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Small Mammal Communities of the Nadym Hills and Changes They Undergo along a Landscape Catena

A. Yu. Levykh[a, *], **D. V. Chernykh**[b, **], **D. V. Zolotov**[b], **and R. Yu. Biriukov**[b]

[a] *Arctic Research Center, Salekhard, Yamalo-Nenets Autonomous Okrug, 629007 Russia*
[b] *Institute for Water and Environmental Problems, Siberian Branch, Russian Academy of Sciences, Barnaul, Altai krai, 656038 Russia*
**e-mail: aljurlev@mail.ru*
***e-mail: chernykhd@mail.ru*

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Abstract—This paper discusses the species composition and population structure of small mammals inhabiting the north-taiga landscape of the Nadym Hills (Yamalo-Nenets Autonomous Okrug, Russia) with an emphasis on catenary patterns in the intralandscape differentiation. Five small mammal species (*Cl. rutilus, S. caecutiens, S. araneus, A. oeconomus,* and *E. sibiricus*) typical for the north-taiga subzone of Western Siberia are recorded in different parts of a northwest-facing landscape catena (upland, saddle, slope, and floodplain). In terms of abundance, the northern red-backed vole (*Cl. rutilus*) predominates in all catena localities and in the landscape as a whole. Other species codominate in certain localities, with the exception of *S. araneus,* who is common only on the upland. Throughout the entire study area and in the upper localities of the catena, *Cl. rutilus* and *S. caecutiens* form the core of small mammal communities. The total abundance of small mammals and the abundance of the dominant species gradually decline along the slope (i.e., from the upland to the floodplain). Resident and propagating small mammal populations are present in all catena localities. The composition, structure, and parameters of small mammal communities change along the slope following changes in afforestation, wetting, plant species richness, vegetation structure, and microtopography. In all catena localities and throughout the entire study area, small mammal communities feature low values of the diversity, evenness, and sustainability indices and high values of the dominance index, which is determined by harsh natural and climatic conditions. However, their generally undisturbed structure is typical for natural subarctic communities, which indicates their sustainability.

Keywords: rodents, insectivores, landscape catena, diversity, sustainability

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INTRODUCTION

Sustainable nature use and biodiversity conservation in northern regions of Russia require knowledge of the impact exercised by modern global environmental and climatic changes that are most pronounced at high latitudes on natural complexes in these regions (Pavlov and Malkova, 2010; Moskalenko, 2012; Tishkov, 2012; Mokhov et al., 2020; Ferronsky, 2013). Accordingly, issues associated with assessing the state of biodiversity and dynamics at different organization levels of living systems and identifying biological indicators reflecting changes in regional landscapes are extremely relevant. Landscape catenae (i.e., series of morphological landscape units from the watershed to the foot of the slope (Chibilyov et al., 1999; Chernykh et al., 2022) can be used as regional models that make it possible to assess the state of biodiversity in modern conditions. The catenary approach assumes that changes in geosystem parameters occur as a result of the redistribution of moisture, loose material, chemical elements, and their compounds between relief elements along the slope vector. Since most of the terrain is represented by slopes of varying steepness, the catena is the most common organizational form of terrestrial landscapes (Mordkovich et al., 1985). Accordingly, the purpose of this study was to examine the species composition and population structure of small mammals as one of the components and status indicators of a typical north-taiga landscape taking into account changes in conditions along the catena vector.

MATERIALS AND METHODS

The field studies were conducted in the north-taiga subzone, northwest of the city of Nadym (Yamalo-Nenets Autonomous Okrug, Western Siberia), within the so-called Nadym Hills. The Nadym Hills are a suitable test polygon for identifying catenary patterns in landscape differentiation. Some of these hills located in the contact zone with the Nadym River valley are composed of light loamy deposits, which makes it possible to consider tops of these hills uplands whose conditions match the zonal values to the greatest possible extent. The test polygon is distinguished by significant (up to 40 m) elevation differences (Gataullin, 1991; *Gosudarstvennaya geologicheskaya karta*..., 2015; Chernykh et al., 2022).

Field landscape studies were conducted from July 13 to July 17, 2021. Six localities have been distinguished along a northwest-facing slope stretching from the top of one of the hills towards the Ngarka-Veloyakha River (a Nadym River tributary), and landscape descriptions of these localities were produced (Table 1). Each locality was described in accordance with the methodology commonly accepted in landscape science (Beruchashvili and Zhuchkova, 1997), including microtopography description, the establishment and description of a soil profile cut, and the description of a botanical sampling plot 10 × 10 m in size.

Small mammals were caught on sampling plots established on four of the six catenary positions (upland (ND-02-21), saddle (ND-05-21), upper part of the slope (ND-06-2), and floodplain (ND-03-21)) (Table 1) from July 13 to July 17, 2021, and from July 9 to July 14, 2022, using lines of break-back traps and pitfall traps (Karaseva et al., 2008; Ravkin and Livanov, 2008). The total exposure was 1075 break-back trap-days (hereinafter trap-days) and 250 cylinder-days (hereinafter cyl.-days); 82 animals were captured. Data on the numbers of exposed traps of different types and animals captured in various habitats in different years are presented in Table 2. The species of captured animals were identified based on a set of morphological characters (Vinogradov and Gromov, 1952; Yudin, 1989).

Abundance was expressed in number of individuals per 100 trap-days (or 100 cyl.-days). To ensure the comparability of abundance estimates with data collected by other researchers, values obtained using break-back traps were recalculated into ind./100 cyl.-days (Ravkin and Livanov, 2008). A complete morphophysiological examination of captured animals was performed (Shvarts et al., 1968). Their relative age was determined based on the thymus gland condition, teeth condition, and skull structure. The spatial distribution of species was quantified using the biotopic allocation index (F_{ij}) (Pesenko, 1982).

The structure of communities was analyzed using diversity indices and multidimensional icon plots constructed on their basis (Bigon et al., 1989; Litvinov, 2004, 2008), sustainability indicators, and integrated community parameters (Gashev, 2000). In accordance with M. Bigon et al. (1989), diversity indices were computed based not only on abundance parameters, but also based on density (ind./km^2) and biomass (g/km^2) values estimated in accordance with Yu.S. Ravkin and I.V. Luk'yanova (1976). Due to the semiarboreal lifestyle of the Siberian chipmunk (*Eutamias* (=*Tamias*) *sibiricus* Laxmann, 1769), its density was estimated on the basis of its occurrence in snap traps using bird density formulas (Ravkin and Livanov, 2008) and assuming that the reliable detection distance does not exceed 25 m for this species. The community of small mammals was considered "a territorial grouping of phylogenetically similar species belonging to the same or adjacent trophic levels" (Brown, 1995; Litvinov, 2004, 2008). A comparative analysis of community structure was performed based on our materials collected in other subarctic regions of Western Siberia in 2019 and 2021–2022.

The total sampling effort was 5875 trap-days and 860 cyl.-days; in total, 441 individuals belonging to 12 species were captured.

Statistical data processing was performed using the following computer programs: Statan (Gashev, 2011), Theriologist's Workplace (Gashev et al., 2012), and Microsoft Excel.

RESULTS

Distinct Features of the Nadym Catena

Let us examine geosystems of the Nadym Hills in the context of environmental factors that have a significant impact on the spatial structure of their small mammal population (Ravkin and Luk'yanova, 1976) and are manifested differentially within the studied catena (Table 1).

Relief

Microtopography changes along the slope vector. On the upland and in the upper part of the slope, mounds are formed at the base of trees, pronounced cryogenic heaving was noted in the saddle, terracing in the middle and lower parts of the slope, and tussocks in the floodplain.

Soils

All catena elements feature an elongated soil profile, a deep upper boundary of perennially frozen and parent rocks, high humus content in upper horizons, and high organic carbon content. The exception is the saddle locality, where perennially frozen rocks are located close to the surface, and parent rocks occur at a depth of less than 1 m. All drained localities of the studied catena, with the exception of the saddle, are distinguished by textural differentiation of the soil profile and the absence of pronounced gleyization traces.

Anthropogenic Impact

The absence of permafrost within the soil profile and the high organic carbon content discovered in the course of landscape studies could be determined by frequent fires (once every 30–50 years) (Mergelov, 2015), resulting in the presence of numerous piece of coal in the soil profile (Chernykh, 2022).

Table 1. Main geosystem characteristics within the Nadym catena

No.	Position, coordinates	Microtopography	Soil	Vegetation	Number of higher vascular plant species
ND-02-21	Upland 65°33′49.17″ N 72°23′24.52″ E	Mounds at tree bases up to 50 cm in height and 50–80 cm in diameter	Podzolic cryometamorphosed loamy	Spruce–birch–larch–Siberian-pine (4Sp3L2S1B) dwarf-shrub–wild-rosemary–green-moss forest CD = 40% TPC GDSL = 90%	12/4/0/8
ND-05-21	Saddle 65°33′54.40″ N 72°23′10.72″ E	Hummocky: irregularly shaped mounds 50 cm in height and 1–1.5 m in diameter.	Gleysol cryometamorphosed humic loamy	Siberian-pine–spruce–larch (4L3S3Sp+B) horsetail–dwarf-shrub–sphagnum forest CD = 20% TPC GDSL = 60%	16/4/2/10
ND-06-21	Upper part of the slope; inclination 5° 65°33′59.17″ N 72°23′3.46″ E	Rare tussocks at tree bases 30–40 cm in height and up to 1 m in diameter	Pale–podzolic on medium loam	Spruce–birch–Siberian-pine–larch (4L3Sp2B1S) moss–dwarf-shrub–horsetail forest CD = 70% TPC GDSL = 98%	12/4/0/8
ND-07-21	Middle part of the slope; inclination 8° 65°34′2.07″ N 72°22′56.13″ E	Slightly manifested terracing: isometric terraces (sags) up to 1 m in diameter	Stagnic cambisol on loamy sediments with sandy interlayers	Birch–spruce–Siberian-pine–larch (4L3Sp2S1B) dwarf-shrub–moss forest CD = 70% TPC GDSL = 70%	15/4/2/9
ND-04-21	Plume; inclination 5° 65°34′4.27″ N 72°22′51.75″ E	Slightly undulating	Sod–pale–podzolic coarse-humus on loamy deposits with sandy interlayers	Larch–spruce–birch (5B4S1L+Sp) dwarf-shrub–horsetail forest CD = 70% TPC GDSL = 90%	28/5/3/20
ND-03-21	Floodplain 65°34′5.37″ N 72°22′49.38″ E	Tussocky	Alluvial stratified on gleyed fine-grained sands underlain by loam	Birch–spruce (6S4B+L) forb–horsetail–shrub–gramineous floodplain forest CD = 80% TPC GDSL = 98%	32/3/5/24

Numbers of higher vascular plant species divided by slashes are given in the following order: total number, arborescent layer, shrub layer, and herbaceous–dwarf-shrub layer; CD is the canopy density and TPC GDSL is the total projective cover of the grass–dwarf-shrub layer.

Table 2. Characteristics of the studied small mammal communities

Characteristics	Year	Habitats				Throughout the entire study area
		Upland	Saddle	Slope	Floodplain	
Number of trap-days	2021	$\frac{75}{48}$	$\frac{75}{30}$	$\frac{50}{20}$	$\frac{25}{10}$	$\frac{225}{108}$
	2022	200	$\frac{200}{122}$	350	100	$\frac{850}{122}$
Number of species	2021	3	3	1	3	5
	2022	0	1	2	2	2
Number of individuals	2021	39	18	4	3	64
	2022	0	9	7	2	18
Number of females	2021	18	10	2	2	32
	2022	–	4	5	1	10
Number of pregnant females	2021	6	3	1	2	11
	2022	–	1	4	1	5
Number of embryos	2021	44	19	7	8	78
	2022	–	7	29	7	43
Number of resorbing embryos	2021	0	0	0	0	0
	2022	–	0	0	0	0
Number of overwintered individuals	2021	18	7	3	1	30
	2022	–	3	6	1	10

The number of trap-days is above the line; the number of cyl.-days is below the line.

Vegetation

The plant species richness gradually increases from the upland to the floodplain. Concurrently, in areas with stagnant and sinter wetting (i.e., in the saddle and in the middle part of the slope, respectively), the local plant species richness is slightly higher than in adjacent localities due to the greater diversity of microbiotopes.

The tree layer in the upper and middle parts of the catena is formed by four species: *Pinus sibirica* Du Tour, *Larix sibirica* Ledeb., *Picea obovata* Ledeb., and *Betula subarctica* Orlova. In addition, *Salix caprea* L. occurs in the lower part of the slope, while the coenosis-forming role of *L. sibirica* sharply decreases in the floodplain since it prefers more stable wetting conditions. The canopy density on the upland is average; in the saddle, it decreases by half, and then it sharply increases and reaches its maximum in the floodplain (Table 1). The shrub layer is absent on the upland and in the upper part of the slope, but it is present in locations with higher moisture supply. For instance, *Betula nana* L. s. str. and *B. czerepanovii* Orlova grow in the saddle. Lower down the catena, *Salix glauca* L., *S. phylicifolia* L. s. str., *Rosa acicularis* Lindl., *Lonicera pallasii* Ledeb., and *Juniperus communis* L. appear in the shrub layer. The grass–dwarf-shrub layer undergoes the most significant changes along the catena vector (Table 1). The following dwarf shrubs predominate among the eight species recorded on the upland and in the upper part of the slope: *Ledum palustre* L., *Vaccinium vitis-idaea* L., *V. uliginosum* L., *V. myrtillus* L., and *Empetrum nigrum* L. In the saddle and in the middle part of the slope, the species diversity in this layer increases due to the presence of swamp species: *Oxycoccus microcarpus* Turcz. ex Rupr., *Petasites frigidus* (L.) Fries, etc. In the lower part of the slope and in the floodplain, as the moisture supply, soil nutrition, and microbiotopic diversity change, species richness increases due to the presence of tall grasses (*Chamaenerion angustifolium* (L.) Scop., *Angelica decurrens* (Ledeb.) B.Fedtsch., *Cacalia hastata* L., *Senecio nemorensis* L., *Thalictrum minus* L*.*, *Veratrum lobelianum* Bernh. etc.), gramineous species (*Calamagrostis* spp. and *Poa* sp.), taiga short grasses (*Trientalis europaea* L., *Lycopodium annotinum* L., etc.), and swamp and meadow forbs (*Equisetum pratense* Ehrh., *Galium boreale* L., *G. uliginosum* L., *Rubus arcticus* L., etc.). The total projective cover of the grass–dwarf-shrub layer reaches its maximum in the upper part of the slope and in the floodplain, while in the wettest localities (i.e., in the saddle and in the middle part of the slop), it decreases (Table 1).

Composition and Population Structure of Small Mammals

In total, five small mammal species have been recorded within the study area; they represent two orders: Eulipotyphla (Laxmann's shrew (*Sorex caecutiens* Laxmann, 1788) and the common shrew (*Sorex araneus* L., 1758)) and Rodentia (northern red-backed vole (*Clethrionomys (=Myodes) rutilus* Pallas, 1779), the tundra vole (*Alexandromys oeconomus Pallas*, 1776), and the Siberian chipmunk (*Eutamias*

(=Tamias) sibiricus Laxmann, 1769)). The name *Clethrionomys* is provided as the main generic synonym of the northern red-backed vole in accordance with B. Kryštufek et al. (2019), who substantiated its validity; other species names are provided in accordance with systematic catalogues (Pavlinov and Lisovsky, 2012; Lisovsky and al., 2019).

S. caecutiens and *A. oeconomus* belong to the trans-palaearctic fauna type, *S. araneus* to the western (European) palaearctic type, and *Cl. rutilus* and *E. sibiricus* to the eastern (Siberian) palearctic type (Yudin, 1989; Volpert and Shadrina, 2002; Bobretsov, 2016).

A typical forest species, *Cl. rutilus*, makes the main contribution to the total abundance of small mammals. In 2021, it demonstrated a broad ecological valence within the study area: *Cl. rutilus* did not give preference to any of the catena localities and only slightly avoided the floodplain ($F_{ij} = -0.44$) (Table 3). The maximum abundance of the species was noted on the upland and in the saddle; then it gradually decreased along the slope vector. The *Cl. rutilus* dominance index changes in a similar way: from 100% in the saddle (2022) and in the upper part of the slope (2021) to 33–50% in the floodplain. The abundance of other species throughout the entire study area is an order of magnitude lower compared to *Cl. rutilus;* however, their abundance levels are comparable to each other. Some catena localities are codominated by different species: upland by *S. caecutiens* (dominance index = 12.8%), saddle by *S. caecutiens* and *E. sibiricus* (11.1 and 5.6%, respectively), upper part of the slope by *E. sibiricus* (14.3%), and floodplain by *A. oeconomus* and *E. sibiricus* (33.3 and 33.3–50%). The analyzed sample indicates the stenotopicity of *A. oeconomus,* who occurs only in the floodplain, and the clear biotopic preference given to this habitat by *E. sibiricus* ($F_{ij} > 0.7$). This can be explained by the ecological and biological characteristics of these species: *A. oeconomus* prefers wet floodplain biotopes, while the floodplain offers more diverse sources of seed foods for *E. sibiricus*. *S. caecutiens* does not demonstrate biotopic preferences in the upper part of the catena and is absent in samples collected on the slope and in the floodplain. *S. araneus* (2.6%) was caught only on the upland. Overall, throughout the study area and in the upper part of the catena (on the upland and in the saddle, where catches were richer), *Cl. rutilus* and *S. caecutiens* form the core of the small mammal community; their cumulative share in the total number of individuals was 92.7, 97.4, and 96.3%, respectively.

In 2021, the total abundance of small mammals in all studied localities of the Nadym catena was an order of magnitude higher than in 2022; this can be primarily attributed to different phases of the population cycle of the dominant species (*Cl. rutilus*), whose abundance fluctuates in a similar way (Table 3). It is obvious that other species feature similar population dynamics: in 2022, their numbers were so low that, despite the sufficient sampling effort, they were absent in catches.

Numerical abundance scores of individual species (Ravkin and Luk'yanova, 1976) vary by years and by habitats. In 2021, *Cl. rutilus* was numerous throughout the study area and in upper parts of the catena (on the upland and in the saddle) and common on the slope and in the floodplain. Other species were rare throughout the entire study area, but common in certain habitats: *S. caecutiens* on the upland and in the saddle (based on the results of the pitfall-trap census, it is abundant in the saddle), *S. araneus* on the upland, *E. sibiricus* in the saddle and in the floodplain, and *A. oeconomus* in the floodplain. In 2022, despite the larger number of exposed trap-days, rodents were not caught on the upland, while insectivores were not caught at all—not in a single habitat—which can be explained by their extremely low abundance levels. Still, *Cl. rutilus* remains a common species both throughout the study area and in all parts of the catena. *E. sibiricus* is common in the floodplain, but rare in the upper part of the slope and throughout the entire study area. In both years, the catches did not include very rare species with an abundance of less than 0.1 ind./100 trap-days (cyl.-days).

The unevenness of the spatial distribution of small mammals (huddling) increases along the slope vector as their total abundance decreases, the microrelief changes, and the species richness in lower vegetation layers goes up; this is manifested in a series of increasing values of the poor aggregation index from upper to lower catena localities (Table 4). High values of the conservatism index reflecting the total proportion of females and overwintered animals (Gashev, 2000) recorded in all habitats indicate that resident and propagating small mammal populations are present everywhere. In both years, the reproductive success index gradually increased along the slope vector; this can be explained by compensatory population processes activated under the conditions of lower population density featured by both small mammals in general and by the dominant species in lower parts of the catena.

Based on their anthropophobia degrees, *Cl. rutilus, A. oeconomus, S. caecutiens,* and *E. sibiricus* belong to the neutral ecological group, while *S. araneus* belongs to the group of synanthropes (Gashev, 2000). Values of the integrated anthropogenic adaptation index, which reflects specific contributions of various ecological groups to the community taking into account their ranked ecological and biological characteristics (K- and r-orientation, anthropophobia degree, consumption degree, preferred humidity, and habitat closeness degree) (Gashev, 2000), are the same for small mammal communities inhabiting all localities of the catena and throughout the entire study area (A = 1.11) and are identical to values obtained for small mammal communities studied by the authors in the natural north-taiga habitats of Western Siberia (vicinity of the

Table 3. Quantitative parameters reflecting the participation of different species in the small mammal community of the Nadym Hills

Species	Parameters	Habitats				
		Upland	Saddle	Slope	Floodplain	Abundance values computed for the entire study area
		2021				
Cl. rutilus	Relative abundance (ind./100 cyl.-days/ind./100 trap-days)	$\frac{44.0}{71.4\ *}$	$\frac{20.0}{32.5*}$	$\frac{8.0}{13.0*}$	$\frac{4.0}{6.5*}$	$\frac{23.6}{38.2*}$
	Density (ind./km^2)	17600	8000	3200	1600	9440
	Body weight (g)	24.54 ± 1.77	20.82 ± 2.17	28.04 ± 4.99	26.76	23.79 ± 0.06
	Biomass (g/km^2)	431904.0	166560.0	89728.0	42816.0	224577.6
	Biotopic allocation index (F_{ij})	0.03	–0.004	0.10	–0.44	–
	Dominance index (%)	84.6	83.3	100.0	33.3	82.8
A. oeconomus	Relative abundance (ind./100 cyl.-days/ind./100 trap-days)	0	0	0	$\frac{4.0}{6.5*}$	$\frac{0.44}{0.72*}$
	Density (ind./km^2)	0	0	0	1600	176
	Body weight (g)	–	–	–	52.38	52.38
	Biomass (g/km^2)	–	–	–	83808.0	9218.9
	Biotopic allocation index (F_{ij})	–1.0	–1.0	–1.0	1.0	
	Dominance index (%)	0	0	0	33.3	1.6
E. sibiricus	Relative abundance (ind./100 cyl.-days/ind./100 trap-days)	0	1.33	0	4.0	0.88
	Density (ind./km^2)	0	53	0	160	35
	Body weight (g)	–	78.91 ± 3.30	–	78.91 ± 3.30	78.91 ± 3.30
	Biomass (g/km^2)	–	4182.2	–	12625.6	2761.9
	Biotopic allocation index (F_{ij})	–1.0	0.44	–1.0	0.91	–
	Dominance index (%)	0	5.56	0	33.3	3.1
S. araneus	Relative abundance (ind./100 cyl.-days/ind./100 trap-days)	$\frac{1.33}{2.73*}$	0	0	0	$\frac{0.44}{0.90*}$
	Density (ind./km^2)	259	0	0	0	86
	Body weight (g)	5.26	–	–	–	5.26
	Biomass (g/km^2)	1362.3	–	–	–	452.4
	Biotopic allocation index (F_{ij})	1.0	–1.0	–1.0	–1.0	–
	Dominance index (%)	2.6	0	0	0	1.6
S. caecutiens	Relative abundance (ind./100 cyl.-days/ind./100 trap-days)	$\frac{1.33}{8.33}$	$\frac{1.33}{33.33}$	0	0	$\frac{0.89}{4.63}$
	Density (ind./km^2)	$\frac{259}{1624}$	$\frac{259}{6499}$	0	0	$\frac{174}{903}$
	Body weight (g)	4.99 ± 0.34	4.99 ± 0.34	–	–	4.99 ± 0.34
	Biomass (g/km^2)	$\frac{1292.4}{8103.8}$	$\frac{1292.4}{32430.0}$	–	–	$\frac{868.3}{4506.0}$
	Biotopic allocation index (F_{ij})	0.23	0.01	–1.0	–1.0	–
	Dominance index (%)	12.8	11.1	0	0	10.9

Table 3. (Contd.)

Species	Parameters	Habitats				
		Upland	Saddle	Slope	Floodplain	Abundance values computed for the entire study area
Cumulative abundance of representatives of all species (ind./100 cyl.-days/ind./100 trap-days)		$\frac{47.7}{8.33}$	$\frac{22.7}{33.33}$	$\frac{8.0}{12.98*}$	$\frac{12.0}{19.47*}$	$\frac{26.2}{4.63/43.12*}$
Cumulative density of representatives of all species (ind./km^2)		19742	14811	3200	3360	10814
Cumulative biomass of representatives of all species (g/km^2)		442662.5	204464.6	89728.0	139249.6	242385.1
2022						
Cl. rutilus	Relative abundance (ind./100 cyl.-days/ind./100 trap-days)	–	$\frac{4.5}{7.3*}$	$\frac{1.7}{2.8*}$	$\frac{1.0}{1.62*}$	$\frac{1.88}{3.05*}$
	Density (ind./km^2)	–	1800	680	400	752
	Body weight (g)	–	20.33 ± 1.77	25.52 ± 1.44	34.5	23.16 ± 1.47
	Biomass (g/km^2)	–	36594.0	17353.6	13800.0	17416.3
	Biotopic allocation index (F_{ij})	–	0.13	0.03	0.15	–
	Dominance index (%)	–	100.0	85.7	50.0	88.9
E. sibiricus	Relative abundance (ind./100 cyl.-days/ind./100 trap-days)	–	0	0.29	1.0	0.24
	Density (ind./km^2)	–	–	12	40	10
	Body weight (g)	–	–	83.23 ± 4.55	83.23 ± 4.55	83.23 ± 4.55
	Biomass (g/km^2)	–	–	998.8	3329.2	832.3
	Biotopic allocation index (F_{ij})	–	–1.0	0.78	0.78	–
	Dominance index (%)	–	–	14.3	50.0	11.1
Cumulative abundance of representatives of all species (ind./100 cyl.-days/ind./100 trap-days)		–	$\frac{4.5}{7.3*}$	$\frac{2.0}{2.78*}$	$\frac{2.0}{1.62*}$	$\frac{2.12}{3.05*}$
Cumulative density of representatives of all species (ind./km^2)		–	1800	692	440	762
Cumulative biomass of representatives of all species (g/km^2)		–	36594.0	18352.4	17129.2	18248.6

Number of trap-days is above the line; number of cyl.-days is below the line. Abundance parameters marked by asterisks were computed based on the results of snap-trap censuses using conversion coefficients; abundance parameters not marked by asterisks were computed empirically based on the results of the pitfall-trap census. The abundance data were converted into ind./100 cyl.-days not taking *E. sibiricus* into account, since the recalculation methodology was developed for terrestrial rodents and insectivores (Ravkin and Livanov, 2008, p. 84). F_{ij} is the biotopic allocation index.

Shukhtungort cordon, Malaya Sos'va State Nature Reserve, Beryozovo district, Khanty-Mansi Autonomous Okrug, and the vicinity of the Sterkh station, Kunovatskii Regional Wildlife Sanctuary, Shuryshkarskii district, Yamalo-Nenets Autonomous Okrug).

The composite well-being index reaches its lowest values in communities inhabiting the saddle (localities with stagnant wetting) and the highest values in communities inhabiting floodplains. Throughout the entire study area, this parameter featured average values in 2022 and below average values in 2021. This can be explained by the harsh natural and climatic conditions of this region.

Let us examine biomass as an emergent property of the studied communities and diversity indices and information multidimensional icon plots constructed for the Shannon (H) and Simpson's (D) species diversity indices and the Shannon (J) and Simpson's (E) evenness indices (Magurran, 1988; Litvinov, 2004, 2008) as a measure of species diversity.

Table 4. Diversity and sustainability indices and integrated parameters reflecting the state of small mammal communities inhabiting the Nadym catena (2021–2022)

Parameters	Year	Habitats				Throughout the entire study area
		Upland	Saddle	Slope	Floodplain	
Integrated parameters						
Reproductive success index (URZ)	2021	3333.33	3000.00	4999.99	9999.99	3437.50
	2022	–	2499.99	7999.99	9999.99	5000.00
Conservatism index (IKV)	2021	0.92	0.94	1.25	1.00	0.97
	2022	–	0.78	1.57	1.00	1.11
Poor aggregation index (B)	2021	0.002	0.009	0.063	0.333	0.70
	2022	–	0.037	0.020	0.250	0.120
Composite well-being index (SSS)	2021	85.50	42.23	–	104.49	35.82
	2022	–	–	86.36	102.72	52.28
Diversity and sustainability indices						
Margalef's species richness index (R)	2021	$\frac{1.26}{0.47/0.35}$	$\frac{1.59}{0.48/0.38}$	–	$\frac{4.19}{0.57/0.39}$	$\frac{2.22}{0.99/0.74}$
	2022	–	0	$\frac{1.18}{0.35/0.24}$	$\frac{3.32}{0.38/0.24}$	$\frac{0.80}{0.35/0.24}$
Shannon species diversity index (H)	2021	$\frac{0.22}{0.17/0.05}$	$\frac{0.24}{0.31/0.24}$	–	$\frac{0.48}{0.37/0.39}$	$\frac{0.28}{0.21/0.15}$
	2022	–	0	$\frac{0.18}{0.04/0.09}$	$\frac{0.30}{0.13/0.21}$	$\frac{0.15}{0.03/0.08}$
Shannon evenness index (J)	2021	$\frac{0.20}{0.15/0.05}$	$\frac{0.22}{0.28/0.22}$	–	$\frac{0.44}{0.34/0.35}$	$\frac{0.17}{0.13/0.09}$
	2022	–	–	$\frac{0.26}{0.06/0.13}$	$\frac{0.43}{0.19/0.30}$	$\frac{0.22}{0.04/0.12}$
Simpson's species diversity index (D)	2021	$\frac{0.27}{0.20/0.05}$	$\frac{0.29}{0.50/0.31}$	–	$\frac{0.67}{0.54/0.54}$	$\frac{0.30}{0.23/0.14}$
	2022	–	0	$\frac{0.25}{0.03/0.10}$	$\frac{0.50}{0.17/0.31}$ 0.17/0.31	$\frac{0.20}{0.03/0.09}$
Simpson's evenness index (E)	2021	$\frac{0.09}{0.07/0.02}$	$\frac{0.10}{0.17/0.10}$	–	$\frac{0.22}{0.18/0.18}$	$\frac{0.16}{0.05/0.03}$
	2022	–	–	$\frac{0.13}{0.02/0.05}$	$\frac{0.25}{0.09/0.16}$	$\frac{0.10}{0.02/0.05}$
Simpson's dominance index (C)	2021	$\frac{0.73}{0.80/0.95}$	$\frac{0.71}{0.50/0.69}$	$\frac{1.0}{1.0/1.0}$	$\frac{0.33}{0.46/0.47}$	$\frac{0.70}{0.77/0.86}$
	2022	–	1.0	$\frac{0.76}{0.97/0.90}$	$\frac{0.50}{0.84/0.69}$	$\frac{0.80}{0.97/0.91}$
Resilient sustainability (UU)	2021	$\frac{0.36}{0.25/0.12}$	$\frac{0.41}{1.22/0.45}$	–	$\frac{2.91}{1.54/1.47}$	$\frac{0.43}{0.30/0.19}$
	2022	–	0.09	$\frac{0.32}{0.11/0.15}$	$\frac{1.22}{0.21/0.46}$	$\frac{0.25}{0.10/0.14}$
Resistant sustainability (UR)	2021	$\frac{1.01}{1.69/0.53}$	$\frac{0.92}{4.20/3.23}$	–	$\frac{1.17}{3.94/5.44}$	$\frac{0.76}{1.03/0.80}$
	2022	–	–	$\frac{0.97}{0.38/1.67}$	$\frac{0.99}{1.72/5.06}$	$\frac{1.07}{0.29/1.42}$
Overall sustainability (U)	2021	$\frac{1.37}{1.94/0.65}$	$\frac{1.33}{5.43/3.68}$	–	$\frac{4.08}{5.48/6.90}$	$\frac{1.19}{1.33/0.99}$
	2022	–	–	$\frac{1.29}{0.49/1.83}$	$\frac{2.21}{1.94/5.52}$	$\frac{1.32}{0.40/1.56}$

Index values computed based on abundance parameters are above the line; values based on density (before the slash) and biomass (after the slash) are below the line.

For all small mammal species and communities as a whole, biomass trends by years and habitats are similar to abundance trends, since the density of species that statistically significantly differ from the dominant in body weight is insignificant (Table 3).

Small mammal communities in individual habitats and throughout the entire study area are distinguished by very low values of the species richness, species diversity, and evenness indices (as well as sustainability indices) and high values of the dominance index (Table 4). This is typical for high-latitude communities due to harsh natural and climatic conditions in their habitats. Concurrently, values of all community diversity and sustainability indices increase from the upland to the floodplain, with the exception of the dominance index, whose changes are inverse to the slope vector and are consistent with changes in diversity. Differences between upland and floodplain communities in diversity indices reach 1.7–3.3 times, in the dominance index 1.5–2.2 times, and in sustainability indices 1.2–13.6 times. Interestingly, resistant sustainability exceeds resilient sustainability by 2.2–3.0 times in communities inhabiting all localities of the catena (except for the floodplain); this is typical for communities inhabiting transformed landscapes and habitats at early succession stages (i.e., young communities) (Gashev, 2000). By contrast, in the floodplain community, the contribution of the resilient component to the overall sustainability is 2.5 times higher compared to the resistant component, which is typical for undisturbed habitats.

According to the methodological approach substantiated by Yu.N. Litvinov (2004, 2008), the shape of multidimensional icon plots can be used as a qualitative characteristic of the information structure and sustainability of communities (samples) and landscapes (sites) (Litvinov, 2004, 2008). Multidimensional icon plots constructed for the studied communities based on the computed abundance, density, and biomass indices have different scales, but a similar shape, which indicates the validity of diversity estimates produced on the basis of the available material (i.e., primary data on numbers of individuals belonging to different species). For communities with the participation of *E. sibiricus* inhabiting the saddle, slope, and floodplain, this indicates inter alia the adequacy of the approach used to estimate the density of this species (Fig. 1).

Multidimensional icon plots constructed for upland, saddle, and floodplain communities are flattened in the horizontal direction, which indicates that their diversity indices exceed their evenness indices. The shape of multidimensional icon plots constructed for these communities is similar to the shape of averaged multidimensional icon plots constructed for subarctic landscapes in the northern part of Central Siberia (Litvinov, 2004) and open landscapes of Western Siberia (Litvinov, 2008); however, compared to the latter, it is more elongated in the direction of Simpson's diversity index, which gives greater weight to common species.

The above-noted similarity with communities of open landscapes can be somewhat explained by afforestation features in the studied localities: low canopy density on the upland and in the saddle and the semiopen floodplain habitat.

Multidimensional icon plots constructed for the slope community are elongated along the vertical axis in the direction of Simpson's evenness index; their shape is similar to averaged multidimensional icon plots constructed for forest communities of Western Siberia (Litvinov, 2008) and mountain taiga communities of the Altai Mountains (Litvinov, 2004). This is consistent with the forest vegetation structure on the slope where canopy density amounts to 70% (Table 1).

The shape of the averaged multidimensional icon plot is consistent with shapes of multidimensional icon plots constructed for a number of subarctic communities in the northern part of Central Siberia (Litvinov, 2004); overall, it is similar to averaged multidimensional icon plots constructed for small mammal communities studied by the authors in the western part of the north-taiga zone of Western Siberia (Malaya Sos'va State Nature Reserve and Kunovatskii Regional Wildlife Sanctuary) and in the mountain tundra of the Polar Urals (Lake Khadatayoganlor); however, it is more harmonious both in diversity and evenness (Fig. 2).

Compared to small mammal communities inhabiting a forest–tundra landscape in the vicinity of the Tazovsky rural locality (upper reaches of the Syambota-Yakha River) and a north-taiga landscape in the foothills of the Polar Urals (Nyrdvomenshor Stream floodplain, Sob River basin), the averaged multidimensional icon plot constructed for the small mammal community of the Nadym Hills is less elongated along the axis of the Shannon evenness index (J), reflecting the evenness of species with low abundance values, but it is more balanced along all other axes (E, H, and D).

Multidimensional icon plots constructed for all small mammal communities of the Nadym Hills are symmetrical along one or both axes. This, along with their similarity to multidimensional icon plots constructed for communities inhabiting natural high-latitude and high-mountain landscapes of Western Siberia and adjacent areas, indicates their undisturbed dominance structure, the decisive effect of natural factors on the small mammal population of the studied biogeocoenoses, and the relative stability of the communities under study.

DISCUSSION

In the course of the census of small mammals conducted in the Nadym Hills in July 2021–2022, 5 spe-

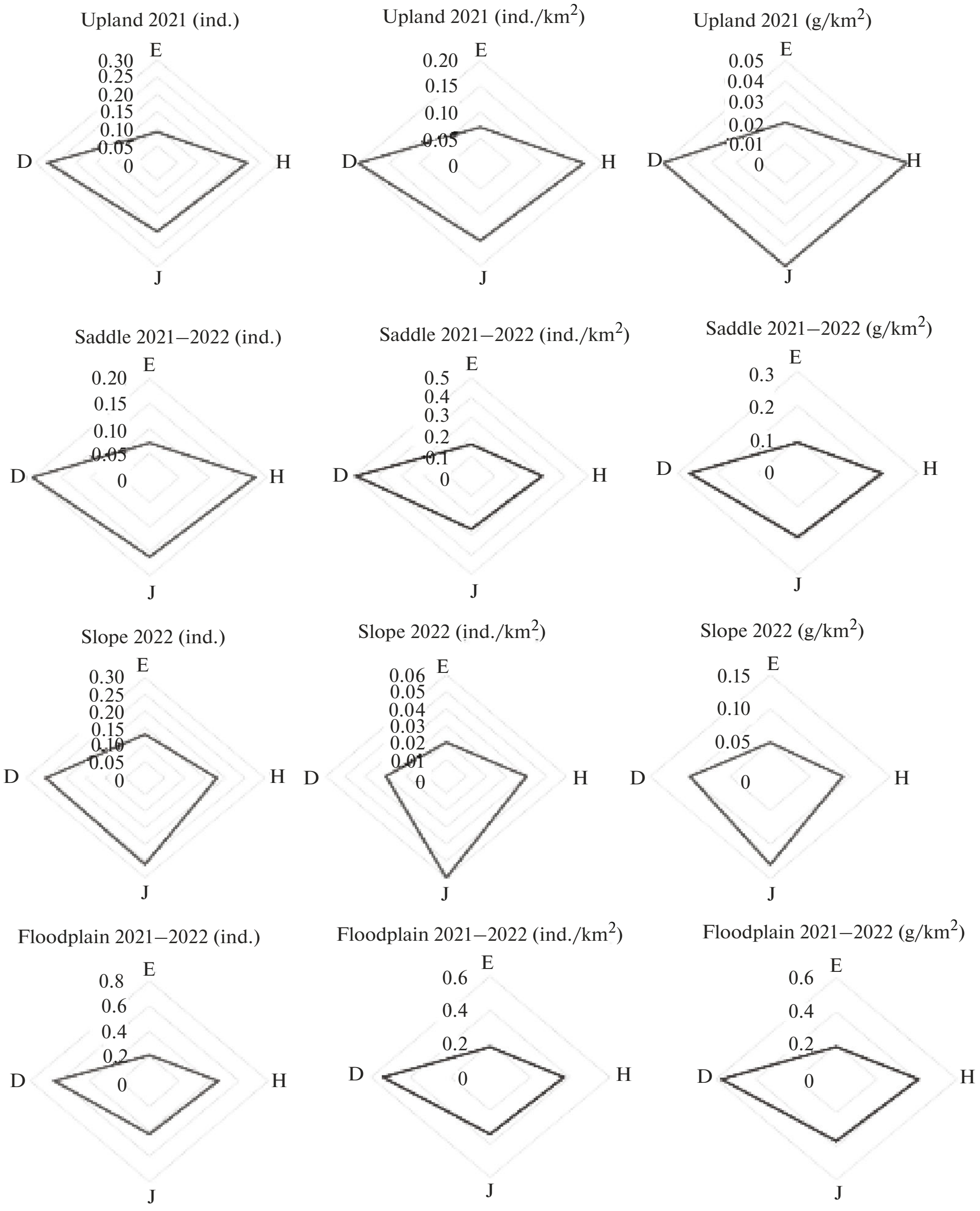

Fig. 1. Multidimensional icon plots constructed for information diversity indices computed for small mammal communities inhabiting different localities of the Nadym catena (multidimensional icon plots in the left row were constructed for indices computed based on abundance parameters; in the central row, based on density; and, in the right row, based on biomass).

cies out of the 16 (17 species taking into account *E. sibiricus*) inhabiting the central part of the north-taiga subzone of Western Siberia were caught, including four species (*Cl. rutilus*, *S. caecutiens*, *S. araneus*, and *A. oeconomus*) out of the nine that form the core of small mammal communities throughout the north-taiga subzone (Starikov and Vartapetov, 2021). The absence of the remaining 12 small mammal species in the catches can be explained by their ecological and/or biotopic preferences and, accordingly, by the heterogeneity of their spatial distribution within the subzone; for some species, this can be explained by their uneven numerical distribution in the latitudinal and longitudinal directions, as well as the phase of low population size amid the universally insignificant abundance of these species.

All the recorded vole and shrew species were described as part of Pleistocene faunas in the northern part of Western Siberia (Smirnov et al., 1986). *E. sibiricus,* a typical species inhabiting modern north-taiga Siberian pine and pine forests (Ravkin et al., 1980; *Mlekopitayushchie*..., 2007), apparently penetrated into the northern regions of the West Siberian Plain later, in the

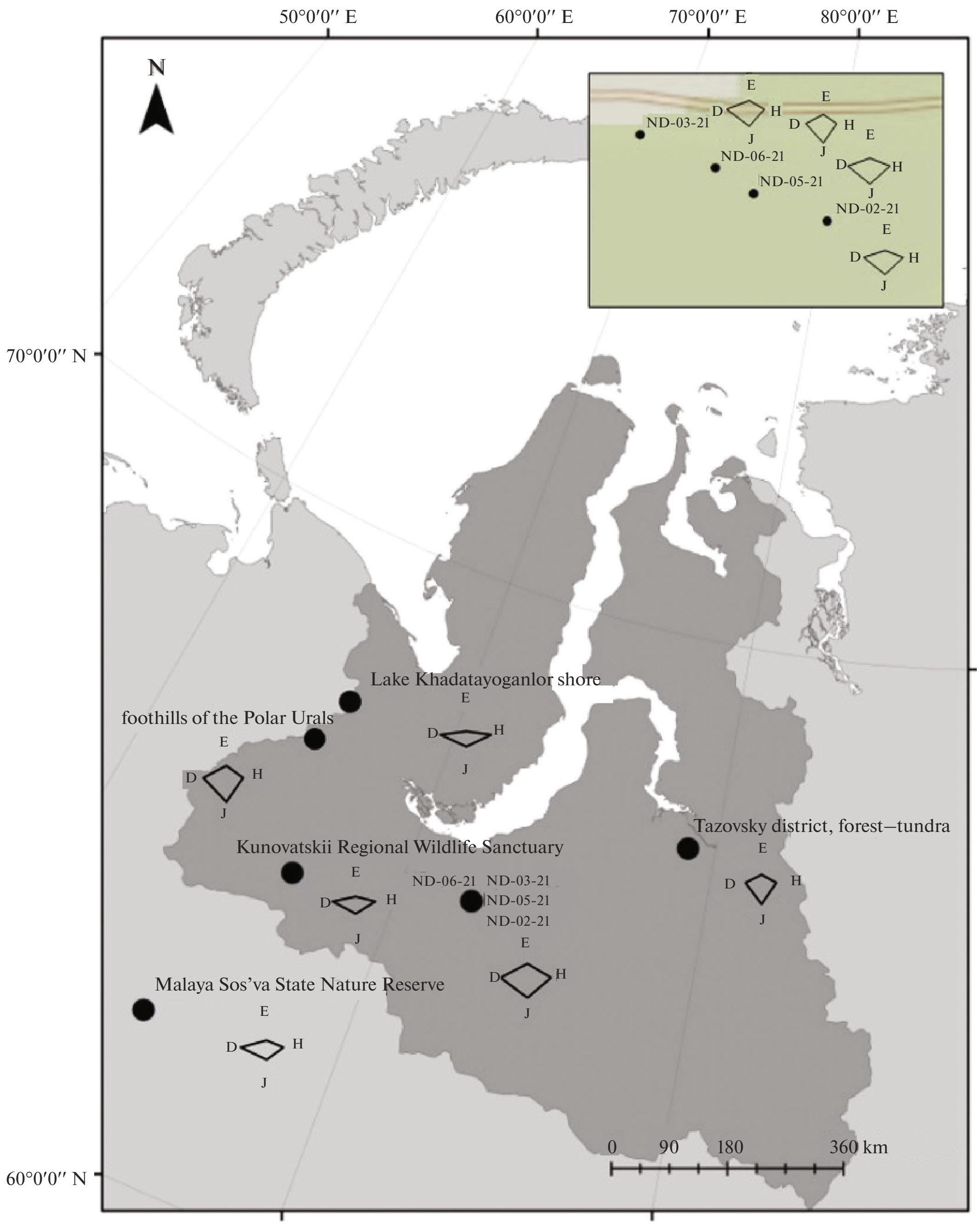

Fig. 2. Map of multidimensional icon plots constructed for small mammal communities inhabiting high-latitude regions of Western Siberia.

course of the formation of the taiga–forest theriocomplex, a derivative from the tundra–steppe and forest–steppe faunal complexes, in the second half of the Holocene (Smirnov et al., 1986). Siberian and transpalaearctic species predominate among the recorded species, which is consistent with the geographical location of the study area and the history of faunas.

The dominance estimates are consistent with the data (Starikov and Vartapetov, 2021) indicating the universal and joint predominance of *Cl. rutilus* and *S. caecutiens* throughout the entire north-taiga subzone of Western Siberia with the maximum proportion of *Cl. rutilus* in the center of the subzone. However, contrary to the data collected by B.P. Starikov and L.G. Vartapetov (2021), in our study, *S. araneus* was recorded as a common species only on the upland, and it is not among the dominants.

The spatio–biotopic and numerical distributions of individual small mammal species by Nadym catena localities correspond to their species-specific ecological and biological features. The composition, structure, and parameters of small mammal communities change along the catena following changes in geosystem characteristics: afforestation, wetting, plant species richness, vegetation structure, and microtopography.

Low diversity and sustainability indices in small mammal communities inhabiting the Nadym Hills are determined by their harsh natural and climatic conditions, which is confirmed by the results of landscape and ecological studies (the presence of areas where perennially frozen rocks occur close to the surface, cryogenic heaving, areas with excessive moistening, low species diversity of higher vascular plants; the numerical predominance of a few plant species; etc.). Relatively higher values of diversity indices and the composite well-being index in the floodplain small mammal community correlate with the greater species and structural diversity of floodplain vegetation and a milder microclimate in this part of the landscape. Relatively higher resistant sustainability and, conversely, lower resilient and overall sustainability in communities inhabiting upper parts of the catena can be somewhat explained by the impact of fires.

The average multidimensional icon plot constructed for the entire small mammal community inhabiting all localities of the Nadym catena is symmetrical along both axes and more harmonious in diversity and evenness than multidimensional icon plots constructed for communities inhabiting its individual localities, which can be explained as follows: being an integral system, the landscape is balanced better than its local geosystems at the intralandscape level. The multidimensional icon plot constructed for the small mammal community of the Nadym Hills is more symmetrical and balanced in diversity and evenness when compared to multidimensional icon plots constructed for communities inhabiting western parts of the northern taiga, forest–tundra, and mountain tundra. This is consistent with the known zonal and provincial heat supply, moisture, and biodiversity distribution patterns in Western Siberia (Parfenova, 2004; Ravkin and Bogomolova, 2016, 2018).

CONCLUSIONS

The species composition and population structure of small mammals inhabiting the Nadym Hills correspond to the zonal–subzonal and provincial location of these hills, the formation history of the taiga faunal complex, the composition of biotopes, and their proportions within the study area.

Patterns determining changes in the composition, population structure, and parameters of small mammal communities inhabiting the Nadym Hills along the slope vector (i.e., from the upland to the floodplain) are consistent with changes in a number of other geosystem characteristics.

In all catena localities and throughout the entire study area, small mammal communities feature a generally undisturbed information structure typical for subarctic landscapes, which indicates their sustainability.

Despite traces of fires noted in the soil structure and their probable impact on the stability of small mammal communities in the upper catena localities, the predominance of anthropogenically neutral species in the studied communities and their low anthropogenic adaptation indicate the absence of a significant economic anthropogenic impact on the studied landscape.

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COMPLIANCE WITH ETHICAL STANDARDS

Conflict of interest. The authors declare that they have no conflicts of interest.

Statement on the welfare of animals. Animal-related experiments were approved by the Institutional Animal Ethical Committee on Biomedical Ethics of Siberian Federal University, Russia (Approval Code: State Standard of Russian Federation No. 33215-2014; Approval Date: 2016-07-01).

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