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GEOGRAPHY

Ecosystems of Eastern Europe in the Holocene Atlantic Optimum Based on Floristic and Theriologic Data

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The Holocene Climatic Optimum falls on the final stage of the Atlantic period (AT3) and is determined by different authors as the interval between about 6000 and 4800–4600 yr ago. This time interval was characterized by the development of Late–Middle Neolithic cultures and inhomogeneous climate. Based on palynologcial spectrum data, the warming maximum was observed 6000–5000 yr ago [1]. However, temperatures were also higher than at present 7900–4600 yr ago, and the global annual average temperature during the Atlantic Optimum increased by 1°C [2].

Reconstructions of plant communities and theriocomplexes in AT3 were carried out in a series of works for the former USSR territory [3, 4]. Unfortunately, vast theriologic and paleofloristic AT3 materials have so far been considered separately, and their combined analysis has not been made. We applied new approaches to the generalization and interpretation of paleofloristic and theriologic data using methods of multivariate analysis for reconstructing the environment of the Bryansk Interstadial (33 to >24 ka ago) and the maximal cooling during the Valdai Glaciation (<24 to 18 ka ago) [5, 6].

We analyzed paleobotanical data from 98 sections (157 samples) and materials from 121 mammal localities of Eastern Europe, which are referred to an interval of 6000–5000 yr ago. Paleobotanical sections comprise 121 flora taxons, including 53 species and 40 generic taxons. Mammal localities include 95 taxons, the majority of them being identified to the species level. The northernmost and southernmost localities are located at 68° N and 42° N, respectively.

At the first stage, paleotheriologic and paleofloristic materials were transformed into a DBMS PARADOX database related to the ARC/INFO cartographic program. The PALEOFAUNA and PALEOFLORA databases comprise information about the species composition of mammals and plants, the geological and geographical position of localities, and absolute and relative ages. Theriocomplexes for different Holocene intervals were distinguished based on the distribution of mammal species of various types of ecology [4]. Data on subfossil pollen spectra were taken into account for plant communities and natural zonation.

A new level of analysis of paleobiological materials was gained by applying a combined approach to the interpretation of paleofloristic and paleotheriologic data using methods of multivariate analysis. Values of spore-and-pollen species spectra were arranged within the interval of 0–1 to avoid the peculiar effect of pollen production by some species. The data were separately arranged for spore-and-pollen spectra based on different methods. Based on the Kendall rank correlation, a matrix of distances between each pair of sections was calculated. The matrix obtained was processed by the method of nonparametric multivariate scaling (MS). The cluster analysis (UPGMA method) with MS axes as variables made it possible to distinguish groups of sections with different qualitative and quantitative compositions of flora. The confidence level of differences between section groups was assessed by the Craskell–Wallace criterion. The Jacquard distance was estimated between all the pairs of mammal localities [8]. Then, the matrix was processed by the MS method. The MS axes were used as variables for classification of localities. Each group of localities was characterized by a specific species composition and frequency. The confidence level of differences between the occurrence frequency of individual mammal taxons in section groups was assessed by Pirson χ^2 criterion.

The analysis of the species composition of mammals and plants in the AT3 interval and their distribution in Eastern Europe allows us to establish the following regularities. No less than seven well-defined types of zonal ecosystems can be distinguished from north to south.

Forest tundras. In the northernmost regions, forest tundras were represented by alternating areas of moss–underbrush tundras and sparse taiga vegetation (pine–birch formations on the Kola Peninsula and spruce–

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Table 1. Occurrence frequency of taxon (%) and number of localities with the given taxon (in parentheses) by groups of mammal localities

Taxons	Groups of localities				χ^2	*p*
	1	2	3	4		
Alces alces (elk)	54.5 (18)	0.0 (0)	0.00 (0)	45.5 (15)	41.7	0.000
Bison bonasus (European bison)	13.3 (2)	0.0 (0)	40.0 (6)	46.7 (7)	13.8	0.003
Bos primigenius (tur)	0.0 (0)	3.9 (1)	11.5 (3)	84.6 (22)	15.6	0.001
Capreolus capreolus (roe)	15.0 (6)	2.5 (1)	0.0 (0)	82.5 (3)	24.05	0.000
Castor fiber (beaver)	40.0 (16)	5.0 (2)	0.0 (0)	55.0 (22)	20.6	0.000
Cervus elaphus (red deer)	0.0 (0)	0.0 (0)	0.0 (0)	100.0 (45)	67.2	0.000
Cricetulus migratorius (grey hamster)	0.0 (0)	66.7 (2)	33.3 (1)	0.0 (0)	10.9	0.012
Cricetus cricetus (common hamster)	0.0 (0)	100.0 (4)	0.0 (0)	0.0 (0)	29.7	0.000
Microtus gregalis (narrow-skulled vole)	0.0 (0)	100.0 (4)	0.0 (0)	0.0 (0)	29.7	0.000
Glis glis (fat dormouse)	0.0 (0)	75.0 (3)	0.0 (0)	25.0 (1)	15.4	0.002
Dryomys nitedula (forest dormouse)	0.0 (0)	66.7 (2)	0.0 (0)	33.3 (1)	8.7	0.033
Mus musculus (house mouse)	0.0 (0)	66.7 (2)	0.0 (0)	33.3 (1)	8.7	0.033
Ochotona pussila (steppe pika)	0.0 (0)	100.0 (4)	0.0 (0)	0.0 (0)	29.7	0.000
Ellobius talpinus (Northern mole-vole)	0.0 (0)	0.0 (0)	100.0 (1)	0.0 (0)	7.2	0.065
Equus hemionus (Asiatic wild ass)	0.0 (0)	0.0 (0)	60.0 (9)	40.0 (6)	39.0	0.000
Felis silvestris (European wildcat)	0.0 (0)	0.0 (0)	0.0 (0)	100.0 (10)	9.5	0.023
Gazella subgutturosa (Persian gazelle)	0.0 (0)	0.0 (0)	80.0 (4)	20.0 (1)	22.5	0.000
Lagurus lagurus (steppe lemming)	0.0 (0)	100.0 (1)	0.0 (0)	0.0 (0)	7.2	0.065
Meles meles (badger)	9.1 (2)	9.1 (2)	0.0 (0)	81.8 (18)	9.7	0.021
Lutra lutra (common otter)	33.3 (5)	6.7 (1)	0.0 (0)	60.0 (9)	-	-
Marmota bobak (steppe marmot)	0.0 (0)	0.0 (0)	0.0 (0)	100.0 (5)	-	-
Rangifer tarandus (reindeer)	83.3 (5)	0.0 (0)	0.0 (0)	16.7 (1)	14.3	0.003
Saiga tatarica (saiga)	30.0 (3)	0.0 (0)	70.0 (7)	0.0 (0)	37.7	0.000
Sciurus vulgaris (squirrel)	0.0 (0)	75.0 (3)	0.0 (0)	25.0 (1)	15.4	0.002
Sicista betulina (northern birch mouse)	0.0 (0)	100.0 (4)	0.0 (0)	0.0 (0)	29.7	0.000
Spalax microphtalmus (northern birch mouse)	0.0 (0)	33.3 (1)	0.0 (0)	66.7 (2)	–	–
Sus scrofa (northern birch mouse)	14.3 (7)	0.0 (0)	2.04 (1)	83.7 (41)	36.4	0.000
Ursus arctos (wild boar)	29.7 (11)	5.41 (2)	0.0 (0)	64.9 (24)	12.1	0.007
Vulpes corsac (European brown bear)	0.0 (0)	0.0 (0)	100.0 (1)	0.0 (0)	7.2	0.065
Vulpes vulpes (corsak fox)	13.0 (3)	0.0 (0)	8.7 (2)	78.3 (18)	8.2	0.042

Note: (χ^2) Pirson coefficient, (*p*) assessment of the possibility of assuming the hypothesis about a random distribution of the taxon frequency by groups.

birch formations on the Baidaratskaya Guba coast). No data on mammals are available for these territories (Table 2, group 1; figure).

Taiga. In the southern area up to 60°–58° N, vast territories were occupied by the taiga ecosystem of pine–birch and larch forests with spruce, fir, and subordinate alder, linden, filbert, and elm. The area south of 66° N was occupied by pine–spruce forests with linden, filbert, hornbeam, and oak. The taiga theriocomplex included reindeer, elk, European bison, roe, brown bear, and others (Table 1, group 1; Table 2, group 2; figure).

Mixed coniferous–broad-leaved forests. Ecosystems of this subzone were represented by two types. Coniferous–broad-leaved and broad-leaved forests with oak, hornbeam, linden, elm, ash, maple, pine, and spruce were developed in the west. The forests were inhabited by elk, European bison, tur, red deer, roe, wild boar, brown bear, wildcat, badger, squirrel, beaver, forest dormouse, fat dormouse, water vole, and others (Table 1, group 4; Table 2, groups 2, 3; figure). Sparse broad-leaved–coniferous and broad-leaved–pine forests with elements of a meadow forest steppe prevailed in the east (east of ~30° E). Tur, roe, squirrel, field

Table 2. Average values of ranks for spore-and-pollen spectra of main plant taxons by section groups

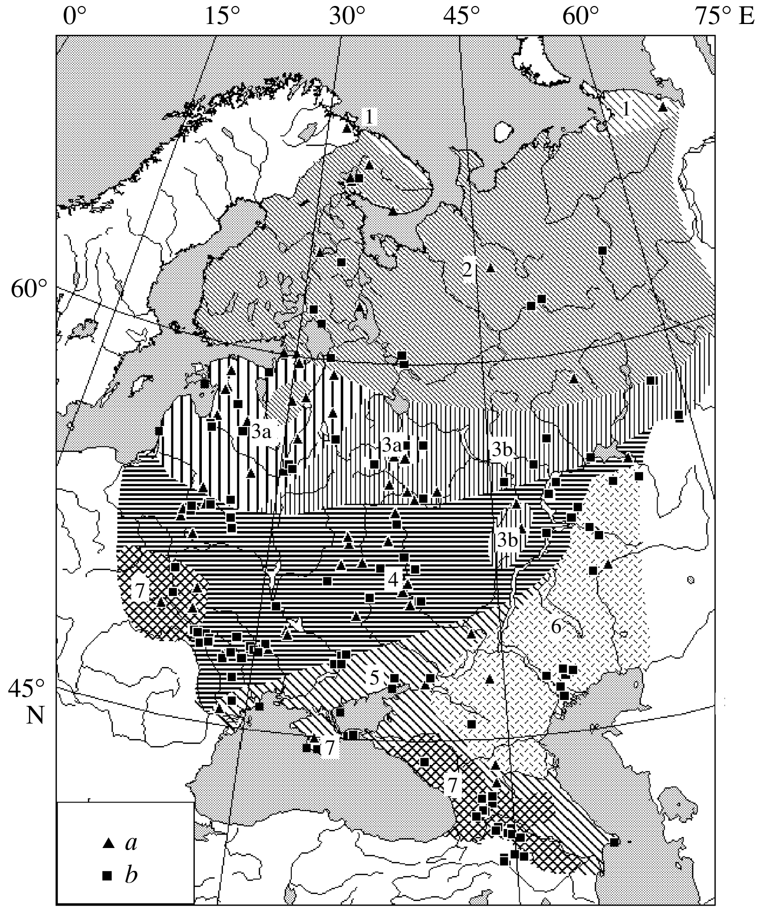
Taxons	Section groups						
	1	2	3	4	5	6	7
Picea (spruce)	0.10	0.37	0.32	0.07	0.03	0.20	0.02
Pinus (pine)	0.40	0.43	0.56	0.21	0.37	0.64	0.10
Betula sect. Albae (birch)	0.68	0.42	0.23	0.18	0.11	0.14	0.12
Betula nana (dwarf birch)	0.54	0.12	0.00	0.01	0.00	0.00	0.00
Alnus (alder)	0.06	0.26	0.43	0.01	0.70	0.25	0.03
Salix (willow)	0.19	0.15	0.13	0.06	0.02	0.00	0.02
Carpinus (hornbeam)	0.25	0.04	0.22	0.00	0.16	0.00	0.03
Quercus (oak)	0.00	0.11	0.44	0.00	0.40	0.00	0.04
Corylus (filbert)	0.02	0.15	0.32	0.01	0.16	0.00	0.02
Tilia (linden)	0.00	0.15	0.22	0.00	0.08	0.00	0.10
Ulmus (elm)	0.07	0.04	0.35	0.00	0.20	0.00	0.01
Caryophyllaceae (pink family)	0.00	0.01	0.01	0.05	0.08	0.20	0.15
Chenopodiaceae (goosefoot family)	0.00	0.05	0.03	0.08	0.08	0.17	0.33
Asteraceae (aster family)	0.04	0.01	0.09	0.05	0.09	0.20	0.15
Cichorium (chicory)	0.00	0.01	0.00	0.05	0.01	0.06	0.34
Artemisia (wormwood)	0.18	0.12	0.08	0.01	0.19	0.43	0.32
Brassicaceae (mustard family)	0.00	0.00	0.00	0.00	0.33	0.00	0.22
Cyperaceae (sedge family)	0.41	0.26	0.16	0.00	0.00	0.14	0.04
Ericaceae (heath family)	0.33	0.02	0.02	0.00	0.00	0.00	0.00
Ephedra (joint fir)	0.00	0.00	0.01	0.00	0.04	0.17	0.37
Poaceae (gramineous)	0.13	0.33	0.16	0.01	0.29	0.58	0.24
Fabaceae (legumes)	0.00	0.03	0.01	0.90	0.09	0.18	0.02
Polygonaceae (buckwheat family)	0.01	0.00	0.02	0.36	0.50	0.00	0.22
Ranunculaceae (buttercup family)	0.23	0.04	0.01	0.25	0.00	0.20	0.12
Bryidae (true mosses)	0.03	0.29	0.11	0.10	0.00	0.46	0.01
Equisetum (horsetail)	0.45	0.17	0.00	0.00	0.00	0.00	0.00
Lycopodiaceae (club-moss family)	0.41	0.06	0.08	0.27	0.08	0.00	0.10
Polypodiaceae (fern family)	0.11	0.32	0.14	0.13	0.09	0.12	0.14
Sphagnum (sphagnum moss)	0.19	0.24	0.04	0.18	0.00	0.15	0.00

mouse, forest dormouse, fat dormouse, water vole, Russian mole rat, common hamster, and others were the dominant animals (Table 1, groups 1, 2; Table 2, groups 3, 4; figure). These distinctions indicate an intensification of the continental nature of the climate from west to east and a decrease in precipitation in the eastern part of the region owing to a weakening of the western atmospheric transfer. The southern boundary of the zone passed at about 53°–54° N.

Forest steppe. Steppe species of plants and mammals dominated south of 53°–54° N. Meadow, forb, and bunchgrass steppes alternating with areas of pine–broad-leaved forests dominated up to 48° N in the western part and up to 51° in the eastern part of the region. The zonal mammal assemblage included tur, roe, forest dormouse, fat dormouse, water vole, Russian mole rat, common hamster, gray hamster, steppe lemming, and others (Table 1, group 4; Table 2, group 6; figure).

Southern forest steppe. The Black Sea, Sea of Azov, present-day Crimean steppes, western Ciscaucasia, and western Caspian Sea regions were occupied by a more xerophile forest steppe where feather–grass and wermuth–grass steppes alternated with hornbeam and oak broad-leaved forests of alder, filbert, and pine groves. European bison, tur, red deer, roe, Asiatic wild ass, wild boar, marmot, Russian mole rat, steppe lemming, and others inhabited this region and Persian gazelle inhabited the western part of the Caspian Sea region (Table 1, groups 3, 4; Table 2, group 5; figure).

Steppe and semidesert. Grass–wermuth, wermuth–goosefoot xerophile steppe, and semidesert occupied the Caspian Sea region, lower reaches of the Volga



Ecosystems of Eastern Europe in the Holocene Atlantic Optimum by theriologic and floristic data. (1) Forest tundra; (2) taiga; (3) mixed coniferous–broad-leaved forests: (3*a*) coniferous–broad-leaved and broad-leaved forests, (3*b*) sparse broad-leaved–coniferous and broad-leaved pine forests; (4) forest steppe; (5) southern forest steppe; (6) steppe and semidesert; (7) mountain and foothill forests and forest steppes. (*a*) Sections with paleobotanical materials; (*b*) mammal localities.

River, and the Ural River basin. Typical representatives of the fauna in this zone were saiga, Asiatic wild ass, Persian gazelle, European bison, tur, corsak, souslik, great jerboa, little earth hare, gray hamster, Northern mole-vole, steppe lemming, social vole, and others (Table 1, group 3; Table 2, group 7; figure).

Foothill and mountain coniferous–broad-leaved forest steppes and forests of the Carpathians, Crimea, and Caucasus. Forest and forest steppe zones of mountain systems, represented mainly by formations with pine, oak, elm, and hornbeam, were inhabited by red deer, roe, European wildcat, wild boar, fat dormouse, and forest dormouse in the Carpathians; obscurus common voles and others in the Crimea; Afghan mole-vole and Radde's hamster in the Caucasus; and Caucasian tur, long-clawed mole-vole and snow vole in the subnival and nival belts (Table 1, group 4; Table 2, groups 3, 6; figure).

Conclusions. Ecosystems of Eastern Europe in the AT3 had a zonal and subzonal structure. According to substantial paleobiological data available, the tundra zone in Eastern Europe was absent at the end of the Atlantic, the forest tundra zone occupying only the northernmost area. During that time, a vast forest zone spanning the entire northern and central parts of the region had already formed. They can be divided into taiga, mixed forest, and broad-leaved forest subzones. The ajoining forest steppe zone south of 52°–54° N extended to the Black Sea coast. This zone included different kinds of forest steppe formed as a result of the hydrothermal regime gradient. Arid steppe and semidesert ecosystems existed in the southeastern part of Eastern Europe.

The zonal structure of AT3 ecosystems is typical for the Pleistocene Interglacial periods [9, 10]. Plants and mammals of a certain group completely occupy or dominate in them. Thus, AT3 ecosystems differ from ecosystems of glacial epochs, in which animal and plant communities were formed from different ecological groups and various geographical zones [11].

The most essential distinctions between the ecosystem chorology of the Atlantic Optimum and Recent period are as follows: (1) the absence of the tundra zone in the northern part of Eastern Europe; (2) narrowing of the forest tundra zone; (3) northward widening of the taiga zone; (4) substantial southward advancement of the forest steppe zone; (5) reduction of the steppe zone that remained only in the eastern part of Eastern Europe. All these features of ecosystems suggest higher temperatures in the studied territory during the AT3. At the same time, the reconstruction indicate that a hydrothermal gradient, probably more pronounced than at present, migrated in the eastward and southeastward directions. This was responsible for the formation of ecosystems of arid steppes and semideserts in the Caspian Sea region and lower reaches of the Volga River. They were similar to ecosystems of Central Asia in terms of fauna.

Thus, based on the combined analysis of voluminous paleobotanical and theriological data, ecosystems of Eastern Europe were reconstructed for the first time for the Atlantic Optimum, the most remarkable warming interval in the Holocene. Methods of multivariate analysis allowed us to obtain the unbiassed structure of the biota. The reconstructions carried out can serve as a model of changes in the natural zonation of Eastern Europe during a potential warming of the climate due to anthropogenic factors.

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