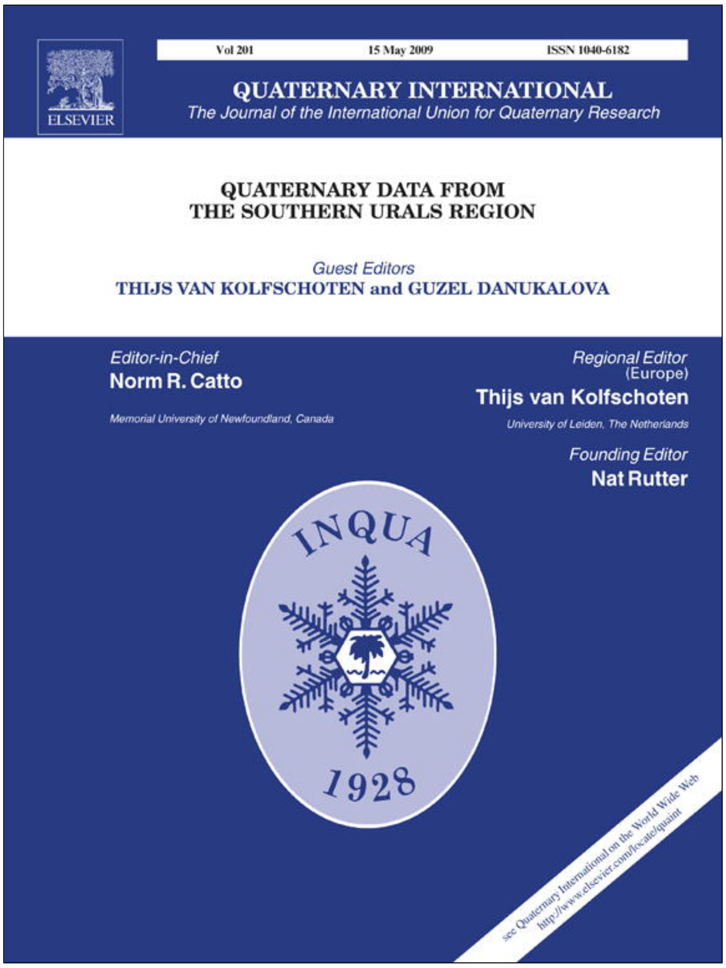
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Ecosystems of Eastern Europe at the time of maximum cooling of the Valdai glaciation (24–18 kyr BP) inferred from data on plant communities and mammal assemblages

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ABSTRACT

Data on Eastern European fossil mammal fauna and palaeoflora dated to the Last Glacial Maximum (24–18 kyr BP) have been summarized using PARADOX and ARC/VIEW software. Palaeobotanical material from 54 sections (197 samples altogether) was studied, along with mammal fossils recovered from 55 localities. This made it possible to compile a series of electronic maps for indicator mammal and plant species for the considered time interval. An analysis of the spatial distribution of species belonging to different ecological groups enabled the identification of principal mammal assemblages and plant communities of the LGM. The whole volume of data was then processed using a range of mathematical techniques. The classes of the palynologically studied sections were analysed integrally with those of mammal localities both in the multidimensional axes space and in physical space (described by their geographical coordinates). Mathematical processing of a considerable amount of palaeobiological data permitted the identification of individual groups of mammals and plants and to make a further comparison between them. In this way, palaeoenvironments of the coldest phase of the Valdai glaciation for the territory of Eastern Europe were reconstructed for the first time by means of simultaneous analysis of theriological and palaeobotanical data using mathematical techniques.

1. Introduction

The Late Valdai was marked by the most severe climate within the Pleistocene, with extensive ice sheets and periglacial landscapes widely spread over the extra-tropical regions of the northern hemisphere. In the stratigraphic scheme of the central Russian Plain, the Late Valdai sediments are defined as the Ostashkov horizon dated from <25 kyr BP to >10 kyr BP (Breslav et al., 1992) and correlated with stage 2 of the oxygen isotope scale (Fig. 1). This stratigraphic horizon includes glacial deposits (till and glaciofluvial sediments) as well as periglacial alluvium of low terraces and loess-soil series. The latter consists (from the top down) of the Altynov loess (loess I), Trubchevsk interstadial soil (~17 kyr BP) and underlying Desna loess (loess II). The time of Desna loess formation is thought to correspond to the maximum Valdai cooling (usually termed Last Glacial Maximum or LGM) (Gerasimov et al., 1980). In this paper we concentrate on the analysis of mammal fauna and flora of this time interval.

There are a number of reconstructions of Late Valdai environments, including those of vegetation, mammal fauna, cryogenic phenomena, loess cover, etc. They have been published in monographs and palaeogeographic atlases (Markov, 1939; Markov et al., 1965; Paleogeography of Europe, 1982; Grichuk, 1989; Atlas of Paleoclimates and Paleoenvironments of the Northern Hemisphere, 1992; Bolikhovskaya, 1995; Dynamics of Landscapes and Climates of northern Eurasia, 2003). New data are now available on the ice sheet limits on land, as well as in the coastal regions and Arctic shelves (Velichko et al., 1997; Svendsen et al., 1999; Siegert et al., 2002). The authors used those data when developing cartographic presentations of the reconstructed LGM palaeo-ecosystems.

In spite of an abundance of palaeobiological materials regarding the LGM in Eastern Europe, no attempt has been made as yet to summarize the large volume of theriological and palaeoflora data and to construct a model to get a better understanding of past environments. This approach was first applied by the authors when reconstructing Russian Plain environments during the Bryansk Interstadial (33 to >24 kyr BP and 24–18 kyr BP) (Markova et al., 2002a,b).

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2. Materials

Fifty-four sections (197 samples altogether) were studied palaeobotanically along with mammal fossils recovered from 55 localities on the Russian Plain dated within the interval 24–18 kyr BP. The palaeobotanical sections contain 183 taxa (88 genera and 67 species); the mammal localities yielded 71 taxa, most of them defined to species level. The northernmost localities are at ~67°N, and the southern ones are in the northern coastal region of the Black Sea and on the piedmont plain of the Caucasus (~45°N).

3. Methods

Data on fossil mammal fauna and palaeoflora have been summarized using PARADOX and ARC/VIEW software. The PALEOFAUNA database includes information on mammal species composition, geological and geographical position of the localities, and absolute and relative ages. The PALEOFLORA database has been developed along the same lines. This made it possible to compile a series of electronic maps for indicator mammal and plant species for the considered time interval. An analysis of the spatial distribution of species belonging to different ecological groups enabled the identification of the principal mammal assemblages and plant communities of the LGM (Markova, 1998a). When analysing plant communities, characteristics of sub-fossil pollen spectra from different natural zones were taken into account (Grichuk and Zaklinskaya, 1948; Monoszon, 1985).

The entire volume of data was then processed using a range of mathematical techniques. Pollen assemblage values were standardized so that biological peculiarities of pollen production in various species are ruled out while the assemblages retained their typical patterns of variation.

A matrix of pair Euclidian distances was obtained for 54 sections with palynological data. The matrix was further treated using a multidimensional scaling technique (MDS) (Deivison, 1988), with the aim of determining a minimum MDS axes number sufficient for the "optimum dimension" data to be adequately described. For this purpose, "stresses" were found for an artificial model (Puzachenko, 2001). The lower ones are values of this index, the higher one is the quality of the MDS model. A "fuzzy set" technique (Kaufman and Rousseeuw, 1990) was applied to the classification of palynologically studied sections. The locality classes thus defined were characterized by median values of pollen assemblages.

A matrix of pair distances (Jakardian matrix) was calculated for 55 localities of mammals (71 taxa) (Zaitsev, 1984). The "optimum dimension" was found from the matrix using the MDS technique (as described above), and localities were classified according to values on the MDS axis.

The classes of the palynologically studied sections were analysed integrally with those of mammal localities both in the MDS axes space and in physical space (described by their geographical coordinates).

4. Mammal assemblages

First, the analysis of mammal range dynamics and species composition in the mammal assemblages dated to the LGM in Easrtern Europe was performed by means of GIS ARC/VIEW.

Fifty-five mammal localities across the Russian Plain are the basis for the mammal composition, diversity and distribution interpretation of the Late Valdai maximum. The climatic conditions between <24,000 and >18,000 yr BP were relatively stable and severe. This permits analysis of the mammal material of this interval as a whole. The mammal localities are located between 24.09–54.00°E, and 44.50–67.00°N. The distribution of mammal sites is irregular. Only a few localities were found in the very north of the Russian Plain, which was covered mostly by ice sheets, while most localities were concentrated in the central and southern parts of the Russian Plain. Several sites were recovered east of the Volga River. Most of the localities are associated with the cultural levels of the Late Palaeolithic and 70% of them have been dated by ^{14}C. Seventy-one mammal taxa were recovered from these sites, including: Insectivora: Eurasian common shrew *Sorex araneus*; arctic shrew *Sorex arcticus*, Russian desman *Desmana moschata*; Lagomorpha: steppe pica *Ochotona pusilla*; European hare *Lepus europaeus*; polar hare *Lepus timidus*; Rodentia: Eurasian beaver *Castor fiber*; bobac marmot *Marmota bobac*; European suslik *Spermophilus (Spermophilus) citellus*, spotted suslik *Spermophilus (Spermophilus) suslicus*, great jerboa *Allactaga major*, steppe sicista *Sicista subtilis*; mole rat *Spalax microphtalmus*; Eurasian grey long-tailed hamster *Cricetulus migratorius*; common hamster *Cricetus cricetus*; water vole *Arvicola terrestris*; Siberian lemming *Lemmus sibiricus*; collared lemming *Dicrostonyx gulielmi*; yellow steppe lemming *Eolagurus luteus*; steppe lemming *Lagurus lagurus*; common red-backed vole *Clethrionomys glareolus*; narrow-skull vole *Microtus (Stenocranius) gregalis*; field vole *Microtus (Microtus) agrestis*; common vole *Microtus (Microtus) arvalis*, root vole *Microtus (Pallasiinus) oeconomus*; Proboscidea: woolly mammoth *Mammuthus primigenius*; Carnivora: arctic fox *Alopex lagopus*; wolf *Canis lupus*, corsak fox *Vulpes corsak*; red fox *Vulpes vulpes*; cave hyena *Crocuta (Crocuta) spelaea*; lynx *Lynx (Lynx) lynx*; cave lion *Pantera (Leo) spelaea*; wolverine *Gulo gulo*; stoat *Mustela erminea*; weasel *Mustela nivalis*; large cave bear *Ursus (Spelearctos) spelaeus*; brown bear *Ursus (Ursus) arctos*; Artiodactyla: elk *Alces alces*; red deer *Cervus elaphus*; reindeer *Rangifer tarandus*; giant deer *Megaloceros giganteus*; ibex *Capra aegagrus*; saiga *Saiga tatarica*; primitive bison *Bison priscus*; wild ox *Bos primigenius*; musk-ox *Ovibos moschatus*; Perissodactyla: woolly rhinoceros *Coelodonta antiquitatis*; Pleistocene wild ass *Equus hydruntinus*; "latipes" horse *Equus latipes*; horse *Equus caballus* and some others.

Several extinct large herbivores *M. primigenius*, *C. antiquitatis*, *B. priscus*, *B. primigenius*, *M. giganteus* and carnivores *C. spelaea*, *P. (Leo) spelaea*, *U. spelaeus* were typical for Late Valdai fauna.

Some of species present an evolutionary stage in their phylogenetic lineage. Thus, collared lemming *D. gulielmi* is the direct ancestor of the modern *D. torquatus*. In the opinion of some scientists, the morphology of several mammals (*M. gregalis*, *L. lagurus*, *A. terrestris*, etc.) differs from the modern ones at subspecies level (Rekovets, 1985).

Materials from the Russian Plain attributed to the Late Valdai glaciation and summarized together in the form of the PALEOFAUNA database permit us to distinguish at least four mammal assemblages. Analysis of the series of electronic maps showing mammal ranges reveals the assemblages as follows:

I. Only subarctic mammals inhabited the narrow belt near the ice sheets: *D. gulielmi*, *L. sibiricus*, *M. (Stenocranius) gregalis*, *R. tarandus*, *A. lagopus*, probably, *O. moschatus* and polar bear *Ursus maritimus* (this last species was found at a slightly earlier site in this belt). The assemblages of subarctic tundra were identified from these data.

II. Further south, the mammals of the subarctic zone coexisted with some steppe animals, a few forest eurytopic mammals, and intrazonal species, including *O. pusilla*; *L. timidus*; *C. migratorius*; *C. cricetus*; *A. terrestris*; *L. sibiricus*; *D. gulielmi*; *L. lagurus*; *C. glareolus*; *M. (Stenocranius) gregalis*; *M. (Microtus) agrestis*; *M. (Microtus) arvalis*, *M. (Pallasiinus) oeconomus*; *M. primigenius*; *A. lagopus*; *C. lupus*, *V. corsak*; *V. vulpes*; *L. (Lynx) lynx*; *G. gulo*; *M. erminea*; *M. nivalis*; *U. (Spelearctos) spelaeus*; *U. (Ursus) arctos*; *A. alces*; *R. tarandus*; *S. tatarica*; *B. priscus*; *B. primigenius*; *O. moschatus*; *C. antiquitatis*; *E. latipes*, and *E. caballus*.

This assemblage was situated between 60–64°N and 53–60°S, its location depended on the southern limit of the ice sheet. It was named the periglacial forest–tundra assemblage.

III. Steppe species were dominant south of the periglacial forest–tundra biome. However, several subarctic, meadow and forest species as well as large herbivores and 'cave' carnivores were also present in this periglacial forest–steppe assemblage, including *O. pusilla*; *L. europaeus*; *L. timidus*; *M. bobac*; *S. (Spermophilus) citellus*; *S. (Spermophilus) suslicus*, *A. major*, *S. subtilis*; *S. microphtalmus*; *C. migratorius*; *C. cricetus*; *A. terrestris*; *L. sibiricus*; *D. gulielmi*; *E. luteus*; *L. lagurus*; *C. glareolus*; *M. (Stenocranius) gregalis*; *M. (Microtus) agrestis*; *M. (Microtus) arvalis*, *M. (Pallasiinus) oeconomus*; *M. primigenius*; *A. lagopus*; *C. lupus*, *V. vulpes*; *C. (Crocuta) spelaea*; *L. (Lynx) lynx*; *P. (Leo) spelaea*; *G. gulo*; *M. erminea*; *M. nivalis*; *U. (Spelearctos) spelaeus*; *U. (Ursus) arctos*; *A. alces*; *C. elaphus*; *R. tarandus*; *M. giganteus*; *S. tatarica*; *B. priscus*; *B. primigenius*; *C. antiquitatis*; *E. latipes*, and *E. caballus*.

The southern limit of this assemblage was at 48°N in the western Russian Plain and extended 1–2° northward onto the eastern Russian Plain. The location of this boundary was similar to the position of the permafrost southern limit during the late Valdai (Nechaev, 1986). The periglacial forest–steppe assemblage is considered to be present here.

IV. On the very south of the Russian Plain the mammal communities were only slightly influenced by the presence of the ice sheet. The periglacial steppe mammal assemblage was distributed south of 48°N. It included *O. pusilla*, *L. europaeus*, ground squirrels *S. (Spermophilus) citellus* and *S. (Spermophilus) suslicus*, *M. bobac*, jerboas of different genera and species *Allactaga*, *Pygeretmus*, moles *Spalax* and *Nannospalax*, *S.subtilis*; *L. lagurus*, *E. luteus*, *C. migratorius*, *C. cricetus*, *M. (Stenocranius) gregalis*, *M. (Microtus) arvalis*; *A. terrestris*; *M. primigenius*; *C. lupus*, *V. corsak*; *V. vulpes*; *C. (Crocuta) spelaea*; *P. (Leo) spelaea*; *U. (Spelaearctos) spelaeus*; *R. tarandus*; *C. antiquitatis*, *B. priscus*, *B. primigenius*, *M. giganteus*; *S. tatarica*; *E. hydruntinus*; and *E. latipes (?=E. caballus)*. The presence of reindeer, as well as that of several large herbivores and 'cave' carnivores, gave the community somewhat eccentric characteristics.

Thus, all of the LGM mammal assemblages display a unique structure, and do not have counterparts in modern biota.

5. Reconstructions of vegetation

Of 56 palynologically studied sections located in Eastern Europe and attributed to the LGM on the basis of geochronological and geological evidence, 22 belong to loess-palaeosoil deposits, and the rest to alluvial, lacustrine and proluvial deposits. Thirty-six sections have been radiocarbon-dated. The age of the rest was inferred from geological and archaeological evidence. The PALEOFLORA database provides the basis for constructing electronic maps showing locations of pollen and spores of indicator species characteristic of certain plant communities. The maps were drawn using cartographic ARC/VIEW software. In addition, we compiled maps of plant communities indicative of certain ecosystems.

When analysing participation of tundra and forest–tundra coenoses in the communities, data both on overall composition of spectra and on percentage of species-indicators of those coenoses were taken into consideration. Thus, modern surface assemblages obtained from tundra and forest–tundra zones show typically the following composition: tree and bush (AP) pollen account for more than 40%, and spores vary from ~20 to 50%, with some microthermal (cold-tolerant) plants also present, such as *Alnus (Alnaster) viridis* ssp., *Selaginella selaginoides*, *Betula nana* (Grichuk and Zaklinskaya, 1948).

The total composition of the pollen spectra suggests tundra and forest–tundra communities occurring north of 48–49°N during the LGM. However, pollen and spores of individual arctic and hypoarctic species are found in the layers of this age over most of the Russian Plain. They include *A. (Alnaster) viridis* ssp., *S. selaginoides*, *Lycopodium pungens*, *Lycopodium appressum*. *A. (Alnaster) viridis* ssp., for example, is a boreal–arctic and arctic–alpine microthermal Eurasian species (Grichuk 1989). At present, only the northwestern part of its distribution range falls within the Russian Plain limits. In the past, during the LGM, this species, typical of northern taiga and forest–tundra, occurred north of 48–49°N. Its pollen has been recorded in the Don lower reaches, in the Dniestr drainage basin and in the Carpathian forelands. Dwarf birch *B. nana* features hypoarctic distribution at present (Alekhin et al., 1957). During the LGM, its distribution coincided with that of *A. (Alnaster) viridis* ssp. The southern limit of *B. nana* on the Russian Plain is at 54–55°N now (Sokolov et al., 1980). At the LGM (24–18 kyr BP) this limit shifted southward to 47°N. *S. selaginoides*, a typical mesophytic plant of tundra and northern taiga, penetrated ~1500 km south of its present-day range (Sladkov, 1951; Grichuk 1989).

Steppe species were also quite common all over Eastern Europe at the studied time interval; they appeared in communities of periglacial tundra–steppe, forest–steppe, steppe, and dry steppe (semi-desert).

As had been previously found by modern surface spectra analysis, the relationship between groups of higher plants pollen typical of modern steppes is as follows: tree species pollen (AP) forms less than 30% (Grichuk and Zaklinskaya, 1948), pollen of herb, grass and subshrubs (NAP) is more than 40–60%, with Chenopodiaceae varying from 10 to 22.5% (Monoszon, 1985). There are some typical steppe and semi-desert species found in the assemblages of the steppe zone, such as *Ephedra*, *Kochia*, *Eurotia ceratoides*. *Ephedra distachya* is a xerophile (semi-xeroplile) subshrub inhabitant of steppe, deserts and open woodlands. At present it is common all over the arid belt of Eurasia, from Moldova to the Altai Mountains and Tuva (see Atlas of Medicinal and Allied Plants of USSR, 1983). In the Late Valdai *Ephedra* was spread over the Russian Plain up to 62°N. Another representative of the Chenopodiaceae family, a xerophyte and meso-microthermal *Eurotia ceratiodes*, is an indicator of wormwood and saltwort desert and steppe communities with some xerophile subshrubs. At present *Eurotia* occurs mostly in the south of Eastern Europe; it can be found in the middle and lower reaches of the Volga, on the Southern Urals, in the Crimea and Caucasus (Sokolov et al., 1980). During the LGM its northern limit shifted considerably (by more than 1000 km) to the northwest and was found at 62°N. Sections with palynological assemblages dominated by steppe species (Chenopodiaceae >20%, grasses, herbs and subshrubs >40%) are mostly located south of 49–52°N, indicating that periglacial steppes were widespread.

Another group of pollen assemblages attributed to the LGM gives an insight into the development of periglacial semi-desert coenoses. In the modern surface samples of the semi-desert, the proportion of Chenopodiaceae exceeds 38%; spores and tree pollen amount to less than 7% each (Grichuk and Zaklinskaya, 1948; Monoszon, 1985; Bolikhovskaya, 1999). During the LGM, semi-desert plant communities occurred primarily at the Black Sea coasts (at 45–47°N), and locally in the southern Oka-Don Plain and in the middle reaches of the Dnieper River.

LGM pollen assemblages with an AP proportion in excess of 60% (including more than 10% of *Picea*) have been recovered only from sections located to the north of the Moscow and in the Podolsk uplands. This does not necessarily mean, however, that tree species were completely absent from other regions of Eastern Europe. They formed a part of periglacial forest–steppe and forest–tundra communities; some forest refugia persisted in mountains and on rugged terrain, primarily on uplands.

As an example, we refer to spruce (*Picea*), a moderately thermophilic forest mesophyte, which at the LGM penetrated far south of its present-day range. It was most common in western and northwestern regions of Eastern Europe and occasionally found in the Black Sea and Sea of Azov coastal regions. No *Picea* pollen has been recorded in the southeastern Russian Plain, with the exception of the middle reaches of the Don River. Another forest mesophyte is larch (*Larix*). Its pollen was found in sections of the LGM deposits at ~52°N, while its modern distribution is mostly in Siberia and covers only the northeastern part of the Russian Plain (north of 56°N and east of 40°E). A typical species of dark coniferous taiga forest, *Pinus sibirica*, was most widely distributed during the Late Valdai and reached as far south as 52°N (its pollen was found in the middle reaches of the Dnieper and upper reaches of the Don). The present-day range of Siberian pine extends from the upper Vychegda River (NE European Russia) eastwards, including almost the whole of Siberia. This suggests a considerable expansion of the species in Eastern Europe during the LGM. An allied species of pine – stone pine (*Pinus cembra*) – occurs at present in the Carpathian Mountains at an altitude of more than 1700 m (Kremer, 1997). It belongs to the Cembrae section in common with Siberian pine. It seems likely that during the LGM, the Carpathians were the southern centre of expansion of *Pinus* sect. Cembrae, as its pollen was found in sections in the Carpathian foreland and along the present-day coasts of the Black and Azov seas.

A moderately thermophilic species the Scots pine (*Pinus silvestris*) was also common during the Late Valdai all over Eastern Europe; this tree species occurred in various environments and preferred moderately dry unconsolidated soils. All these tree species were components of periglacial forest–steppe and forest–tundra landscapes. Mosaic landscapes, where steppe and tundra communities alternated with pine and birch open woodlands, extended southwards to 49°N.

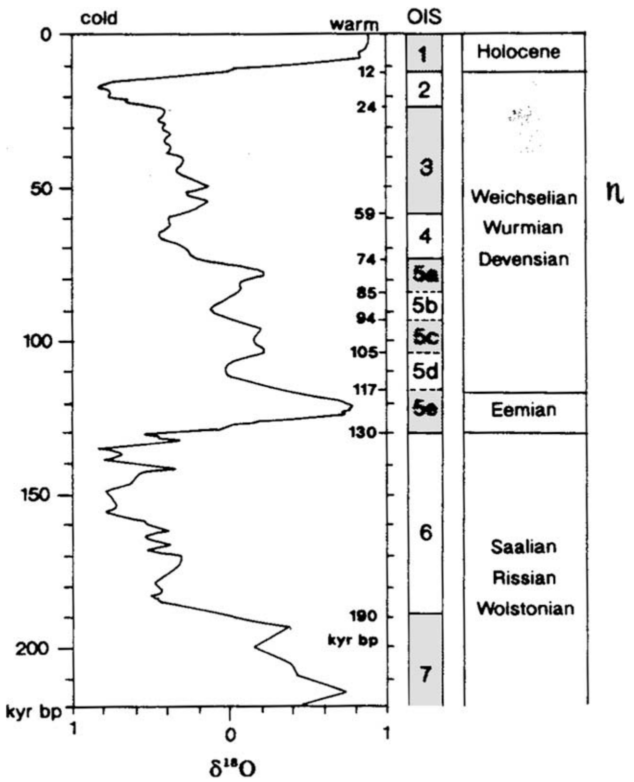

Fig. 1. Orbital-based chronostratigraphy (SPECMAP) of the last 200,000 yr; after Imbrie et al. (1984). Ages in millennia (kyr). Bottom: normalized benthonic ?^{18}O. Oxygen isotope stage boundary ages (small numbers) after Martinson et al. (1987).

The question of the presence of broadleaved species in the Late Valdai vegetation is still open. Many specialists think that broadleaved pollen recovered from sediments of this age was redeposited (Grichuk et al., 1969; Pashkevich, 1977, 1987; Semenenko et al., 1981; Deviatova, 1982; Zelikson, 1986). In the authors' opinion, pollen redeposition is possible in the case of sections located within the limits of the ice sheet or at its margin, where unconsolidated sediments underwent intensive erosion and redeposition.

An analysis of elecronic maps showing the occurrence of broadleaved species (*Tilia*, *Carpinus*, *Corylus*, *Quercus* and *Ulmus*), together with classifications using the fuzzy set technique, revealed a distinct pattern which was taken into consideration when reconstructing palaeovegetation in unglaciated areas.

Minor amounts of *Ulmus*, *Quercus*, *Carpinus*, *Acer*, *Corylus*, and *Tilia* pollen have been found in sediments dated to the beginning of the Late Valdai in the central Russian Plain (middle reaches of the Dnieper River, the Central Russian Upland, the Moscow Upland), on the Neman Upland, in Moldova and the Sea of Azov coastal areas. As for the LGM proper (21–18 kyr BP), *Ulmus*, *Tilia*, *Corylus*, and *Carpinus* disappeared from most of Eastern Europe. *Quercus*, *Tilia*, and *Acer* are found in pollen assemblages from Moldova, *Ulmus*, *Tilia* and *Carpinus* in the Azov region; and *Ulmus*, *Tilia* and *Acer* in the middle reaches of the Dnieper (49–51°N).

The analysis performed permitted identification of five refugia of northern taiga and forest vegetation on the Russian Plain; those are the Moscow Upland, the Central Russian Upland, the middle reaches of the Dnieper River, the Donetsky Ridge, and the Podolian Upland. The refugia were inherited from the Bryansk interval (33–24 kyr BP) (Markova et al., 2002a).

Table 1
The frequency of mammal taxa in different groups (I–VI) of localities, which are the most important for revealing the LGM ecosystems.

	Mammal localities		
	I	II	III
Mammuthus primigenius	22	17	11
Bos primigenius	2	9	0
Megaloceros giganteus	0	0	4
Rangifer tarandus	9	7	11
Gulo gulo	2	0	7
Canis lupus	0	17	0
Alopex lagopus	2	20	0
Vulpes corsac	0	0	4
Ursus arctos	0	2	7
Lepus timidus	0	0	4
Marmota	0	0	6
Lagurus lagurus	0	2	6
	IV	V	VI
Talpa	4	0	0
Bison priscus	0	9	7
Bos primigenius	7	0	9
Ovis	4	0	0
Alces alces	0	0	7
Cervus elaphus	2	0	7
Vulpes vulpes	4	0	0
Ursus arctos	2	2	0
Crocuta spelaea	4	0	0
Panthera leo spelaea	4	0	0
Lepus europaeus	4	0	0
Ochotona pusilla	9	0	0
Pteromys volans	4	0	0
Spalax	7	0	0
Clethrionomys glareolus	4	0	0
Clethrionomys rufocanus	9	0	0
Clethrionomys rutilus	9	0	0
Microtus agrestis	7	0	0
Microtus oeconomus	7	0	0
Microtus gregalis	11	0	0
Cricetus cricetus	4	0	0
Lemmus sibiricus	7	0	0
Eolagurus luteus	4	0	0
Lagurus lagurus	7	0	0

Qualitative and quantitative analysis of palynological data summarized in the PALEOFLORA database permitted identification of the following plant assemblages, which have no analogues in modern vegetation:

- Shrub tundra, locally with forest–tundra vegetation, with some admixture of steppe species (northern Byelorus – north of 54–56°N, Tver, Yaroslavl, Kostroma, and Vologda regions).
- Periglacial forest–tundra (open pine and birch forests), locally with tundra–steppe patches (53–56°N). This assemblage occupied mostly western and eastern regions of the Russian Plain and wedged out towards its central part.
- Periglacial forest–steppe (open pine and birch woodlands with some communities of herb-rich steppes, as well as meadow and tundra–steppe plant communities) – 49–53°N. This assemblage is distinguished by a higher proportion of steppe elements, while the amount of tundra species is lower compared to the periglacial forest–tundra.
- Periglacial steppe with *Artemisia* and Chenopodiaceae, with some tundra species (47–49°N).
- Periglacial semi-desert (45–47°N)
- Refugia of northern taiga and forest vegetation.

It follows from the above that vegetation zones found on the Russian Plain were completely restructured during the LGM. Pollen records indicate a wide expansion of arctic and northern taiga species towards the south and southeast as far as 47°N, penetration of steppe plants to the north and northwest up to 62°N, and destruction of the forest zone at the Late Valdai maximum.

6. Ecosystems at the time of the maximum Valdai cooling

When considering species composition and diversity of mammals and plants at the maximum cooling of the Valdai, together with specific features of species ranges, not only qualitative methods have been applied (as described above), but first and foremost mathematical techniques. It was primarily by means of the latter that the results stated below were obtained.

Not less than five distinct ecosystems are identified:

1. A strip in the immediate vicinity of the ice sheet margin was inhabited mostly by subarctic and some steppe mammals; tundra–steppe plant communities were dominant. These data are corroborated by classifications derived using modelling techniques (Table 1, *groups I, II, V*; Table 2, *group I*). There was subshrub tundra with isolated patches of birch and pine woodlands inhabited primarily by tundra mammal species. Periglacial tundra–steppe was reconstructed (Fig. 2).
2. Farther south, mammals and plants characteristic of the subarctic belt coexisted with typical steppe animals and plants and with some everybionts – periglacial tundra–forest–steppe ecosystem (Table 1, *groups I, II, IV, V*; Table 2, *groups III, IV, VI*. Fig. 2). The southern limit of this biome ran approximately along 52–53°N in the west and farther north in the eastern Russian Plain.
3. South of this biogeographic province, steppe species of Mammalia and plants became dominant in the biocoenoses, though subarctic species were also present in small amounts, as well as some forest and meadow species, thus forming a periglacial steppe community. The southern limit of this ecosystem was at 48°N in the west and shifted by about 2° northwards in the Volga drainage basin. The boundary mostly coincided with the southern limits of permafrost (Atlas of Paleoclimates and Paleoenvironments of the Northern Hemisphere, 1992).
4. Finally, in the southern Russian Plain a dominance of steppe and semi-desert species of plants and mammals is recorded; that suggests ecosystems of steppes and semi-deserts spread south of 48°N (Table 1, *groups I, II, III, IV, VI*; Table 2, *groups II, V*; Fig. 2). A distinctive feature of this ecosystem was an abundance of species belonging to the "mammoth" assemblage, many of which became extinct at the end of the Pleistocene.
5. Refugia of forest and forest–steppe vegetation dominated by pine, occasionally with some broadleaved species, are reconstructed in the Crimea, in the Transcarpathian region, in the Caucasus, on the Central Russian Upland, the Donetsky Ridge, and in the middle reaches of the Dnieper River. A number of mammals typical of nemoral forests also retreated to mountain regions. The proportion of steppe mammals and of species belonging to the "mammoth" assemblage was also high (Table 1, *groups IV, V, VI*; Table 2, *group VII*; Fig. 2).

7. Conclusions

A drastic restructuring of the biota of Eastern Europe and the whole Northern Hemisphere took place during the Valdai glaciation, including its coldest phase (24–18 kyr BP). The response of individual species of mammals and plants is proven to have been varied in direction and scale, which resulted in the appearance of completely new biomes having no modern analogues (Semken, 1988; Baryshnikov and Markova, 1992; Musil, 1985; Markova et al., 1995; FAUNMAP Working Group, 1994; Markova, 1998b). The ranges of subarctic mammals and plants extended noticeably southwards. Contrary to this, representatives of steppe fauna and flora penetrated far westward and northward from their present locations and have been recorded within the forest zone of today. Forest species of flexible ecology and those of taiga changed their ranges insignificantly; this suggests preservation of forested areas within the limits of the modern forest zone. A few forest–steppe mammals and plants also changed their ranges but slightly, though their northern limits shifted somewhat to the south. Species typical of broadleaved forests practically disappeared from the Russian

Table 2
The content (%) of indicative plant pollen in different groups (I–VII) of LGM localities.

Taxa	Groups of localities						
	I	II	III	IV	V	VI	VII
Abies	0.03	1.09	1.03	0.00	0.00	0.00	0.00
Alnus (Alnaster) viridis ssp.	1.71	1.03	0.38	1.57	0.09	0.13	0.65
Alnus	4.92	5.84	7.73	0.98	0.07	7.51	0.50
Artemisia	19.81	14.66	3.46	12.59	0.99	35.96	31.86
Betula nana	10.98	0.89	6.29	4.45	0.04	3.13	4.67
Betula	50.09	14.15	23.48	2.23	1.63	17.27	9.03
Botrychium	0.89	3.06	0.24	0.13	0.04	0.02	0.01
Bryidae	51.64	54.17	5.27	0.21	0.31	5.50	0.14
Caryophyllaceae	0.37	0.11	0.17	0.00	0.05	0.09	0.11
Chenopodiaceae	5.92	22.14	2.13	32.48	2.28	27.33	30.89
Compositae	24.59	24.16	20.59	55.05	2.38	44.54	39.33
Corylus	0.91	0.16	0.96	0.09	.08	3.38	1.39
Cyperaceae	22.36	5.07	4.06	0.00	0.57	5.79	0.22
Ephedra	0.08	0.34	0.08	0.22	0.06	0.00	0.06
Fabaceae	0.00	1.81	0.31	0.04	0.05	0.31	0.00
Gramineae	16.94	12.73	5.72	6.91	1.18	6.98	16.19
Lycopodiaceae	2.13	1.53	0.20	0.16	0.05	0.04	0.07
Picea	10.95	7.62	2.96	0.13	0.05	14.19	7.53
Pinus	23.93	65.09	26.00	1.69	0.81	33.13	79.39
Plumbaginaceae	0.00	0.64	0.01	0.07	0.09	0.00	0.00
Polygonaceae	0.01	0.92	1.68	0.00	0.52	0.02	0.00
Polypodiaceae	22.73	10.55	8.56	0.29	0.18	1.09	0.15
Quercus	0.41	0.34	0.05	0.07	0.05	3.13	0.22
Rosaceae	0.00	8.12	0.43	0.01	0.13	0.28	0.00
Selaginella	0.35	1.04	0.08	0.00	0.10	0.00	0.00
Sphagnum	19.71	0.88	2.04	0.10	0.05	0.22	0.06
Tilia	0.29	0.13	0.03	0.02	0.05	2.04	1.33
Ulmus	9	0.37	2.00	0.04	0.06	3.00	1.06

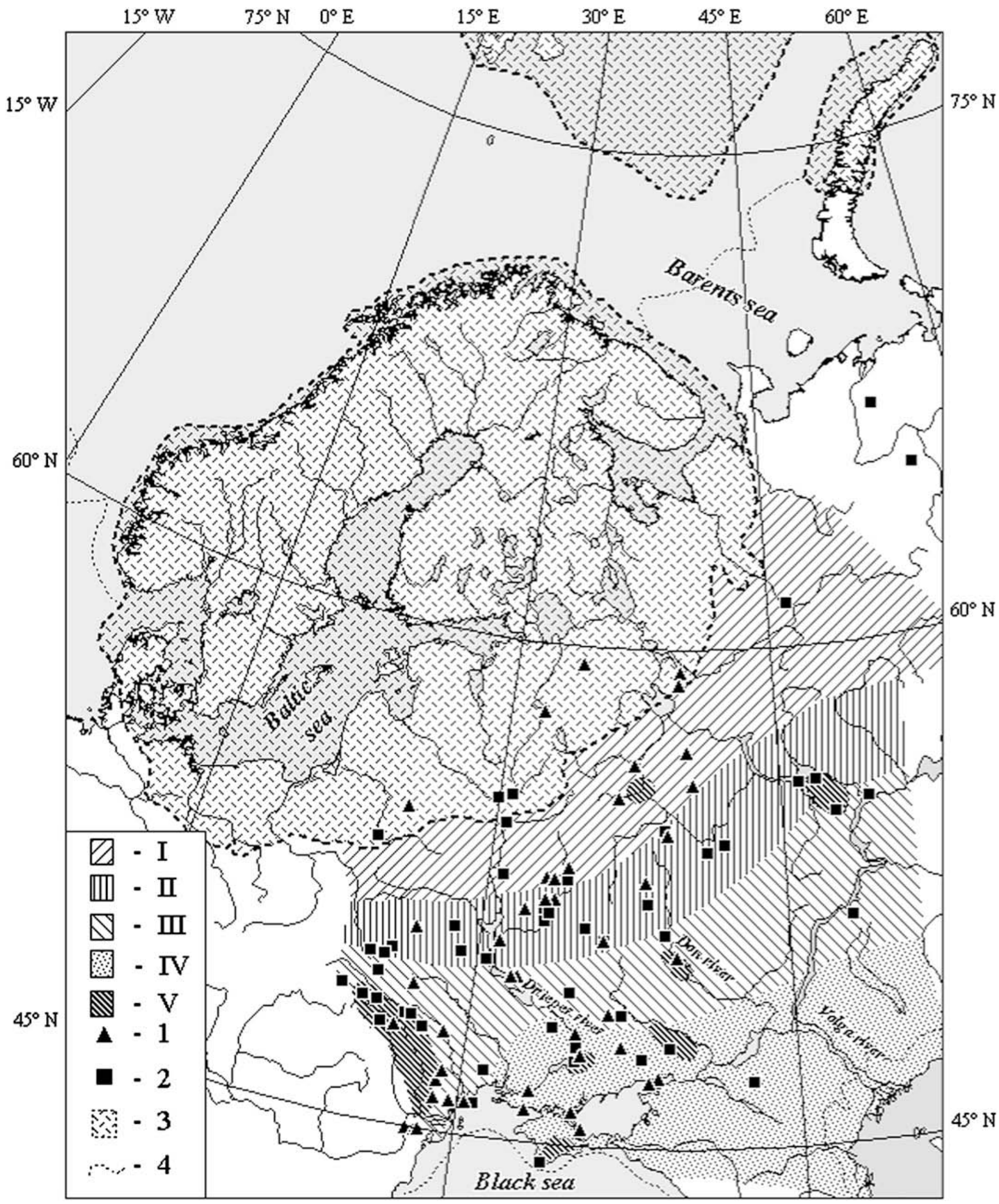

Fig. 2. LGM ecosystems: I, periglacial tundra–steppe; II, periglacial tundra–forest–steppe; III, periglacial forest–steppe; IV, steppe and semi-desert; V, refugees forest and forest–steppe vegetation; 1, mammal localities; 2, plant localities; 3, LGM ice sheet limits; 4, LGM coastlines.

Plain and persisted only in mountain refugia of the Carpathians, Crimea and Caucasus. The structure of periglacial tundra–forest–steppe and forest–steppe biomes was not unlike that of large ecotones.

Thus, specific characteristics of East European biota at the coldest phase of the Valdai glaciation have been established by analysing the whole volume of data (Fig. 2). Ecosystems of the Russian Plain at the time of the Valdai glaciation were stable enough and persisted with minor modifications through almost 90 thousand years (that is, throughout the whole Valdai epoch). Even during interstadials the biota structure underwent only slight changes (Markova et al., 2002b). During glaciation there were a variety of landscapes, though their differentiation was not so clearly pronounced as during interglacial epochs. There was no continuous forest zone in Eastern Europe at the LGM, though a few refugia of forest flora existed on highlands and mountains marked by a diversity of local habitats. In addition, some forest species survived near water bodies where remnants of tree and shrub communities persisted. Mathematical processing of a considerable amount of palaeobiological data permitted us to identify individual groups of mammals and plants and to make a further comparison between them. In this way, palaeoenvironments of the coldest phase of the Valdai glaciation were reconstructed for the first time by means of simultaneous analysis of theriological and palaeobotanical data using mathematical techniques. Such an approach allowed us to avoid any bias when reconstructing palaeoenvironments of Eastern Europe.

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