the Holocene climatic optimum (*c.* 7–6 ka BP). It is worth noting that definite forest-tundra characteristics were recorded in the rodent assemblages in the north of the region (Pymvashor, layer 3) as early as the beginning of the Holocene, at the Preboreal/Boreal boundary; the assemblages were closer in composition to those of the modern taiga than to those of the present-day tundra.

As a result of our multidimensional analysis, the localities can be classified into three main clusters (Fig. 5): (1) Holocene localities; (2) sites of Pleistocene age attributed to extremely cold periods; and (3) Pleistocene localities belonging to intervals with a milder global climate, including all the tundra-like faunas. In Makhnevskaya Cave, the fauna of layer 9 suggests warmer conditions than those reconstructed for that time interval. The Pizhma 1 and Sokoliny localities were included in cluster 3 for the same reason.

In the group of Holocene localities (three in total), one (Koziy, 1b) stands alone as corresponding to a colder climate of the Holocene inception, as indicated by the dominance of narrow-skulled voles (*Microtus gregalis*) in the assemblage. Furthermore, the southernmost locality in cluster 2 (Rasik 2b) differs from the others in composition; it features a sizeable number of steppe species against a rather low proportion of collared lemming.

In Fig. 6, each cluster is plotted as a function of taxon occurrence. In the faunas of cluster 1, forest species are dominant, with their proportion showing a regular increase from cluster 1b to 1a. The rodent communities of cluster 2 are dominated by the collared lemming, which is typical for the extremely cold climate of the arid arctic desert and tundra.

In the faunas of cluster 3, the dominant species are the Siberian lemming (*Lemmus sibiricus*) and narrow-skulled vole. In addition, meadow voles (*Microtus*) and red-backed voles (*Clethrionomys*) are present in small quantities. It should be noted that the desman found in the Sed'yu locality belongs to that cluster. This desman finding indicates the presence of water bodies that did not freeze to the bottom, as well as the presence of trees and shrubs along floodplains.

Multidimensional analysis not only enables the study of general aspects of the changes in micromammal assemblage within the framework of a single model, but also provides an insight into the specific features of individual species trends. All species of small mammals can be classified into two groups: species for which the abundance is controlled mainly by climatic changes, and those influenced mainly by other factors (Table 5).

A distinguishing characteristic of the first group is the strong correlation of species occurrence with the main geographic and climatic indicators (E1, K1, PC1; Table 5). This group consists primarily of abundant and more common species, such as *Dicrostonyx*, *Clethrionomys rufocanus*, *Myopus*, *Arvicola terrestris*, *Microtus oeconomus*, *Microtus agrestis* and *Clethrionomys rutilus-glareolus*. However, the second and third most frequently occurring species (the narrow-skulled vole and Siberian lemming) do not appear to be strongly dependent on climate. The species-indicators of dry environments (grey hamster, steppe lemming, pika) also appear to be distinctive and relatively independent of the main climatic trends.

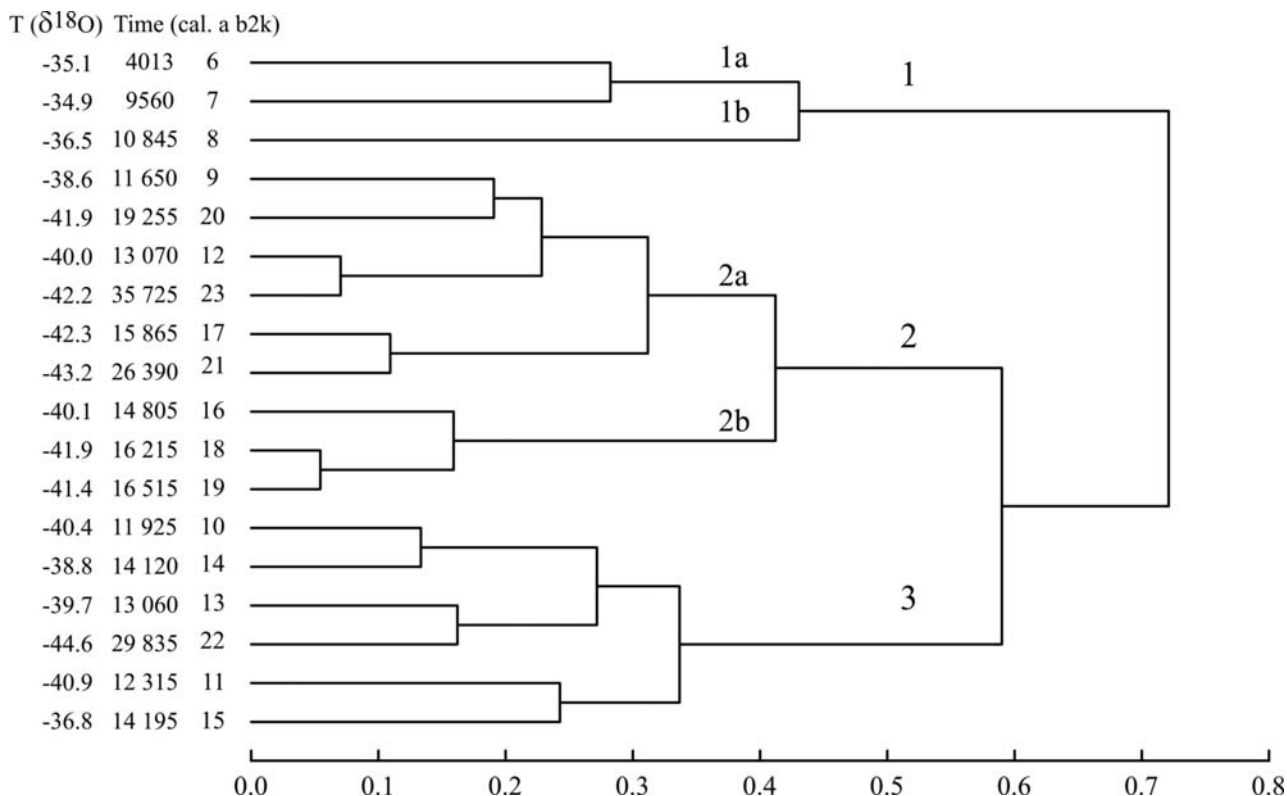


Fig. 5. Classification of the localities ('distant neighbour' method, Euclidean metrics) on the basis of axes of multidimensional scaling (E1–E4, K1–K5). Indications as in Fig. 2.

Analysis of the variation in large mammal species composition over time (Table 6) shows the existence of two distinct faunal assemblages in northeastern Europe (Mammoth and Holocene assemblages). The Mammoth assemblage persisted up to the Younger Dryas. The Holocene assemblage existed at least since the beginning of the middle Holocene. The data available on the mammal faunas of the Younger Dryas, Preboreal and Boreal are rather scarce and do not permit a detailed analysis of the transition from the Mammoth assemblage to that of the Holocene.

## Discussion

### *Small mammals*

This section discusses the history of the small mammal fauna composition through several time-slices. The choice of time-slices was based on commonly accepted intervals identified in the evolution of the environment and climate, without special consideration for key moments in the transformation of the fauna.

*Middle Valdai.* – The oldest small mammal assemblage considered was recovered from the Middle Valdai deposits in the Kur'yador locality (Kochev

1993) and from a horizon between the Middle Valdai and the LGM in the Makhnevskaya 2 cave, horizon 9 (Fadeeva & Smirnov 2008). The small mammal assemblage in Kur'yador is dominated by collared lemmings and narrow-skulled voles (39% each), while the proportion of Siberian lemming is slightly lower (22%), indicating relatively harsh environments. In the fossil assemblage from the Makhnevskaya 2 cave (horizon 9), tundra species prevail, including the collared lemming, Siberian lemming and narrow-skulled vole, in approximately equal quantities (34, 26 and 26%, respectively). Other species are present in smaller proportions, such as Middendorf's vole (4%), red-backed voles (*Clethrionomys*, 1%), root vole (*Microtus oeconomus*, 5%), water vole (*Arvicola terrestris*, 0.6%), pika (*Ochotona*, 1%), *Cricetulus* (0.7%), steppe lemming (*Lagurus*, 0.3%), and field vole (*Microtus agrestis*, 0.2%).

It is noteworthy that most of the species from those assemblages are cold-tolerant, which suggests the presence of tundra-like landscapes. Middle Valdai spores and pollen are found in radiocarbon-dated peat at the Kur'yador locality (Guslitser & Duryagina 1983; Duryagina & Konovalenko 1993). The analysis of that sequence made it possible to recognize six phases in the vegetation evolution, including warm intervals when

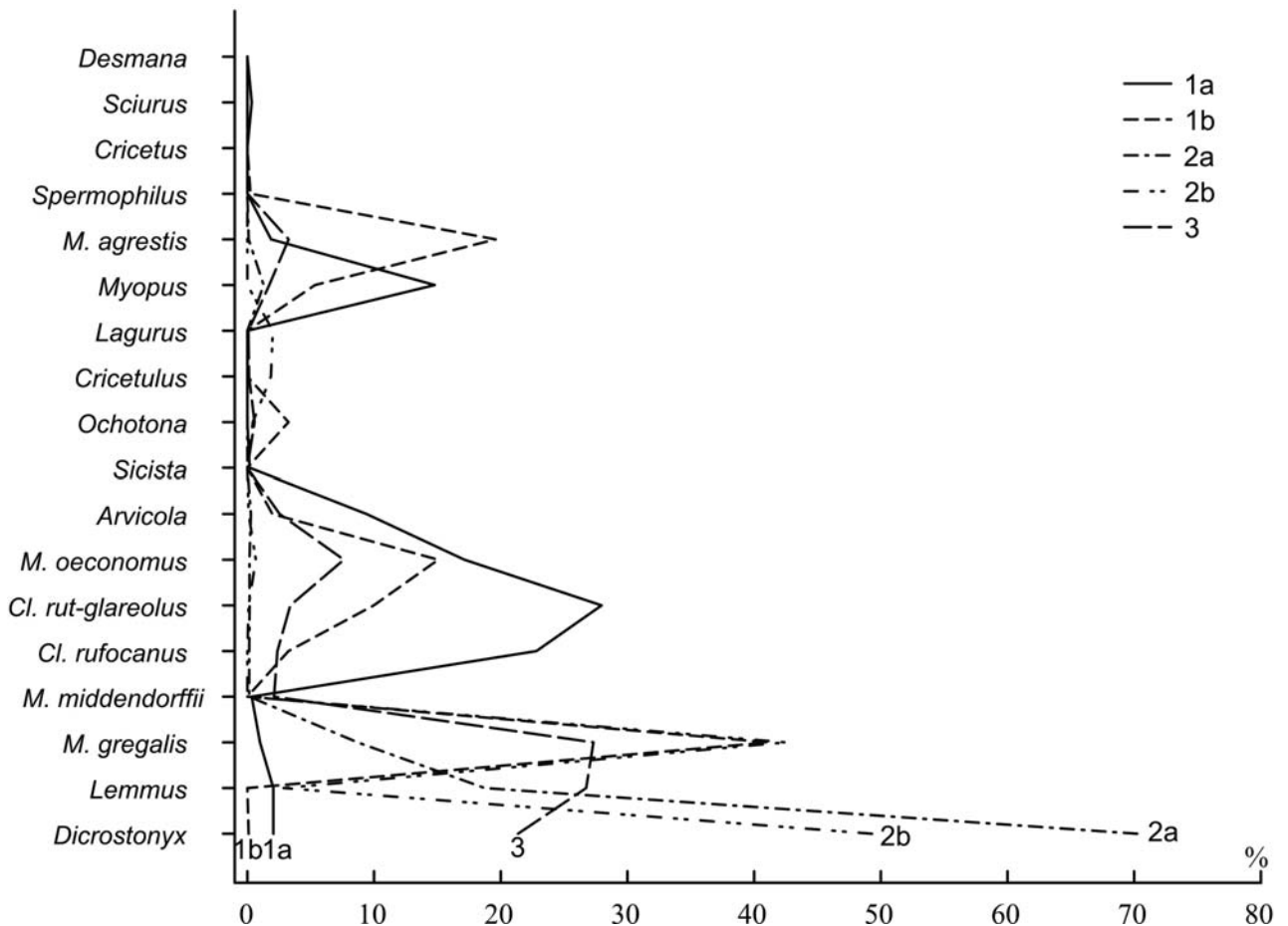


Fig. 6. Characteristics of composition of the micromammalian fauna of various clusters.

the north taiga and forest-tundra communities were widely spread over the region and cold intervals when they were replaced by tundra communities with steppe xerophytes. The climate was colder than today, even at the climatic optimum of that interstadial, and the region was dominated by treeless or poorly forested landscapes. Unfortunately, because a clearly defined chronology of the warm and cold phases during the Middle Valday in the region is lacking, it is difficult to correlate a particular faunal assemblage with a particular climatic event with certainty.

**LGM.** – The LGM period in the faunal history is correlated with material obtained from layer 6 in the Pymvashor locality (Smirnov *et al.* 1999) and with brown loam ‘B’ in Medvezh’ya (Bear) cave (Smirnov 1996). Only three rodent species (collared and Siberian lemmings and narrow-skulled vole) have been found in layer 6 at Pymvashor. The collared lemming remains are not just the most numerous but are clearly dominant: they account for nearly 90% of all the identified molars. The remaining 10% are from Siberian lemmings (9%) and narrow-skulled voles (1%). The

fossil assemblage recovered from brown loam ‘B’ of Medvezh’ya cave is somewhat different from the above assemblage in composition and ecological structure. The remains of eight small mammal species have been found there. Again, the collared lemming is the most abundant (74%), followed by the narrow-skulled vole (14%) and Siberian lemming (10%). The wood lemming (*Myopus* sp.) can be considered as a common species (1%), while the two species of red-backed voles (*Clethrionomys*) and Middendorf’s vole are rare (less than 0.6% each). Apparently, that stage in the micromammalian history is noted for a composition of impoverished species, with one cryoxerophilous species (collared lemming) being dominant; such a composition may have resulted from the extreme climatic conditions, which were most severe at this time.

The composition of the fossil assemblages agrees well with palaeoenvironmental reconstructions, which are indicative of the coldest climate for the entire period. At the LGM, the European northeast was characterized by shrub tundra with local patches of forest-tundra or tundra-steppe vegetation, as well as periglacial tundra-forest-steppe, a combination of tundra and

Table 5. Coefficients of Spearman's rank correlation for frequencies of the most abundant species and factors of spatio-temporal trends in the composition of communities.

Factor	<i>Dicrostonyx</i>	<i>L. sibiricus</i>	<i>M. gregalis</i>	<i>M. middendorffii</i>	<i>Cl. rufocanus</i>	<i>Cl. rutilus-glaucobus</i>	<i>M. oeconomus</i>	<i>A. terrestris</i>	<i>O. pusilla</i>	<i>C. migratorius</i>	<i>L. lagurus</i>	<i>Myopus</i>	<i>M. agrestis</i>	<i>S. vulgaris</i>
E1	-0.97	-0.22	-0.18	0.21	0.83	0.83	0.84	0.79	0.04	-0.25	-0.25	0.72	0.90	0.58
E2	0.09	0.33	-0.80	-0.10	-0.15	-0.24	-0.19	0.34	-0.47	-0.54	-0.54	-0.10	-0.09	0.15
E3	-0.23	0.77	0.44	0.41	0.03	0.03	0.25	0.09	0.27	-0.03	-0.04	-0.15	0.31	-0.53
E4	-0.33	0.17	0.27	-0.04	-0.17	-0.11	0.15	0.52	0.31	0.28	0.27	-0.30	0.13	0.04
K1	-0.84	-0.24	-0.27	0.26	0.93	0.91	0.80	0.62	0.04	-0.45	-0.46	0.90	0.87	0.58
K2	0.15	-0.64	-0.24	-0.56	-0.24	-0.22	-0.37	-0.16	-0.09	0.32	0.32	-0.10	-0.43	0.51
K3	-0.46	-0.07	0.45	0.34	0.17	0.33	0.55	0.25	0.57	0.61	0.60	-0.10	0.33	-0.07
K4	-0.19	0.17	-0.46	0.14	-0.14	-0.14	0.10	0.66	-0.28	-0.13	-0.14	-0.13	0.10	0.22
K5	0.03	0.06	0.40	-0.64	-0.33	-0.34	-0.17	-0.18	0.29	-0.06	-0.05	-0.13	0.06	-0.15
PC1	-0.82	-0.22	-0.41	0.24	0.90	0.84	0.78	0.74	-0.12	-0.53	-0.53	0.83	0.88	0.58
PC2	0.41	0.03	-0.61	-0.55	-0.41	-0.53	-0.63	-0.04	-0.57	-0.44	-0.43	-0.18	-0.45	0.23
PC3	0.11	0.49	-0.45	0.08	0.01	-0.06	-0.14	-0.08	-0.45	-0.61	-0.61	0.09	0.07	-0.10
PC4	-0.29	0.54	-0.03	0.24	0.05	-0.00	0.28	0.49	0.04	-0.26	-0.26	-0.16	0.33	-0.15
PC5	-0.10	0.27	0.21	-0.49	-0.21	-0.22	-0.03	0.05	0.37	-0.31	-0.32	-0.03	0.18	-0.13

steppe communities with small areas of open forests of pine and birch (Grichuk 1982; Simakova & Puzachenko 2008a).

*Lateglacial.* – The Lateglacial is characterized by material recovered from horizons 27, 24 and 21 of the Rasik rockshelter (the Perm Region, western forelands of the Urals) (Fadeeva & Smirnov 2008). The remains of nine small mammal species have been found there, including the collared lemming (42–57%), Siberian lemming (2–4%), narrow-skulled vole (35–46%), red-backed vole (0.3%), water vole (0.3%) and root vole *Microtus oeconomus* (2%), as well as the steppe lemming (1.7–2.3%), pika (0.3–1%) and grey hamster (1.5–2.4%). A distinctive feature of those assemblages is a more steppe-like structure, with collared lemming and narrow-skulled vole both dominating, and the presence of some steppe species (pika, grey hamster and steppe lemming). The assemblages consist of moderately cryophilic and xerophilic (steppe-like) species. These data on mammals contradict the results of pollen studies (Arslanov *et al.* 1981; Grichuk 1982; Simakova & Puzachenko 2008b). Most of the latter references define the Lateglacial as a period with prevailing periglacial forest-tundra, that is, a combination of shrub tundra, pine and birch open woodlands and tundra-steppe vegetation (mostly in the north), along with pine-birch and pine-spruce open forests (in the south), with patches of tundra and meadow.

*Bolling-Allerød interstadial complex.* – The assemblages dated to this interval are known from localities in the extreme north (Pymvashor, layer 5), in the south (Makhnevskaya 2 cave, horizon 6), and in the central part of the region (Sed'yu 1; Medvezh'ya, the brown loam layer A). They show remarkable regional variations. Layer 5 at Pymvashor (Smirnov *et al.* 1999) yielded remains of collared lemming (46%), Siberian lemming (36%) and narrow-skulled vole (19%). The fauna from Makhnevskaya 2, horizon 6 (Fadeeva & Smirnov 2008), is dominated (77%) by tundra species (in a broad sense, including the narrow-skulled vole) in equal proportions. Specific for this fauna (as distinct from other assemblages of the same age) is the presence of steppe species (0.5%), such as the grey hamster, steppe lemming and *Spermophilus*, along with forest (4%) and near-water (18%) species. The fauna from brown loam A in Medvezh'ya cave has a similar composition (Smirnov 1996). There are also co-dominant species, such as the collared lemming (18%), Siberian lemming (28%) and narrow-skulled vole (33%) in the assemblage, as well as some remains of forest (13.3%) and near-water (7.5%) species.

The fauna recovered from the Sed'yu 1 locality is markedly different. It comprises 16 small mammal species belonging to three orders: rodents, lagomorphs and insectivores. The remains of Siberian lemming far



Table 6. Large mammal taxa of the European Northeast during the Late Pleistocene and Holocene. ‘+’ = species found; ‘-’ = species not found; ‘±’ = species not found, but its presence is highly probable; ‘?’ = species not found, but its absence is highly probable.

Species	Pleistocene					Holocene		
	MW	LGM	LGT	BØ-AL	YD	PB-B	AT-SB	SA
<i>Lepus timidus</i> L.	+	+	+	+	+	+	+	+
<i>Castor fiber</i> L.	+	-	-	-	?	+	+	+
<i>Marmota bobak</i> Müller	+	-	-	-	?	?	-	-
<i>Canis lupus</i> L.	+	+	+	+	+	+	+	+
<i>Alopex lagopus</i> L.	+	+	+	+	+	+	+	+
<i>Vulpes vulpes</i> L.	+	-	+	+	±	±	+	+
<i>Ursus arctos</i> L.	+	-	+	+	±	+	+	+
<i>Ursus spelaeus</i> Rosenmüller	+	-	-	-	-	-	-	-
<i>Ursus savini</i> Andrews	+	-	-	-	-	-	-	-
<i>Martes</i> sp.	+	-	+	+	?	+	+	+
<i>Gulo gulo</i> L.	+	+	+	+	+	+	+	+
<i>M. erminea</i> L.	+	+	+	+	+	+	+	+
<i>M. nivalis</i> L.	+	+	+	+	+	+	+	+
<i>M. eversmanni</i> Lesson	+	+	+	+	±	±	-	-
<i>M. putorius</i> L.	-	-	-	-	-	±	+	+
<i>Meles meles</i> L.	-	-	-	+	?	±	+	+
<i>Lynx lynx</i> L.	-	-	+	+	?	±	+	+
<i>Panthera spelaea</i> Goldfuss	+	+	+	+	?	?	-	-
<i>Mammuthus primigenius</i> Blumenbach	+	+	+	+	±	?	-	-
<i>Equus</i> sp.	+	+	+	+	±	?	-	-
<i>Coelodonta antiquitatis</i> Blumenbach	+	+	+	+	?	?	-	-
<i>Cervus elaphus</i> L.	+	-	-	-	?	?	-	-
<i>Alces alces</i> L.	+	-	+	+	?	+	+	+
<i>Rangifer tarandus</i> L.	+	+	+	+	+	+	+	+
<i>Bison priscus</i> Bojanus	+	+	+	+	+	±	-	-
<i>Saiga tatarica</i> L.	+	+	+	+	+	±	-	-
<i>Ovibos moschatus</i> Zimmermann	+	+	+	+	+	±	-	-

exceed those of all other species in abundance (61.5%): desman, collared lemming, wood lemming, narrow-skulled vole, root vole, Middendorf’s vole, red-backed voles, European water vole, steppe pika and field vole. In our opinion, the specific features of that assemblage are the result of specific natural environments as well as of taphonomic factors. This fossil assemblage represents a very specific type of community with a clear predominance of cryohydrophilous species, such as the Siberian lemming. Close analogues of this fauna can be found among modern communities inhabiting the northern arctic tundra (Petrov 1994, 2002).

According to palynological data (Arslanov *et al.* 1981; Grichuk 1982; Nikiforova 1982; Velichko *et al.* 1997, 2002; Simakova & Puzachenko 2008c), shrub tundra and periglacial forest-tundra, locally with patches of tundra-steppe, dominated northeastern Europe. Most common were communities with *Betula nana*, *Salix*, *Ericales*, *Hippophae rhamnoides*, *Juniperus*, *Rubus*, *Helianthemum*, *Armeria*, *Sphagnum* and *Selaginella*, along with pine-birch. Taking into account the latitudinal variations, the structure of small mammal assemblages is in reasonable agreement with the pollen-based reconstructions of vegetation; the specific features of the Sed’yu 1 fauna require further investigation.

*Younger Dryas.* – The assemblages assigned to the Younger Dryas are known from layer 5 of the Pizhma 1 rockshelter (Ponomarev *et al.* 2005) and layer 2 of the Sokoliny rockshelter (Ponomarev 2005). In layer 5 of Pizhma 1, a large fraction of all remains (nearly 96%) is accounted for by three species: the collared lemming (46.4%), Siberian lemming (18.6%) and narrow-skulled vole (30.7%). Moreover, other remains have occasionally been found, including that of the wood lemming (*Myopus*) (2%), red-backed voles (*Clethrionomys*), field vole (*Microtus agrestis*), root vole (*Microtus oeconomus*) and water vole (*Arvicola terrestris*) (not more than 0.6% each). It can easily be seen that the structure of the community from layer 2 of the Sokoliny rockshelter is quite different from that of Pizhma 1. This assemblage is also dominated by tundra species, but their proportion is lower (only 57.8%, with the narrow-skulled vole prevailing in this group (34%)). Forest species account for 31.7%, and meadow species for 10.5%.

On the whole, the cold-tolerant composition of the assemblages in the central and northern parts of the region suggests mostly cold and dry conditions. As follows from palynological data, the Younger Dryas cooling resulted in the birch forests becoming more and more open, while the tundra and steppe plant communities penetrated into the free areas (Arslanov *et al.*

1981; Nikiforova 1982; Velichko *et al.* 1997, 2002; Kremenetsky *et al.* 1998; Kaakinen & Eronen 2000; Bohncke 2008; Golubeva 2008). Shrub tundra and larch–pine–birch woodlands developed along with the steppe communities.

*Preboreal.* – Two faunal assemblages dated to the Preboreal are known in the region: the Koziy locality (Fadeeva & Smirnov 2008) and layer 4 of the Pymvashor locality (Smirnov *et al.* 1999). The Koziy fauna is of a peculiar type, dominated by the narrow-skulled vole (41%); *M. agrestis-arvalis* (19.6%), root vole (15%), red-backed voles (13%), wood lemming (5%), pika (3%), water vole (2%), ground squirrel *Spermophilus* (0.2%) and collared lemming (0.1%) have all been collected. The assemblage may be described as forest-steppe, and, more specifically, as moderately xerophilous.

The assemblage from Pymvashor layer 4 resembles that from layer 5 of Pizhma 1. At the latter site, the following assemblage was found: collared lemming (49.1%), Siberian lemming (21.2%), narrow-skulled vole (10.6%), wood lemming (6.7%), root vole (1.1%), water vole (1.7%) as well as red-backed and field voles (0.6% each). During the Preboreal, the shrub tundra was succeeded by forest-tundra floristic associations; locally, there existed pine–birch forests, sometimes with spruce, alternating with tundra-steppe communities. It should be noted that, in the north of Eastern Europe, floristic elements of the periglacial tundra-steppe persisted in the vegetation until the Boreal (Arslanov *et al.* 1981; Nikiforova 1982; Velichko *et al.* 1997, 2002; Kremenetsky *et al.* 1998; Kaakinen & Eronen 2000; Simakova & Puzachenko 2008d; Golubeva 2008).

*Boreal.* – The Boreal fauna is known from layer 3 of Pymvashor (Smirnov *et al.* 1999), where an essentially all-forest assemblage was found, which included the remains of red-backed voles (33.3%), root vole (32%), water vole (12.9%), wood lemming (8.8%), collared lemming (4.1%), Siberian lemming (4.1%), narrow-skulled vole (2%), field vole (2%), Middendorf's vole (0.7%) and northern birch mouse (*Sicista betulina*). As can be observed from this list, the forest and riparian species are dominant, while the proportion of tundra dwellers is insignificant.

During the Boreal period, the taiga forests became the prevalent vegetation type; they expanded northwards as far as the arctic sea coast (Arslanov *et al.* 1981; Nikiforova 1982; Velichko *et al.* 1997, 2002; Kremenetsky *et al.* 1998; Kaakinen & Eronen 2000; Simakova & Puzachenko 2008c; Golubeva 2008).

*Subboreal.* – The Subboreal assemblage was recovered from the deposits of Bolshaya Makhnevskaya cave (Fadeeva & Smirnov 2008), located in the extreme south of the region (in the Uralian forelands). The

assemblage is completely dominated by red-backed voles (68%); the proportion of wood lemming is also considerable (21%), while squirrel (0.7%), field vole (2%), water vole (6%), root vole (2%) and northern birch mouse (0.4%) are present in much smaller amounts. Such an appearance of a small mammal assemblage is typical for the taiga zone for the entire Holocene since the Boreal period.

One more climatic optimum is recorded during the Subboreal. At that time, dark coniferous forests, and also broadleaf trees, spread over the greater part of the territory. The southern taiga biome reached as far as 64–65°N, and the northern taiga expanded to the coasts of the Barents Sea. In the southernmost areas there were subtaiga forests of broadleaf species (Surova *et al.* 1975; Arslanov *et al.* 1981; Nikiforova 1982; Velichko *et al.* 1997, 2002; Kremenetsky *et al.* 1998; Kaakinen & Eronen 2000; Golubeva 2008).

#### Large mammals

The species composition of the Mammoth assemblage varied with time during the period considered. Different assemblages existed at different chronological intervals.

The Middle Valdai interval is noted for the greatest species diversity in the assemblage. It included 24 species, such as cave bear (*Ursus spelaeus*), small cave bear (*Ursus savini*), red deer (*Cervus elaphus*) and beaver (*Castor fiber*); those species do not occur in the faunas of the LGM or LGT. Both species of cave bear became extinct at the boundary of the Middle Valdai and LGM (Pacher & Stuart 2009). The LGM assemblage characteristically included 15 species (Table 6). Note that remains of fox (*Vulpes vulpes*), brown bear (*Ursus arctos*), and species of the genus *Martes*, which commonly occur in other Late Pleistocene faunas, have not been found here. That variant of the Mammoth mammal assemblage was the poorest in species composition.

During the Lateglacial, the large mammal fauna became slightly more diversified in species composition owing to the appearance of fox (*Vulpes vulpes*), brown bear (*Ursus arctos*), moose (*Alces alces*) and some species of the *Martes* genus. The fauna included 20 species altogether (Table 6). The species diversity of the assemblage increased in the Bølling–Allerød interval, when the European badger (*Meles meles*) appeared.

The data on the Younger Dryas fauna are scarce. Radiocarbon dates have been obtained from the bones of bison (*Bison priscus*, 10 255±90 a BP, TUa-1396; Svendsen *et al.* 2010), saiga (*Saiga tatarica*, 10 345±55 a BP, AAR-11364; Campos *et al.* 2010a) and musk ox (*Ovibos moschatus*, 10 755±65 a BP, AAR-12058; Campos *et al.* 2010b) recovered from Medvezh'ya cave. Some dates obtained from mammoth bones (*Mammuthus primigenius*) are known from the adjacent

territories of the northern Russian Plain, and Yamal and Gydan peninsulas; most of them date to *c.* 10 ka BP (Arslanov *et al.* 1982; Stuart *et al.* 2002; Yashina 2002). It seems that mammoth inhabited NE Europe during the Younger Dryas. Horse (*Equus* sp.) bones from a location on the eastern slope of the Northern Urals were dated to  $8020 \pm 120$  a BP (SOAN-5138; Bachura & Kosintsev 2007). This suggests that the wild horse also lived in NE Europe during the Younger Dryas, and most probably during the early Holocene as well. Taking into account the deterioration of the global climate during the Younger Dryas, it is believed that the fauna of that time was less diversified than that of the previous warm Bølling–Allerød period.

As for the early Holocene (Preboreal–Boreal), not much is known about the large mammal fauna composition (Kosintsev 2007b). The radiocarbon dates mentioned above on bison, saiga and musk ox bones belong to the middle–second half of the Younger Dryas. Therefore, it is quite possible that those species still inhabited NE Europe during the Preboreal. Mammoth and horse bones from the adjacent regions were  $^{14}\text{C}$ -dated to the Preboreal/Boreal. Hence, it is conceivable that those species dwelled here during the Preboreal. It follows from palaeoenvironmental reconstructions that NE Europe was covered with pine–birch forests during the early Holocene, in combination with tundra–steppe communities (Kosintsev *et al.* 2008). This strongly suggests that the region was inhabited by fox (*Vulpes vulpes*) and lynx (*Lynx lynx*), and most probably also by Eversmann's polecat (*Mustela eversmanni*) at that time. From the beginning of the middle Holocene, the large mammal fauna acquired a species composition typical for the Holocene. It is noted for the presence of species related to tree and shrub habitats, such as beaver (*Castor fiber*), brown bear (*Ursus arctos*), common marten (*Martes martes*), badger (*Meles meles*), moose (*Alces alces*) and a small admixture of open landscape inhabitants. Among the latter, polar fox (*Alopex lagopus*) is present only in the north of the region. The species composition of the mammal assemblage did not change throughout the middle–late Holocene (Table 6).

The data available for the large mammal fauna do not allow an analysis as detailed as that for the small mammal faunas. However, it is possible to compare their general development over the last 35 000 years, from the Middle Valday to the late Holocene. Both the small and large mammals show a decreasing species diversity at the LGM, and an increase during the Bølling–Allerød. At the beginning of the Holocene, the number of species related to forest and shrub vegetation increased, and that of those typical of open environments decreased. During the early Holocene, open-landscape inhabitants, namely steppe animals such as horse and saiga, completely disappeared from the fauna.

## Conclusions

Independent models show that trends in the history of small mammal assemblages are relatively stable. Therefore, it is reasonable to apply various multidimensional analysis methods. This allows the assessment of consistency and validity. It also allows the description of more detailed variations in the input variables.

The main temporal trends in the development of mammal assemblages appear to be strongly correlated with global climate changes. This shows that palaeoclimatic conditions can be inferred from the analysis of local faunal assemblages in the past.

In addition, significant deviations in local fauna composition from our model are observed at specific latitudes/longitudes. This is observed at Rasik, Makhnevskaya and Sokoliny. Deviations from the more general trend require a more detailed investigation.

Based on climatic regimes, we could assign the local faunas to three groups: (1) a Holocene assemblage, (2) an assemblage typical for the extremely cold periods during the Late Pleistocene (the 'stadial' assemblage), and (3) an assemblage of moderately cold periods of the Late Pleistocene (the 'interstadial' assemblage). Each of the three assemblages features a typical composition of fauna with specific indicator species. The geographical factor also appears in the classification. This enables, for example, the recognition of steppe assemblages in the Rasik locality, which is south of the studied region.

Some changes in taxa, both of common and relatively rare species, cannot be described in the framework of the 'allochthonous' model based on temperature variations (a factor that is external with reference to the ecosystem). It is quite possible that the determining factors for those species are alterations in the ecosystem structure itself, or variations of biotic and/or abiotic component interactions in the ecosystem. Technically, in multidimensional models describing variations in the composition of local faunas, the factors that are uncorrelated with temperature/climate tend to act as indicators of temperature-independent historical changes in the faunal structure. Such factors are discovered by our investigations. In general, they underscore the significance and place of the 'autochthonous' mechanisms in the historical dynamics of faunal assemblages.

The entire region studied can be divided into two parts, according to their faunal characteristics: the greater northern (subarctic) subregion, and the smaller southern subregion (south of 60°N). The Late Pleistocene assemblages in the southern part included species such as steppe lemming, *Cricetus*, *Cricetulus* and *Spermophilus*, which were not found in the north. In addition, the subregions show different Late Pleistocene assemblages: the collared lemming dominated in the north, while in the southern part either the narrow-skulled vole was dominant, or there was a



co-dominance of the collared lemming and narrow-skulled vole. During the early Holocene, peculiar communities dominated by the narrow-skulled vole existed in the south, while typical forest assemblages were already in place in the north.

We observe some critical moments in the evolution of micromammalian fauna, which were non-synchronous in different parts of the region. The most significant transformation concerns the changes of dominants from the species characteristic for the mammoth steppe (narrow-skulled vole, collared lemming, Siberian lemming) to forest species. These changes took place as early as 8000 years ago in the north but only by 6000 years ago in the south (Smirnov 2004).

Changes on a smaller scale took place at the transition from the LGM to the Lateglacial: the collared lemming was replaced as dominant by co-dominating collared lemming and narrow-skulled vole over the major part of the region (before 12 000 years ago), and later, between 12 000 and 10 000 years ago, the two co-dominants gave way to the narrow-skulled vole as the single dominant in the south of the region.

The changes in the large mammal fauna were analogous to those in the small mammal fauna. In both faunas, the most dramatic transformation took place during the early Holocene. Less important alterations occurred at the transitions from the Middle Valday to the LGM and from the LGM to the Lateglacial. Unlike the small mammal fauna evolution, changes in the large mammal fauna occurred more or less simultaneously over the region. Therefore, we conclude that changes in both small and large mammals in NE Europe proceeded in close harmony, that is, synchronously and unidirectionally during the last 35 000 years.

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## Supporting Information

Additional Supporting Information may be found in the online version of this article:

*Table S1.* Modern mammal fauna of the European Northeast.

*Table S2.* Environmental preferences of the modern mammal species of the European Northeast.

*Table S3.* Radiocarbon dates for Quaternary mammal remains from localities in the European Northeast.