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RESEARCH ARTICLE

Small mammal communities of Tuva Republic (Southern Siberia, Russia) in a changing climate

Sergey O. Ondar[1], Sergey N. Kirpotin[2, 3], Andrey S. Babenko[2],
Bogdan A. Mikhaleiko[2], Nikolay I. Putintsev[1], Aleksey V. Surov[4],
Orlan Ch. Oidupaa[1], Andrey M. Samdan[1], Aivar V. Kuular[1],
Bailak S. Mondush[1], Dayana S. Ondar[1], Pradip Kumar Kar[5],
Aldynay O. Khovalyg[1], Anatoly F. Chuldum[6]

1 *Tuvan State University, 36 Lenina St., Kyzyl, 667000, Russia*
2 *National Research Tomsk State University, 36 Lenina Ave., Tomsk, 634050, Russia*
3 *The Institute for Water and Environmental Problems of the Siberian Branch of the Russian Academy of Sciences (IWEP SB RAS), 1 Molodezhnaya St., Barnaul, 1656038, Russia*
4 *A.N. Severtsov Institute of Ecology and Evolution, Russian Academy of Sciences, 33 Lenina Ave., Moscow, 119071 Russia*
5 *Parasitology Research Laboratory, Department of Zoology, Cooch Behar Panchanan Barma University, Panchanan Nagar, Vivekananda St., Cooch Behar, West Bengal , 736101, India*
6 *Tuvinian Institute for Exploration of Natural Resources of the Siberian Branch of Russian Academy of Sciences (TuvIENR SB RAS), 117a Internationalnaya St., Kyzyl, Tuva Republic, 667007, Russia*

Corresponding author: Bogdan A. Mikhaleiko (xoxoxanas123@gmail.com)

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Abstract

An important indicator of the integrity of the biosphere is biological diversity. Rapid changes in global climate directly affect the biodiversity of ecosystems as a whole. Tuva is a region with unique landscapes that determine the biodiversity of flora and fauna with globally significant endemic and rare species. The patterns of formation and development of communities of small mammals are considered; the role of factors of the physical-geographical environment, phylogeographic distribution of individual species and their phylogenetic relationships in the formation of certain communities is presented as part of the general law of the formation of biological diversity. The modifying influence of global and regional climate factors is shown, which leads to the exchange of communities within bioclimatic zones: the relative abundance and expansion of the range of humid territories increases; with the expansion of the pika's range, the ranges of specialized seed eaters also expand; an expansion of the ranges of forest species into the steppe zone and a reduction in the number of species in desert and dry steppe zones is recorded.

Keywords
Small mammals, boundary space, zoogeographic boundary, orography, transect, ecological and phylogenetic relationships, co-evolutionary relations, ecosystem transformation, Tuva

Introduction

Small mammal communities are one of the main populations of terrestrial vertebrate species and play an important role in the biodiversity of Tuva's ecosystems. Currently, 52 species of small mammals belonging to 3 orders have been noted here, which, due to their characteristics, serve as a convenient model group for studying the processes of fauna formation and the organization of vertebrate communities in heterogeneous conditions of a complexly dissected physic-chemical and biogeographic transition space. A number of works are devoted to the study of this issue (Yudin 1979; Shvetsov 2001; Dayrat 2005; Vinogradov 2010; Davison et al. 2011), but a comprehensive analysis of this region has not been carried out until recently.

The research area is a border between the taiga, steppe and desert sub-districts of Eurasia, including the mountain systems of the Western and Eastern Sayan, the East Tuvan Highlands, the Tannu-Ola ridge and four large intermountain basins – the dry-steppe Tuvan, semi-desert Ubsu-Nur, taiga Togin and forest-steppe Turan. According to the longitude gradient from north to south and the latitude gradient from west to east, the degree of continentality of the climate and the general xerophytization of landscapes increases. The most important meridional zoogeographic boundary of the Palearctic also passes here – the Yenisei zoogeographic boundary, which arose in the Late Cenozoic as result of differences in the geological history of the mountains of southern Siberia (Revushkin 1987; Shvetsov 2001; Vinogradov 2010).

From the orographic point of view, the studied territory consists of rows of mountain chains with an absolute height of up to 4 thousand m separated by intermountain basins from 500 to 1500 m above sea level.

The Tuvan basin is bounded from the north by the Western Sayan, from the northeast by the Academician Obruchev range, from the east by the spurs of the Sangilen highlands, from the south by the Western and Eastern Tannu-Ola ranges. According to the floristic division of the land, the Tuvan basin, the northern macro slope and the highlands of the Tannu-Ola is part of the Altai-Sayan province of the Circumboreal region of the Boreal Sub-Kingdom. To the south of Tannu-Ola is the Ubsunur basin, the northern relatively small part of which enters Russia, and the main part continues into the basin of Large Lakes located between mountain systems Mongolian Altai and Khangai. The low-mountainous part of the southern macro slope of Tannu-Ola and the basin of Large Lakes (including the Ubsunur basin) belongs to the Mongolian province of the Central Asian sub-district of the Iran-Turan region of the Ancient Mediterranean sub-kingdom (Vinogradov 2010; Ondar 2015; Namzalov et al. 2019; Kirpotin et al. 2021).

The transitional space between North and Central Asia is a convenient model territory for searching for spatial boundaries where there is a qualitative change in the species composition of small mammal communities, their connections with the main bioclimatic gradients of the environment, primarily with the hydrothermal regime and the nature of vegetation cover.

The goal of this work is to analyze the features of the composition and structure of communities of small mammals (insectivores, hares and rodents) in Tuva (Fig. 1), the history of fauna formation and identify current trends in connection with a new cycle of temperature increase in the region.

Special attention was paid to the promotion of environmental and phylogenetic relationships between the structure of small mammal communities and landscape features of their habitats, as well as to the story of their formation (Ochirov et al. 1975; Erbajeva et al. 2000; Williams et al. 2002; Lyapunov 2003; Lebedev et al. 2007; Atopkin 2007; Lavrov et al. 2008; Kovalskaya et al. 2011; Ondar 2015; Bannikova et al. 2018; Poplavskaya et al. 2018; Frisman et al. 2019; Lebedev et al. 2019).

Figure 1. Geographical location of the Republic of Tuva.

Materials and methods

To achieve this goal, small mammals were counted at 5 key sites located along model profiles of the meridional direction in all altitude zones – from high-altitude tundra to steppe basins (Fig. 2).

The actual materials of the work were collected within the framework of comprehensive multi-year studies carried out in the period from 2007 to 2023 on the territory of Tuva. The work also uses materials collected by various authors in this territory in the 1950s and 1980s, These data available in the sources obtained in the second half of the last century (Yudin et al. 1979; Yakimenko 2003; Galewski et al. 2006; Atopkin et al. 2007; Lebedev et al. 2007; Kovalskaya et al. 2011; Boyarkin 2012; Bannikova et al. 2018; Poplavskaya et al. 2018; Kislyi et al. 2019; Lisovsky et al. 2019; Frisman et al. 2019; Chabovsky et al. 2019; Lebedev et al. 2019; Ondar et al. 2021).

The studies were carried out in key areas along the transect laid through typical biotopes of the studied territory (Fig. 2). Animals were captured using the standard method of fishing grooves (50 m in length, with 5 cones) (Vinogradov 2010) and crushers in a single period (the growing season is since July to August). The data from the sites were averaged, and the materials collected in different habitats of the same site were combined, which made it possible to minimize errors associated with differences in volumes and timing of capture, as well as with different phases of the number of individual populations. In total, more than 6.456 cone-days and 2.437 pressure-days were worked out. The total volume of the studied material amounted to 2.844 individuals belonging to 52 species of small mammals.

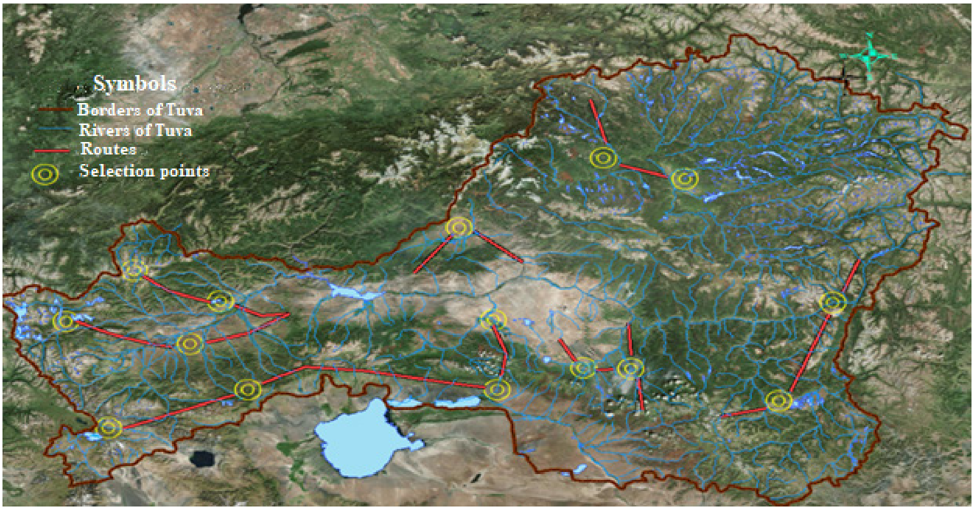

Figure 2. Overview map and research routes.

To characterize the structure of community dominance, a modified score was applied based on the dominance index (Vinogradov 2010; Ondar et al. 2021), which reflects the ratio of species in communities (I.D., %): 4 – dominant (I.D. > 10), 3 – ordinary (10 > I.D. > 3), 2 – rare (3 > I.D. > 1), 1 – single (1 > I.D.), 0 – not marked, – no data. The determination of the similarity of small mammal communities in different key sites was calculated by the Chekanovsky-Sorensen index for quantitative features. The analysis of changes in the composition of fauna occurring over time is calculated by the Cody index: B = (g(n) + p(n)) / 2, where g(n) is the number of species added to the transect; p(n) is the number of species eliminated in the same transect (Vinogradov 2010).

Among the variety of external factors influencing the formation of the composition and structure of small mammal communities, climate is of particular importance as a directly acting factor determining the altitude range of the entire bioclimatic link of mountain landscapes. Therefore, when selecting key sites, the scheme of bioclimatic zones of the mountains of Southern Siberia, developed at the V.N. Sukachev Institute of Forest SB RAS, was used (Fig. 3) (Shvetsov 2001; Vinogradov 2010), where the following facies are distinguished: a) humid – northeastern Tuva (Todzhinskaya basin), the boundary of the site is outlined by a dark green line; b) semi-humid – Turan basin, northern macro slopes of Tannu-Ola, light green line; c) semi-arid – Tuvan basin and Mongun Taiga, red and brown line; d) arid – Ubsu-Nur basin, yellow line.

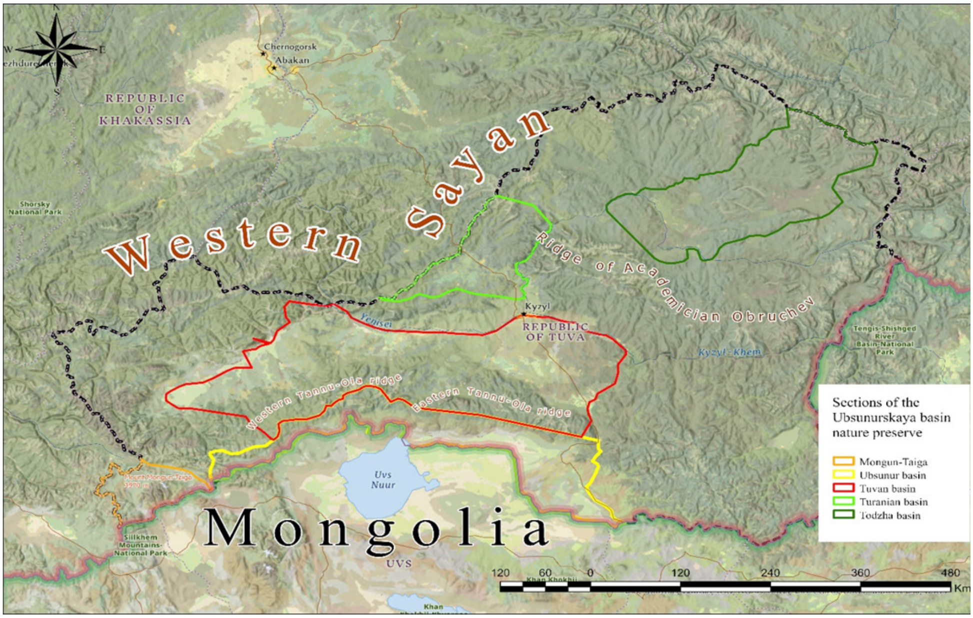

Figure 3. The location of key sites (1–5) relative to the geographical and climatic facies (humidification sectors) of the mountains of Southern Siberia. Dark green line – humid Todzha basin, light green line – semigumid (moderately humid), Turanian basin, red and brown line – semiarid (insufficiently humid) Tuvan basin and the Mongun-Taiga, yellow line – arid, Ubsu-Nur basin (Vinogradov 2010; Lebedev et al. 2019).

The geographical and climatic facies (humidification sectors) are marked on the schematic map of the basins and the Mongun-Taiga massif in accordance with the nature of the hydrothermal regime, the composition of the vegetation cover and the type of soil. The principle of allocating key areas is related to the approach of laying a profile – from a high (dominant ridges) to a low point (bottoms of basins) above sea level in the north-south direction. The main climatic indicators within the facies have their own characteristics. The humid facies is characterized by a sum of active temperatures of 1200–1700° and precipitation of 450–800 mm. Within the semi humid facies, the sum of active temperatures reaches 1200–1600°, and precipitation decreases to 300–500 mm. The semiarid facies, confined to the southern macro slopes of the ridges and elevated intermountain steppe basins, is characterized by the sum of active temperatures of 1100–1600°, precipitation – 350 mm. The arid facies is characterized by the sum of active temperatures of 1000–1300°, the amount of precipitation is less than 200 mm.

The methodology of molecular genetic analysis. Molecular genetic analysis for the study of the genetic structure and analysis of phylogenetic lines of populations of the following species: *Cricetulus barabensis* (Pallas, 1773), *Cricetulus longicaudatus* (Milne-Edwards, 1867), *Phodophus campbelli* (Thomas, 1905), *Lasiopodomys gregalis* (Pallas, 1779), *Alexandromys oeconomus* (Pallas, 1776), *Urocitellus undulatus* (Pallas, 1778) were used muscle tissue samples fixed in 96% ethanol.

Total DNA was isolated using a set of reagents Diatom DNA Prep 200 OOO Isogen Laboratory (Moscow, Russia) according to the manufacturer's instructions. The resulting DNA solutions were stored at a temperature of –18°C. The mtDNA locus was used as a marker of phylogenetic lines: the complete cyt b gene (1140 bp). Primers described in the article were used to amplify cyt b (Matveevsky et al. 2014). PC reaction conditions: I – 94° – 3 min. II – (94° – 1 min, 54° – 1 min, 72°– 1 min 40s) x 30 cycles; III – 72° – 3 min.

When determining the nucleotide sequences of mtDNA, the obtained PCR products were purified by re-precipitation in an ethanol-acetate buffer with washing with 70% ethanol. The result was visualized by electrophoresis in 1.5% agarose gel in the presence of ethidium bromide. The purified PCR product was used as a matrix for staging termination reactions with each of the two primers used for locus amplification. The terminating reaction was carried out on the basis of a set of reagents BigDye Terminator v.3.1 (Applied Biosystems, USA) according to the manufacturer's instructions. Nucleotide sequences were determined by capillary electrophoresis on automatic analyzers. Nucleotide sequences were determined on an automatic analyzer AB 3130 and AB 3500 (USA). For each sample and site, the determination was done twice – with the formulation of a reaction with a direct and reverse primer. The combination of the obtained individual sequences and their alignment were performed using the BioEdit v.7.0.1 program (Hall 1999) with manual correction (Galewski et al. 2006; Conroy et al. 1999; Buzan et al. 2008; Brumstein 2009).

To study the structure of time series and build models of the dynamics of the number of small mammals, a 2,367-year tree-ring chronology was used for the Altai-Sayan region (Mongun-Taiga mountain range) (Myglan et al. 2012).

Discussion

A brief geological history of the research area

The orographic and tectonic structure of the research area belongs to one of the most complex in the world. The modern macro-relief of Tuva and Southeastern Altai was formed mainly during the Mesozoic and Cenozoic. Orogenic activation of the territory occurred along the lines of the oldest tectonic faults, which caused the intensity of block uplifts of varying degrees (Ondar et al. 2021). In the Mesozoic, at the end of the Jurassic or Early Cretaceous, a platform mode is established. During this period, the processes of denudation leveling prevailed against the general background of the slow arched uplift of the territory. The relief as a whole consisted of low-ridge and hilly-humped elevations against the background of vast leveled plains.

At the beginning of the Jurassic, the lowlands were dominated by hilly-flat terrain, at the same time, the mountain elevations that separated them reached a height of 2000–3000 meters. The Tuvan basin with the surrounding hills was the most elevated. In the presence of connections between the Tuva depressions and the Pre-Altai zones of Mongolia, there was a flow of the Praenisei system to the south, into the Basin of Large Lakes and further to the southeast through the depressions of Central Mongolia towards Western Trans Baikal.

The territory located to the east of the Yenisei, together with the Altai-Sayan mountain country, begins to rise. The Ulugh-Khem depression lags somewhat behind the general movement, and perhaps some of the intermountain depressions and individual parts of the Prisayan trough. Probably, in the Early Cretaceous, the alluvial-lacustrine Tuvan basin had a drainage character.

The beginning of the Eopleistocene (2–0.6 million years ago) was marked by small block uplifts and the accumulation of alluvial sand-pebble and gravel deposits in the still weakly embedded ancient valleys of the Todzhinsky basin, as well as dense blue loams that preserved the pollen of Eopleistocene plants. At the same time on Sangilen, in the basin of Lake. The area formed in the graben at the junction of tectonic zones of two directions was layered with lake loam.

The further increase in tectonic stresses led to rapid and deep (in the central parts of the mountain structures – up to 1000 m) erosive dismemberment. During this period, powerful coarse proluvial breccias of brownish tones accumulate along the formed erosive-tectonic and tectonic stages on the sand-pebble deposits of the first half of the Eopleistocene. Such deposits are typical along the southern side of the Tannu-Ola, in the far west of Tuva in the valleys of Mogen Buren and Karga, as well as on the outskirts of Sangilen. The deposits was overlain by the Lower Pleistocene glacial complex. In the valleys of large rivers (Biy-Khem, Ulug-Khem, Khemchik, Balyktyg-Khem), a basement of 80–150-meter terraces of the upper (pre-glacial) complex is formed and brown pebbles are deposited in the lower part of the section of these terraces. At the same time, deposits of boulders and pebbles of the lake were formed. Noyon-Khol and Ham-Cheeses containing pollen of broad-leaved plants.

The presence of brown pebbles of Eopleistocene age in buried valleys in the Tuvan and Ubsu-Nur basins, at an altitude of several hundred meters above water level and within the highly elevated watersheds of Tannu-Ola, indicates the existence of post-Pleistocene movements.

Simultaneously with the uplift of mountain ranges and the isolation of tectonic basins in the north-east of Tuva, grandiose volcanic eruptions occurred, under the tuffs and lavas of which the ancient surface of the alignment and the deluvial and alluvial deposits overlapping it were buried. The volcanic-clastic strata (tuffs, lavas, tuff-alluvium) are deposits synchronous with the intensification of tectonic stresses in the Eopleistocene time (Ondar et al. 2021).

The start time of the Tannu-Ola lifts, judging by the findings of fauna in the continental sediments of the Ubsu-Nur basin, is defined as the Pliocene (5.3–3.6 million years ago) and forms a fairly high-level botanical and geographical boundary, dividing territories belonging to different sub-kingdoms of the Holarctic kingdom. As a result of the the Tannu-Ola erection, the Tuvan basin, which is a northern enclave of Mongolian landscapes, was isolated (Myglan et al. 2012; Matveevsky et al. 2014; Lebedev et al. 2019).

A special biogeographic boundary in the studied territory is the large river of Northern Asia – the Yenisei, on its left and right parts there are intermountain depressions – Tuva and Turanskaya.

On the southwestern edge there is a high-altitude isolated Mongun-Taiga massif, in a sharply continental arid province in the center of the Altai-Sayan mountainous country and is separated from the western and northwestern territories with a continental climate by the Shapshal Ridge and the Tsagan-Shibetu Ridge. The tendency to uplift and tectonic instability of the mountain range have persisted to this day, as evidenced by tremors with a force of up to 10 points.

Results

Formation of small mammal communities in Tuva in a changing climate

The formation of modern communities of small mammals has a long history. In paleontological finds in the Tuvan (Taralyk-Cher) and Ubsu-Nur basins (Holu) of the late Miocene-Pliocene, chipmunks, jerboa and hamsters were already present (Lavrov et al. 2008). Abrupt climate changes towards cooling, aridization and mountain formation, which actively manifested themselves at the turn of the Late Pliocene and Early Pleistocene, initiated the transformation of the structure of communities of living organisms, which fully took shape in the Pleistocene.

The changes in the natural environment and climate during the Pleistocene were directional. Accordingly, adaptations and life forms were associated with low heat supply and an increasing continental climate. The general direction of the process was complicated by periodic fluctuations, which were caused by the alternation of relatively dry and wetter climatic phases. The structure of the vertical belt was more complicated than the modern one. Throughout the Middle and Late Pleistocene, the mosaic of communities was preserved, which was determined by the peculiarity of the climate, differences in the exposure of slopes, the orientation of ridges and river valleys.

The basis of the plant communities of the mountainous region were autochthonous coniferous forests. The introduction of steppe and semi-desert mammal species came from the south – from Kazakhstan and Mongolia, through a system of pronounced intermountain basins. Elements of tundra and boreal communities partially penetrated from the Yenisei territories, some of them descended from the char belt, which was a refuge for them during the interglacial epoch. Even small changes in average annual temperatures and humidity led to increased expansion of one or more zonal ecosystem types and created a common unique mosaic of landscape conditions.

The study of the evolution of a species over large geographical areas is useful not only for comparative phylogeography, but also for solving problems of allopatric speciation and intraspecific taxonomy. At the same time, the identification of genetic differentiation of species is an effective tool in the study of the processes of community formation and speciation in general, due to various environmental factors, including changes in climatic conditions. Based on the data of genomic analysis, a scheme for the formation of the modern range of small forest and field mice was developed (Atopkin et al. 2007). Thus, phylogeographic studies of two Western Palearctic species of *Sylvaemus*: *S. sylvaticus* (Linnaeus, 1758) and *S. flavicollis* (Melchior, 1834), with which *S. uralensis* (Pallas, 1811) is sympathetic in the European part of its range, have shown that global climatic changes played a significant role in the formation of the genetic and geographical structure of their populations (Atopkin et al. 2007).

According to the findings of the Lower Pleistocene deposits in the research area, the population of terrestrial small mammals was dominated in forest communities. During the entire Pleistocene, there was a gradual increase in the number of steppe species of small mammals and a simultaneous decrease in the number of forest species. At the same time, glaciations of various types in the Eurasian continent determined latitudinal migrations from both the west and the east.

Also, for the studied communities of small mammals, a significant genetic differentiation of populations is a characteristic feature. The degree of depth of genetic variation in the mitochondrial genome shows long-standing isolation under Pleistocene refugium conditions and the history of post-Pleistocene settlement.

Sylvaemus uralensis and *Apodemus agrarius* (Pallas, 1771) were recorded by different authors on the periphery of the research area, but were not recorded in Tuva. The appearance of the first specimens of these species was recorded in 2018–2019 in the Todzhinsky basin. The low level of gene flows and the absence of "southern" genetic links between the European and Asian races of *S. uralensis* suggests that the migration of the animal in the southern direction was less intense in the Pleistocene and later, to maintain contact between the races. The differentiation of the geographical races of *S. uralensis* occurred over 2 million years ago, perhaps as a result of the emergence of an ecological barrier between the races in the form of a dry climate zone with an increase in the proportion of steppe landscapes. The ecological conditions in the Asian and European parts of Russia allowed the geographical races of the lesser forest mouse to evolve separately from each other for a long time in different climatic zones, as result of which they achieved such differentiation at the mtDNA level that allows them to be considered species at the stage of formation. Contact between the races apparently did not resume, despite the recent demographic changes within each of them, so we should expect the formation of two independent species from two geographical races of the lesser forest mouse in the studied territories.

The interspecific genetic distances in *Apodemus* vary more widely (d=7.7%–20%), compared with species of the genus *Sylvaemus*. The topology of *Apodemus* species in different phylogenetic reconstructions is preserved with high statistical support at the level of species clusters. The species are joined into two large groups (without statistical support). The first group includes the species *A. agrarius*, *A. chevrieri* (Milne-Edwards, 1868) and *A. speciosus* (Temmnick, 1844), the second – *A. peninsulae* (Thomas, 1907), *A. argenteus* (Temmnick, 1844), *A. draco* (Barrett-Yamilton, 1900) and *A. semotus* (Thomas, 1908). The divergence time of the *Apodemus* species group, according to the values of genetic distances according to mtDNA data, is 3–8 million years, and the time of divergence of geographical isolates of *A. agrarius* is about 300 thousand years ago (Frisman et al. 2019).

The vast continental range of the field mouse is divided into two isolated parts. In the presented study, we tried to identify the initial stages of the formation of intraspecific genetic subdivision due to the geographical barrier. The studied animals were represented by the six equal samples from both parts of the continental range. The population level of subdivision of the species was revealed, reflecting the course of settlement of the field mouse from east to west. The greatest polymorphism at five loci is observed in the eastern, older part of the range. Specific alleles are present in both the eastern and western isolates, but their number is lower in the latter.

The hypothesis of two-fold and multidirectional migration of representatives of the Hedgehog and Squirrel families through the Beringian land in the Pliocene is supplemented with facts (Lyapunova 2003). Recent molecular genetic studies indicate a monophyletic North American origin of the genus *Marmota*, and in the region the oldest find of the Mongolian marmot *Marmota sibirica nekipelovi* (Yerbayeva, 1966) from the Tologoi (southern Siberia), dated to the Early Pleistocene (Devyashin et al. 2019). The origin of the Khangai subspecies *Marmota sibirica caliginosus* (Bannikov & Skalon, 1949) is associated with the psychroarid regions of Central Asia (Tuva, western and central Mongolia). In the Holocene, the habitat of the grey Mountain Asian or Altai marmot *Marmota baibacina* (Kastschenko, 1899) occupied the mountain ranges of Altai, Sayan and Tien Shan, Eastern Kazakhstan and southern Siberia (Tomsk, Kemerovo and Novosibirsk regions). The Tuvan "pulsating" range of the Altai marmot enters the southwestern mountainous part (the Mongun-Taiga massif, the spurs of the Western Sayan). The genus of mountain voles (*Alticola*) is of Central Asian origin. It is shown that the Olkhon vole is a valid species, forming with the Khangai vole *A. semicanus* (Allen, 1924) and *A. tuvinicus* (Ognev, 1950) a single group of closely related species, sister to the flat-headed vole *A. strelzowi* (Kastschenko, 1901) (Atopkin et al. 2007). The topology of phylogenetic trees constructed using maximum likelihood (ML) and nearest neighbor binding (NJ) methods turned out to be similar. Four distinct clusters of mitotypes with high bootstrap supports include five clades (Fig. 4).

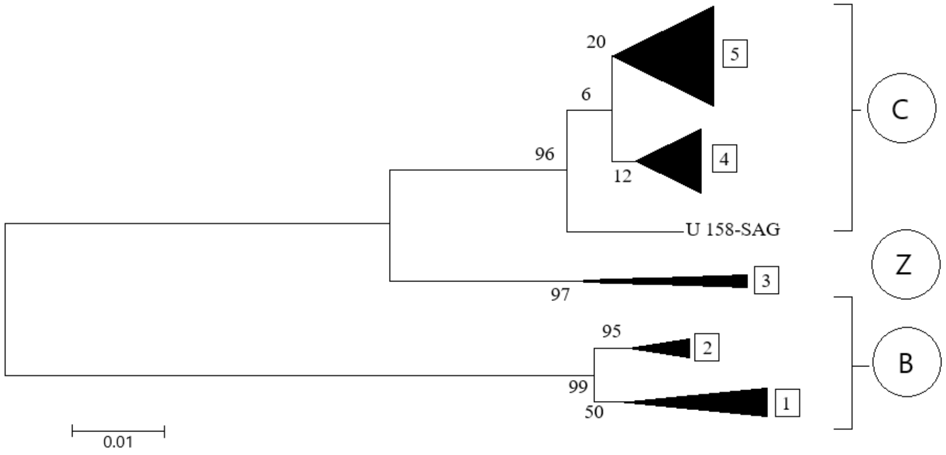

Figure 4. Phylogenetic tree (ML) of the long-tailed ground squirrel CP haplotypes combined into 5 clades (indicated by numbers within the framework). The numbers in the nodes are bootstrap indexes. The letters in the circles indicate groups of populations: B – eastern populations (Baikal Region, Olkhon Island – Irkutsk region, Eastern Mongolia), C – Central populations (Tuva basin, Western and Central Mongolia, Western Buryatia west of the Selenga River), Z – western populations of Altai (Chabovsky et al. 2019).

The first two clearly isolated clades (the distance between them, dp = 0.026±0.004, to the remaining clades: 0.066–0.073) represent exclusively eastern populations in the Baikal region, on Olkhon Island (Irkutsk region) and in eastern Mongolia (Figs 4, 5).

The second clade, found exclusively in the Baikal region and on Olkhon Island, differs from the sister first clade and from all the others in significantly lower haplotypic and nucleotide diversity. In the Baikal region, including on Olkhon Island, representatives of both clades meet syntopically.

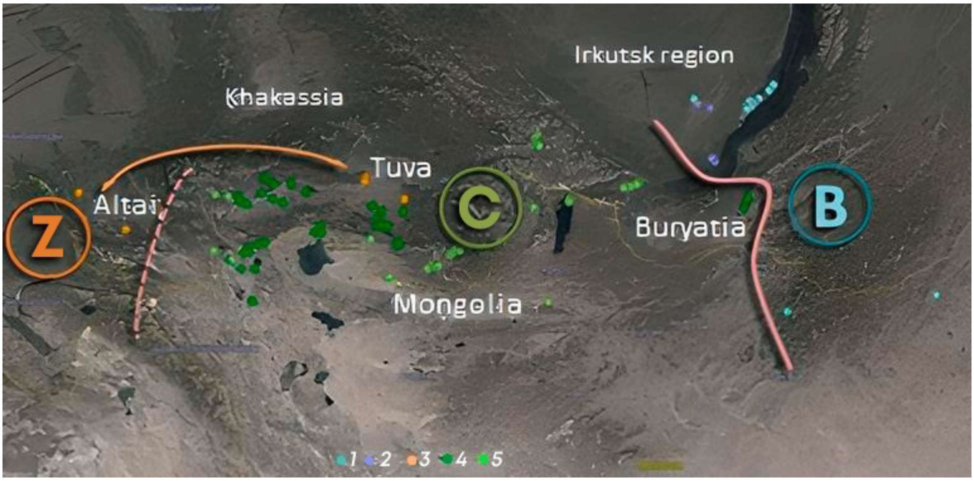

Figure 5. Phylogeography of the long-tailed ground squirrel based on the results of the analysis of the variability of the control region (mtDNA D-loop). 1 – clade 1, 2 – clade 2, 3 – clade 3, 4 – clade 4, 5 – clade 5. The letters in the circles correspond to the groups of clade in Fig. 6. The lines limit the groups of populations. The arrow shows the torn area of the Altai clade 3 (Chabovsky et al. 2019).

The third clade, the Altai, represents Western populations and is much more diverse than all the others. It is well genetically isolated from other clades (dp = 0.039–0.071) and unites two branches: the Altai proper and the branch geographically remote from it and isolated by the Yenisei on its right bank in the central group of populations.

The fourth and fifth clades, occupying a vast central area between western and eastern populations from western Tuva and Mongolia to western Buryatia (to the Selenga River), are weakly genetically isolated from each other (dp = 0.022±0.004, distances to others: 0.039– 0.073). Rather, they are geographically separated from each other, although they occur syntopically in places: the fourth clade occupies the central and western parts of Tuva and Mongolia, the fifth – the central and eastern parts of Tuva, central Mongolia and western Buryatia to the Selenga River. The central treasures border the Baikal and East Mongolian treasures in the east, and the Altai treasure in the west and north (Fig. 4).

Studies of the phylogeographic structure of Tuva communities have shown the following (see Suppl. material 1: Table 1). The modern mixed-origin fauna of small mammals includes 52 species of three orders: hares (Lagomorpha) (4 species), rodents (Rodentia) (41 species) and insectivores (Eulipotyphla) (8 species). Hare-like mammals are represented by 1 genus and 4 species, rodents – by 28 genera and 41 species, insectivores – by 4 genera and 8 species. In the early generalizing summaries of small mammals for Tuva, 47 species were presented (Conroy et al. 1999; Williams et al. 2002). Five more species were added as previously undescribed for this territory or as new ones, the species independence of which is shown by new morphological and molecular genetic methods (Yakimenko 2003).

Using correlation analysis methods, similarity coefficients were calculated between individual areas of the territory, which showed significant differences in the structure of small mammal communities (Fig. 6, 7, 8, 9). Minimal similarity is revealed between the following communities: with coefficient (9) of the Todzhinsky basin and the Mongun Taiga massif (0,253–0,337–0,356–0,416); from (5) Ubsu-Nurskaya and Todzhinskaya basin (0.253–0.337–0.356–0.416); from (5) Ubsu-Nurskaya and Todzhinskaya basin (0.376–0.384–0.423–0.386); from (10) the Tuvan basin and the Mongun-Taiga massif (0.333–0.375–0.4–0.419); from (2) Tuva and Todzhinskaya basins (0.384–0.437–0.431–0.412). The maximum similarities between the studied communities were noted for the following populations: with a coefficient (3) of the Tuvan and Turan basins (0.477–0.455–0.482–0.487), Ubsu-Nur and Turan (0.407–0.403–0.442–0.433); from (7) the Ubsu-Nur basin and the Mongun-Taiga massif (0.4–0.426–0.441–0.453); from (10) the Turan basin and the Mongun Taiga massif (0.32–0.4–0.42–0.418); from (8) the Togin and Turan basins (0.441–0.444–0.457–0.435); from (1) Tuva and Ubsu-Nur basins (0.375–0.342–0.432–0.447).

Also, when conducting cluster data analysis in the 1950s and 1960s, according to the "near neighbor" principle, two clusters were obtained using an agglomerative hierarchical classification algorithm, the distance between which is P=0.0886. The usual Euclidean distance is used as the distance between objects.

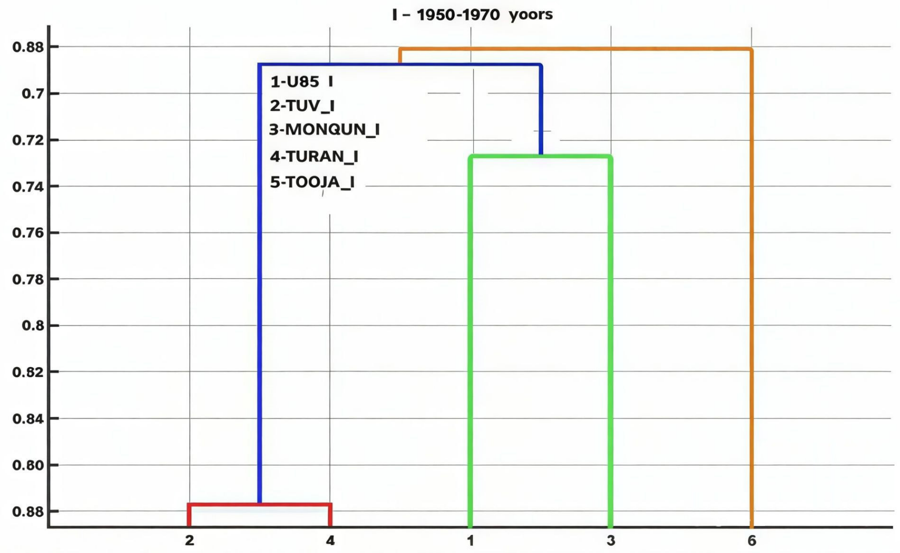

Figure 6. Dendrogram of the degree of similarity of small mammal communities in the basins and mountain range of Tuva in the 1950s and 1970s. The numbers correspond to the numbers of bioclimatic zones.

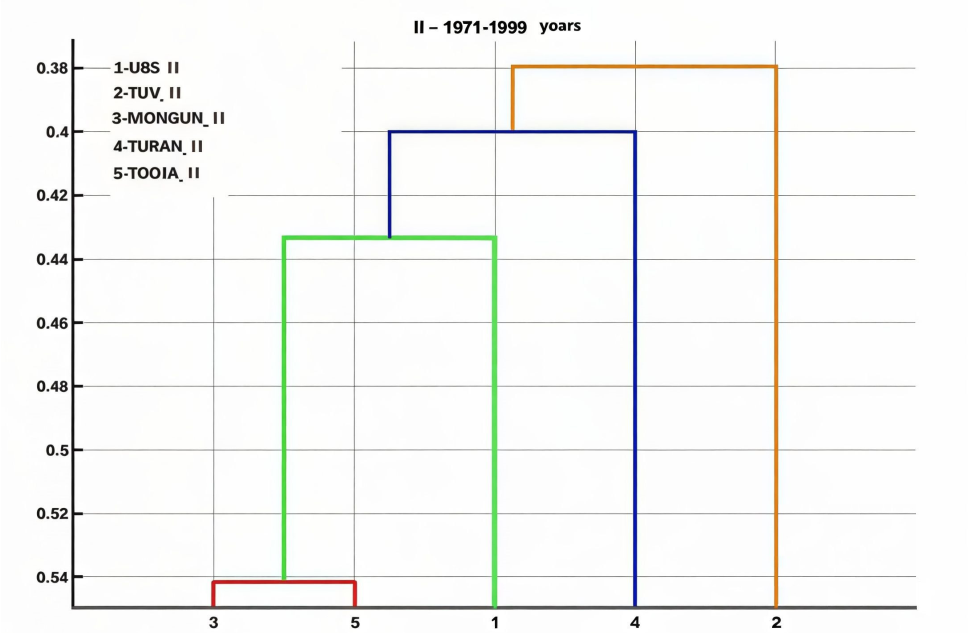

Figure 7. Dendrogram of the degree of similarity of small mammal communities in the basins and mountain range of Tuva in the 1971s and 1999s. The numbers correspond to the numbers of bioclimatic zones.

The results of the hierarchical classification of the coefficients of similarity of sites in the 1950s and 1960s are presented in Fig. 6 in the form of a dendrogram, where as a result we get 2 clusters: S(1,2,7,6,5,4,8,3,9), S(10).

The communities of small mammals of the Tuvan and Turan, Todzhinsky and Turan basins have a higher level of communication within the semiarid and humid, humid and semigumid climatic facies, as well as between the Ubsu-Nur basin (arid facies) and the high-altitude Mongun-Taiga massif (semiarid facies), etc.

When conducting cluster analysis of plots in 1980–2021, according to the "near neighbor" principle, they are also grouped into two clusters (S(1,7,6,9,2,8,4,5,10), S(3)), the distance between which is P=0.0533.

In all the compared sites, from the 1950s to the present, there is a tendency to increase the similarity coefficients, which is associated with the continued formation of the structure of small mammal communities in the studied region. In the cluster, the Tuva basin, which is a transitional area from the boreal forest zone to the semi-deserts of Central Asia in the semiarid zone, had the greatest difference with the dry settled Mongun-Taiga mountain range.

To identify changes in species composition occurring along the main environmental gradients, a graph of the spatial distribution of small mammal communities in the Tuvan mountain region based on the values of the Cody index was constructed (Fig. 10).

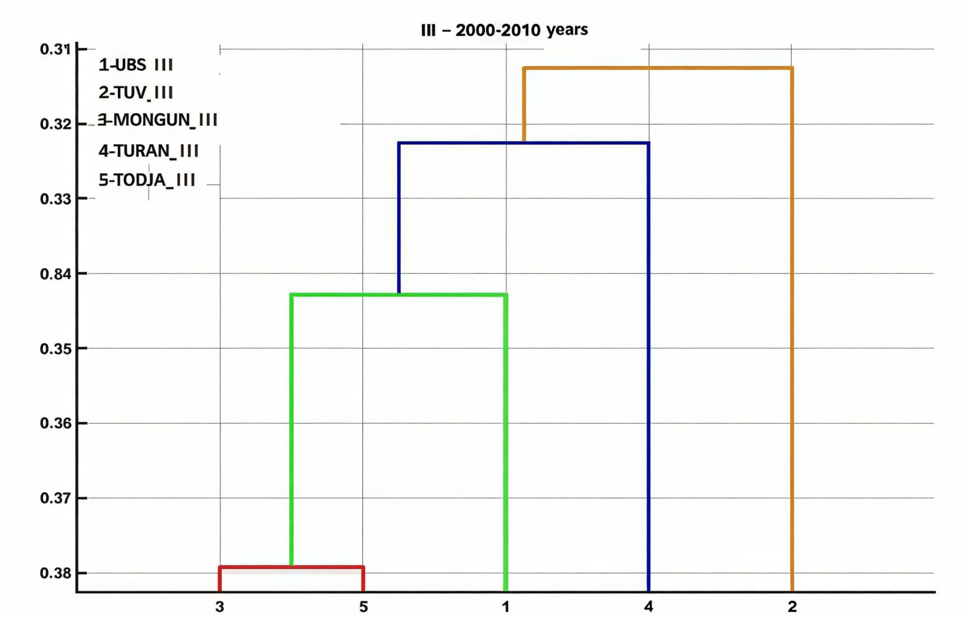

Figure 8. Dendrogram of the degree of similarity of small mammal communities in the basins and mountain range of Tuva in the 2000s and 2010s. The numbers correspond to the numbers of bioclimatic zones.

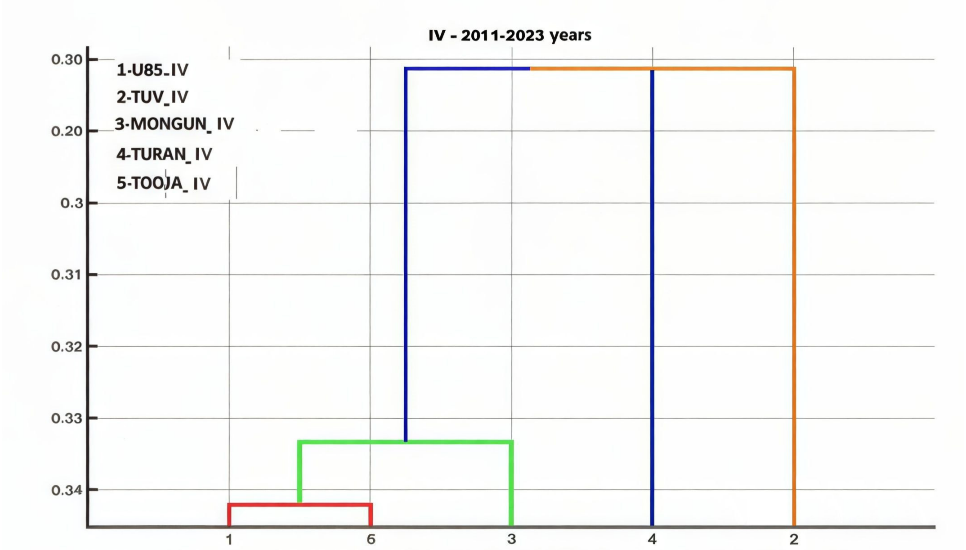

Figure 9. Dendrogram of the degree of similarity of small mammal communities in the basins and mountain range of Tuva in the 2011s and 2023s. The numbers correspond to the numbers of bioclimatic zones.

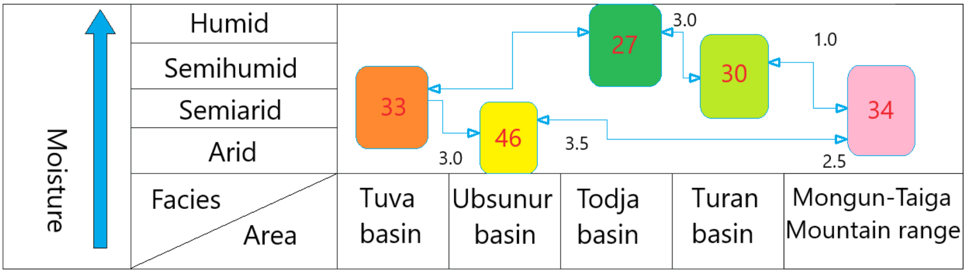

Figure 10. The degree of change in the species composition of small mammal communities in the meridional direction according to the values of the Cody index (numbers above the arrows).

The number of small mammal species noted at the sites red Figure 7 shows the directions of exchange or migration to certain communities. From the standpoint of historical zoogeography and phylogeography, the region since the Late Cenozoic is an area of junction of several faunal groups, which, according to the conditions of formation, can be conditionally divided into groups of North Asian mountain-taiga, forest and forest-steppe, southern Central Asian dry-steppe, semi-desert/desert and mountainous, western broadleaf, forest-steppe, steppe and eastern coniferous-broadleaf origin.

Semi humid territories are the basis for the formation of communities of forest and forest-steppe complexes. The northern group includes insectivores: *Talpa altaica* (Nikolsky, 1883), *Sorex tundrensis* (Merriam, 1900), *Ochotona hyperborea* (Pallas, 1811), *Myopus schisticolor* (Lilljeborg, 1844), voles: *Craseomys rufocanus* (Sandevall, 1811), *Myodes rutilus* (Pallas, 1779), *Alexandronomus oeconomus* (Pallas, 1776), *Agricola agrestis* (Linnaeus, 1761) and *Apodemus peninsulae* (Thomas, 1907).

The southern group of species consists of: *Ochotona daurica* (Pallas, 1776), *Ochotona alpina* (Pallas, 1773), *Ochotona pallasi* (Gray, 1867), *Allactaga sibirica* (Forster, 1778), *Dipus sagitta* (Pallas, 1773), *Cricetulus longlcaudatus* (Milne-Edwards, 1867), *Phodopus campbelli* (Thomas, 1905), *Phodopus roborovskii* Satunin, 1903, *Cricetulus barabensis* (Pallas, 1773), *Alticola tuvinicus* (Ognev, 1950), *Alticola strelzowi* Kastschenko, 1901, *Alticola macrotis* (Radde, 1861), *Alticola barakshin* Bannikov, 1947, *Alticola semicanus* Allen, 1924; *Meriones unguiculatus* (Milne-Edwards, 1867), *Meriones* (*meridianus*) *psammophilus* (Milne-Edwards, 1871), *Cardiocranius paradoxus* (Satunin, 1903), *Allocricetulus curtatus* (Allen, 1925), *Alexandromys mongolicus* (Radde, 1861) and *Urocitellus undulates* (Pallas, 1779). The communities of small mammals of the Ubsu-Nur basin, the basis of which is the southern Central Asian complex, due to the high landscape diversity, accepts elements from other geographical and climatic facies. At the same time, the Tannu-Ola ridge is not a physical and geographical barrier for small mammal communities. This is evidenced by the results of studies of the genetic structure of populations of small mammal species. The Mongun Taiga massif also includes the southern (Central Asian) complex, mainly petrophilic (rocky) species, at the heart of the communities.

The group of species whose origin is associated with the western direction (Europe and Kazakhstan) is represented by: *Sorex minutus* (Linnaeus, 1766), *Sorex araneus* (Linnaeus, 1758), *Neomys fodiens* (Rennant, 1771), *Sicista subtilis* (Pallas, 1773), *Sicista betulina* (Pallas, 1779), *Lagurus lagurus* (Pallas, 1773), *Lasiopodomys gregalis* (Pallas, 1779), *Arvicola amphibius* (Linnaeus, 1758), *Micromys minutus* (Pallas, 1771), *Sylvaemus uralensis* (Pallas, 1811).

The eastern group (ancient Beringia and the Baikal region, Far East) is represented by: *Ondatra zibethicus* (Linnaeus, 1766), *Apodemus agrarius* (Pallas, 1771), *Marmota sibirica* (Radde, 1862), *Marmota baibacina* Kastschenko, 1899, *Eutamias sibiricus* (Laxmann, 1769), *Ellobius tancrei* (Blasius, 1884), *Alexandromys alpinus* (Lissovsky et al. 2018), *Mus musculus* (Linnaeus, 1758), *Hemiechinus auritus* (Gmelin, 1770), *Sorex caecutiens* (Laxmann, 1788), *Sorex minutissimus* (Zimmermann, 1780), *Apodemus agrarius* (Pallas, 1771).

Since the arena of evolution affects the adaptive norms that arise in it, and their totality – biota – in the order of feedback affects the properties of the arena itself, to the extent that the reproduction of organisms – carriers of adaptive norms – reproduces their characteristic community in a number of generations, where each of the members of the community seeks to strengthen integrity through various kinds of biotic interactions.

The observed increase in annual positive temperatures over the past 100 years (Fig. 11), the displacement of the boundaries of bioclimatic zones in the research area (Fig. 12) affected the structure and manifestation of various responses of small mammal communities. The tree-ring chronology developed for the Altai-Sayan region (Fig. 11) indicates the onset of another cycle of temperature increase in the studied area. Unlike previous cycles, the curve of change has some features – the time scale of positive temperatures has expanded, the lower peaks of the curves have become insignificant, the tendency to further increase remains today.

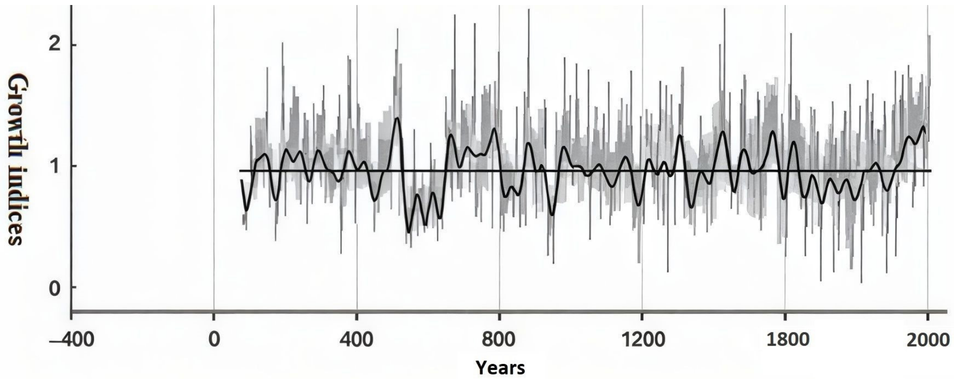

Figure 11. 2367-year tree-ring chronology for the Altai-Sayan region (Mongun-Taiga mountain range) (Myglan et al. 2012).

This is evidenced by special studies on the structure of vegetation cover (Myglan et al. 2012; Artyomov 2015). In all the studied highlands (the Mongun-Taiga mountain range, the Western and Eastern Sayan ridges, Western and Eastern Tannu-Ola and the Sangilen highlands), an increase in the upper boundary of the forest is noted, the onset of cedar woodlands on glacial tundra, and shrub tundra rise to the heights occupied by dryad tundra (Fig. 12).

Thus, the high mosaic of landscapes and biotopes is one of the main factors in the differentiation of small mammal communities. Thus, the dry, settled southern slopes of Tannu-Ola (Ubsu-Nur basin) and Mongun-Taiga differ sharply from other mountain structures in terms of the composition of the animal population and have greater species diversity due to the addition of species of southern (Central Asian) origin. They are represented by rocky, petrophilic and desert species. The desert lowlands, mountains and low ridges with a weakly expressed vertical belt, which are characterized by the precipitation of some high-altitude belts (forest), as well as the desolate lower parts of the slopes of high mountain elevations bordering the mountainous semi-desert, are located in the arid bioclimatic zone. Many processes in these areas are caused by climatic factors such as aridity and poor water availability against the background of high air temperatures, which ecologically brings open biotopes of arid slopes closer to the conditions of the surrounding semi-desert and allows some lowland desert species to settle along them to significant heights. At the same time, it is necessary to point out the ecological specifics of the arid mountains as a rocky natural formation, which directly affects the composition of small mammal communities.

Figure 12. A typical picture of the upper part of the high mountain ranges of Tuva (Sangilen highlands, altitude above sea level – 2133 m, 2019).

Conclusion

The research conducted by the authors on the formation of small mammal communities in the Tuvan mountain region has shown exceptional complexity both in the structure of populations at the genetic level and in geographical distribution. Significant factors are the climatic changes that occurred during the periods under consideration, as well as the complex Late Cenozoic geological history of the territory, which determined the strong fragmentation and sharp mosaic of landscapes. At the same time, the mountain-forming stage of the relief development led to the formation of biogeographic boundaries that determined the directions of migration of small mammal communities in the research area.

The phylogeographic history and phylogenetic relationships of small mammal species in the region indicate the dominance of allochthonous trends in the early stages of the formation of the structure of their communities, which is replaced in the Late Pleistocene and Holocene periods by autochthonous (Central Asian) trends. The responses of small mammal communities are associated with chromosomal evolution, observed in many species – *Cricetulus barabensis*, *C. longicaudatus*, *Phodophus campbelli*, *Lasiopodomys gregalis*, *Alexandromys oeconomus*, *Ellobius tancrei*, *Mus musculus domesticus*, *Sorex araneus*, *Sicista subtilis*.

With the change in climatic indicators, there is an exchange between communities of bioclimatic zones, which has become more and more directional in recent years. Thus, since the 1970s, the relative abundance and range expansion in most model points of species of moistened areas – nival meadows, real, high-altitude and/or meadow steppes – *Lasopodomys gregalis*, *Apodemus penninsulae*, *Marmota sibirica*, *Mus musculus*, *Urocitellus undulatus*, *Sisista subtilis*, *Microtus minutus* and *Ochotona daurica* has been increasing. The latter species (*Ochotona daurica*) expands its range to the north. On the right bank of the Yenisei, the species appeared in the 70s of the last century, which currently occupies the entire steppe of the eastern part of the Turan basin. Along with the expansion of the range of the pika, the ranges of specialized seed-eating hamsters of the genus *Cricetulus* are also expanding in most areas of Tuva, *Phodopus* in the Ubsu-Nur basin; the expansion of the ranges of forest species into the steppe zone is recorded brown-toothed (*Sorex tundrensis*, *S. arenarus*, *S. caecutens*, *S. minutus*, *S. minutissimus*), voles – *Myodes rutilus*, *Craseomys rufocanus*, steppe mouse (*Sisista subtilis*). This trend is especially noticeable in the steppe zone of the Tuvan basin of the northern macro-scopes of the Eastern Tannu-Ola; the appearance of typical forest species – *Sylvaemus uralensis* and *Apodemus agrarius* in the humid zone (Todzhinskaya basin) is noted; the number of desert and dry steppe species – *Allactaga sibirica*, *Lagurus lagurus*, *Ellobius tancrei* in the Ubsu-Nur basin, as well as most species of mountain voles – *Alticola barakshin*, *A. semicanus*, *A. tuvinicus* (Ubsu-Nur basin and the Mongun Taiga massif); grey marmots – inhabitants of mountain steppes – *M. baibacina*, which is possibly related to an anthropogenic factor; the range of species of deserts and semi-desert steppes is locally expanding – *Dipus sagitta*, *Meriones unguiculatus* in the Ubsu-Nur basin.

The above circumstances have generally led to geographical rearrangements of the ranges of small mammals, which then actively participate in the transformation of ecosystem spaces and noticeably change many biotic and abiotic parameters.

Thus, the study of phylogeography, phylogenetic relationships, the genetic and spatial structure of populations of small mammal communities, as well as the dynamics of the transformation of interspecific relationships are especially relevant in studies of biodiversity and their dependence on changing climate conditions.

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Supplementary material 1

Table 1. Relative abundance and distribution of small mammal communities in Tuva

Authors: Sergey O. Ondar, Sergey N. Kirpotin, Andrey S. Babenko, Bogdan A. Mikhaleiko, Nikolay I. Putintsev, Aleksey V. Surov, Orlan Ch. Oidupaa, Andrey M. Samdan, Aivar V. Kuular, Bailak S. Mondush, Dayana S. Ondar, Pradip Kumar Kar, Aldynay O. Khovalyg, Anatoly F. Chuldum
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