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The importance of ecotonic habitats in the spatial organization of the Late Pleistocene ecosystems of Yakutia

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Abstract. The mosaic of the existing vegetation cover of Yakutia in the Late Pleistocene is due to a combination of arid climate, as well as because of permafrost spreading and frequent fires. The combination of these factors creates necessary conditions for the formation of ecotone natural systems represented by dissipative plant communities. Sparse plant communities are characterized by the absence or weak expression of phytocenotic bonds. Their formation occurs stochastically under the absolute influence of external factors and is genetically entirely dependent on the surrounding vegetation, which acts as a donor of patient and ruderal species. Such processes were characteristic of the Late Pleistocene ecosystems of the Northern Hemisphere. A low productivity of such biotopes did not allow them to act as the main pastures for the representatives of the mammoth megafauna, apart from the saiga and bighorn sheep, but contributed to the increase in the biodiversity of the late Pleistocene ecosystems.

1. Introduction

In the 70s of the twentieth century, the concept of “zone ecotone” was introduced into scientific circulation. This concept meant a transitional state of the natural zone, characterized by the mixing of two different formations, for example, in the form of a mosaic cover [1]. One of the factors determining the existence of ecotone communities is the unstable extreme abiotic environment. Such border communities are usually formed by adding more ancient elements adapted to the microclimatic parameters, with evolutionarily new ones, for example, mixing ancient steppe groups with younger tundra. It was massively distributed in the Late Pleistocene in the Northern Hemisphere.

The mammoth faunistic complex biodiversity significantly exceeded the modern faunas of tundra, deciduous forests, taiga and steppes, which are now common in the same geographical latitudes. It is assumed that the high mosaicity of the vegetation cover due to the currently unparalleled natural and climatic conditions was the cause of such faunistic wealth.

2. Materials and Methods

The paleo-faunistic composition of the orictocoenosis of Yakutia was refined in the course of expedition studies, during which the osteological remains of large Late Pleistocene mammals were collected. In recent years, new osteological remains of *Saiga tatarica* L. and *Ovis nivicola* Eschscholtz have been found, it has greatly expanded the concept of their Late Pleistocene ranges. The age of the finds was determined by radiocarbon analysis. The choice of the saiga and bighorn sheep as an object of research



due to the fact that the saiga is absent in the contemporary fauna of Yakutia, but it is widespread in the steppe zone of Eurasia, and bighorn sheep strictly adheres to the mountain habitat of Northeast Asia.

The description of modern vegetation of Yakutia was carried out by generally accepted geobotanical methods. Paleontomological information is taken from open sources. Reconstruction of quantitative indicators of reconstructed paleoflora was carried out by the method of terioindication [2, 3].

3. Results

During the expeditionary work of 2014-2015, fossil finds of bighorn sheep (*Ovis nivicola Eschscholtz*) were discovered in Khangalassky and Tattinsky districts in the territory of Central Yakutia. The interest to these finds is due to the fact that these animals do not live in these areas at the present time; and there is no mountain relief, which is a prerequisite for modern populations of bighorn sheep. The dating showed that the finds belong to the late Pleistocene. Saiga finds made in recent years on the Bolshoi Lyakhovsky Island and on the Adycha River of the Verkhoyansk District also belong to the Late Pleistocene. Fossil finds of saiga in Yakutia are rare, but they give a general idea of the range of this animal in the Late Pleistocene to the north. More than that, the remains of the saiga have not yet been found in the Aldan-Amga interfluvium and to the south (Central Yakutia) [4].

The contemporary cryoxerophilic communities in the Kolyma basin developing on higher ground with a deflated snow cover in winter and an increased summer draining of the soil surface are less productive [5]. Based on the zooindication features of the pill beetles (*Morychus viridis*) widespread in the Late Pleistocene orictocenosis, the widespread associations formed by *Carex argunensis* Turcz. ex Trev. and *Polytrichum piliferum* Hedw in the Late Pleistocene are assumed [5]. Based on the characteristics of the modern disjunctive area of *Carex argunensis* with the presence of a relict population in the upper reaches of the Kolyma and the frequency of occurrence of residues of *Morychus viridis* Kuzm. et Kor. in the Late Pleistocene orictocenosis, we can assume that in silt, unproductive and rarefied communities involving this sedge were much more common than at present.

4. Discussion

Extreme climatic conditions of the Late Pleistocene of Yakutia were characterized by severe winters, low precipitation, continuous development of the cryolithozone [6].

Extremely low winter temperatures along with low snowfall, which contributed to the soil cooling, and summer desiccation to cryochrons of the Pleistocene led to the extinction of the dominant plant communities on the gentle elevations of the relief, where mountain-steppe, mountain-tundra and ruderal plants, phytocenotically unrelated to each other, occupied free ground in that time. One of the main factors for selecting plants for growing in such empty or ruderal habitats was xerophile combined with tolerance for cooling in winter in the absence of snow cover. This feature could be developed evolutionarily only in mountain dry and cold enough conditions. This is similar to the microclimatic conditions of contemporary *Morychus viridis* habitats, which were characterized by low snowfall and strong winter winds, summer dryness, a wide distribution of sparse chionophobic groups in the vegetation in the stochastic combination of steppe and tundra plants [5].

Sparse plant communities are characterized by the absence or weak expression of phytocenotic links. Their formation occurs stochastically under the absolute influence of external factors and is genetically entirely dependent on the surrounding vegetation serving as a donor of pioneer and ruderal species adapted to the climatic and edaphic conditions, which are decisive in such dissipative communities [7].

Under the conditions of the Late Pleistocene Yakutia, such biotopes could be populated as synusia groups *Carex argunensis*, *Dryas punctata* Juz., *Selaginella rupestris* (L.) Spring., *Empetrum nigrum* L., various steppe cereals, and individual wormwood, willows, grains, and haze species, creating a mixed type of vegetation.

A low productivity of such biotopes did not allow them to act as the main pastures for representatives of the mammoth megafauna, possibly other than the saiga. Since the 19th century, the saiga has been one of the main reasons for the tundra-steppe appearance of the mammoth fauna, personifying its steppe part. But contemporary studies of the ecology and biology of this animal indicate that it is not related to

the steppe, but more to semi-desert communities [8]. B. D. Abaturov and colleagues [9, 10] conducted very interesting studies on the saigas' food preferences, as a result of which it turned out that saigas try to avoid eating cereals in the presence of haze and buckwheat ones in pastures. As a result of research, it is also found that saigas prefer biotopes that have undergone pasture digression with a large number of weeds: *Kochia prostrata* (L.) *Scrad.*, *Ceratocarpus arenarius* L., *Bassia sedoides* (Pall.) *Asch.*, *Chenopodium album* L. of the haze family, *Polygonum aviculare* L., *Polygonum patulum* M. Bieb. from the buckwheat family, *Potentilla bifurca* L. from *Rosaceae*, and others. Some of these species are noted in the paleofloristic complex of the Late Pleistocene of Yakutia, such as *Polygonum aviculare*, *Descurainia Sophia* L., and others (such as *Kochia prostrata* being present in the contemporary Yakut flora), and it was likely more widespread in the Late Pleistocene. Thus, a saiga with a wider distribution of ruderal communities in northeast Asia was provided with food supply to a sufficient extent. It should be noted here that *Kochia prostrata* necessarily grows in the contemporary saiga reproductive stations [8].

The saiga's remains in the Pleistocene sediments of Yakutia indicate a wide distribution of ruderal communities, composed of the haze, buckwheat, cruciferous, aster, and cereals in the Late Pleistocene. It is possible that these remains indicate being even more widespread than they are now, despite the increased anthropogenic load on the phytocenoses, which has recently led to an increase in the areas of ruderal communities of anthropogenic origin. Most likely, this is due to the fact that exogenous factors in the formation of vegetation cover prevailed over endogenous factors in the Late Pleistocene. In turn, this led to an increase in the role of stochastic communities of price-phobic ruderals in the regional natural system and, accordingly, a decrease in the role of climax communities.

The presence of saiga in the Late Pleistocene faunistic complex of northeastern Asia also indicates a low snow cover in winter. This correlates well with the hionophobia of the *Carex argunensis* associations, possibly widespread in the Late Pleistocene, judging by the number of *Morychus viridis* in oritocoenosis and the presence of not only the saiga antelope but also the bighorn sheep and the musk ox in the fauna. The musk ox, being a typical tundra species, also prefers a zone of polar deserts with a very rarefied vegetation cover and low snow cover. That is, both saiga and musk ox are those species which depend on the height of snow cover in winter, and they are adapted to winter pastures of semi-desert type with a sparse cover. A bighorn sheep, also being a part of the mammoth faunistic complex, belongs to the same animals. In the Late Pleistocene, winters were characterized by low snowfall [6], and the areas of ruderal and wasteland dissipative communities in the Late Pleistocene of Yakutia surpassed the contemporary areas.

5. Conclusion

A wide distribution of ruderal and cryoxerophytic grass wading communities in the late Pleistocene of northeastern Asia is confirmed by the finds of saiga, *Morychus viridis*, as well as a large number of macro-remains of haze, buckwheat, and crucifers in the Late Pleistocene oritocoenosis. In complex, all these findings, as well as the presence of cohabitation of saiga and bighorn sheep, indicate a wide distribution of stochastic ruderal and cryoxerophytic grass wastelands. Such communities could form and spread due to extreme macroclimatic factors (low winter and high summer temperatures, little snow in winter), leading to cooling in winter and drying of the upper soil horizons in summer. Also, the following influenced their formation: a spread of permafrost with cryogenic processes of swelling, leading to the formation of micro and meso-positive landforms; a trampling of grass by large herd mammals (mammoths, bison), which initiated and enhanced the processes of pasture digression.

The biodiversity of the Late Pleistocene ecosystems in Yakutia was much higher than the current one. Similarly, a spatial organization of landscapes was more complex than it is at present. Contemporary microgroupings of xerophilous steppe, mountain-steppe, and ruderal plants in the Late Pleistocene were more widespread, creating an ecotonic effect and diversifying the ecological niches of some large mammals, such as the saiga and bighorn sheep. It is possible that even more numerous mammoths with bison found their feeding stations in the Late Pleistocene, presently represented by intrazonal or azonal plant communities occupying small areas.

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