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Landscape-biotopic distribution of *Formica uralensis* Ruzsky, 1895 (Hymenoptera: Formicidae) in the Russian part of Altai

Ландшафтно-биотопическое распределение *Formica uralensis* Ruzsky, 1895 (Hymenoptera: Formicidae) на российской части Алтая

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Key words: Ants, distribution, range, ecological preferences, environmental factors, Altai mountain region.

Ключевые слова: муравьи, распределение, ареал, экологические предпочтения, факторы среды, Алтайская горная область.

Abstract. The territory of the Altai mountain region, characterised by high landscape diversity, is a convenient natural model for investigating ecological preferences and specificity of biotopic distribution of individual ant species. The results are presented of a study of the landscape-biotopic distribution of the transpalaearctic ant *Formica uralensis* Ruzsky, 1895, known for highly specific ecological preferences in different parts of its range. The environmental factors determining the nature and specificity of its biotopic distribution were identified. A generalised analysis of our own and literature data on the abundance of *F. uralensis* in the Russian Altai revealed four groups of habitats, different in the degree of favourable environmental conditions for this species: optimal, suboptimal, pessimal and extreme. It was found that the variability in the abundance of *F. uralensis* across habitats is most associated with the type (subtype) of the vegetation cover, differences in heat availability and moisture supply of the territory, and landscape differentiation at the type and subtype levels. In the studied part of Altai, as well as throughout its range, *F. uralensis* inhabits a wide range of habitats including bogs, where its abundance is low. This confirms the validity of the hypothesis that *F. uralensis* has specific adaptations to overwatered habitats (e.g. wetland). However, the results obtained do not exclude the possibility of the existence of two cryptic species with specific ecological preferences, but this issue requires a separate detailed study using molecular genetic methods.

Резюме. Благодаря высокому ландшафтному разнообразию территория горного Алтая является удобной природной моделью для изучения экологических преференций и специфики биотопического распределения отдельных видов муравьёв. Представлены результаты исследования ландшафтно-биотопического распределения транспалеарктического вида муравьёв *Formica uralensis* Ruzsky, 1895, известного специфичными экологическими предпочтениями в разных частях своего ареала. Выявлены факторы среды, определяющие характер и специфику его биотопического распределения. Обобщённый анализ собственных и литературных данных по обилию черноголового муравья на российской территории Алтая, выявил четыре группы местообитаний, различных по степени благоприятности условий среды для обитания этого вида: оптимальных, субоптимальных, пессимальных и экстремальных. Установлено, что изменчивость обилия черноголового муравья по местообитаниям в наибольшей степени сопряжена с обликом растительного покрова, различиями в тепло- и влагообеспеченности территории, а также дифференциацией ландшафтов на типовом и подтиповом уровнях. Как и на всём протяжении ареала, *F. uralensis* обитает на изученной части Алтая в широком спектре местообитаний, и в том числе на болотах, где его обилие невелико. Это подтверждает справедливость гипотезы о том, что *F. uralensis* обладает специфическими адаптациями к обитанию в переувлажнённых (например, заболоченных) местообитаниях. Однако полученные результаты не исключают возможности существования двух видов-двойников с разными экологическими предпочтениями, но этот вопрос требует отдельного детального изучения с использованием молекулярно-генетических методов.

Introduction

Formica uralensis Ruzsky, 1895, has long been of interest to researchers due to its biological peculiarities and the specificity of its distribution [Dlussky, 1967; Zakharov, Dlussky, 2013]. This ant belongs to the transpalaearctic species [Dlussky, 1967; Zakharov, Dlussky, 2013], standing out among them by the peculiar and, at first glance, contradictory character of ecologi-

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cal preferences in different parts of its range [Dlussky, 1967]. It is known that along the borders of its range (except for the southern one), in particular in Europe, in the north of the Urals and Primorye, *F. uralensis* is found predominantly in upland bogs [Dlussky, 1967; Stankiewicz et al., 2005; Punttila, Kilpeläinen, 2009; Wegnez, Mourey, 2016]. At the same time, at the southern border of its range — in Southern Siberia, Northern Kazakhstan and Northern Mongolia — this species inhabits a variety of xerophytic habitats from steppe birch and pine forests to meadows and true steppes [Pleshanov, 1966; Dmitrienko, Petrenko, 1976; Antonov, Pleshanov, 2008; Blinova, 2012; Zakharov, Dlussky, 2013; Aibek, Yamane, 2015].

The specific character of the biotopic distribution of *F. uralensis* raises a natural question as to whether its original habitat was steppes or raised bogs. Various assumptions have been made in an attempt to find the key to its solution. In particular, this phenomenon was explained as a result of habitat change during postglacial dispersal and displacement of *F. uralensis* to bogs by dominant ants of the *Formica rufa* group [Bisgaard, 1944]. Later, R. Rosengren [Rosengren, 1969] suggested that *F. uralensis* had always been adapted to living in wetlands, but he specified that this hypothesis could be fully tested only by analysing the ecological preferences of the species throughout its range [Rosengren, 1969].

Currently, a considerable amount of data has been accumulated on the occurrence of *F. uralensis* in both the European and Asian parts of its range (Fig. 1). However, the available publications usually discuss the fauna of individual regions [Ruzsky, 1905; Dlussky, 1967; Collingwood, 1979; Kvamme, 1982; Zryanin, Zryanina, 2007; Ryabinin, Novgorodova, 2013; Borowiec, 2014; Paukkunen, Kozlov, 2015; Radchenko, 2016; Dubovikoff, Yusupov, 2017] and relatively rarely contain information on the relative abundance of *F. uralensis* [Blinov, 1991; Gubin, Dlussky, 1991, Malozemova, 1991; Gridina, 2003; Adakhovskiy, 2024]. The data allowing us to get an idea of the biotopic distribution of *F. uralensis* east of the Urals have been obtained mainly for the southern part of its range: Mongolia [Pfeiffer et al., 2003; Bayartogtokh et al., 2014; Aibek, Yamane, 2015], northern Kazakhstan [Reznikova, 1983], the steppe basins of Tuva and Khakassia [Zhigulskaya, 1968], Kuznetsk-Salair mountain region [Blinova, 2011, 2012], Western Transbaikalia [Dmitrienko, 1979; Sokolovskij, 2011], and the Baikal region in general [Antonov, Pleshanov, 2008]. There is also some information on the abundance of *F. uralensis* within the taiga zone of Western and Eastern Siberia [Dmitrienko, Petrenko, 1976; Omelchenko, 1996]. The rest of the territory still remains poorly studied in this respect, which does not allow us to get a clear idea of the biotopic preferences of *F. uralensis* in the entire range.

At the same time, the diversity of natural conditions within the mountain areas, and in particular in the Altai mountain region, creates a unique opportunity for a different solution to this problem. When studying the landscape-biotopic distribution of *F. uralensis* in Altai, where all types of habitats of this ant are represented — from steppes to various forests and swamps, it is possible to almost fully appreciate not only the ecological preferences of this species, but also its potential for resettlement and occupation of new territories.

The aim of this work is to investigate the landscape-biotopic distribution of *F. uralensis* in the territory of Russian Altai, to identify its preferred habitats and the environmental factors determining the nature and specificity of its landscape-biotopic distribution.

Materials and methods

Study area

The research was conducted in the Altai Republic (Russia) and in the adjacent part of the Altai Territory (Krasnoshchekovsky, Altai and Solton districts, Russia). According to the physical geographic zoning, the surveyed territory belongs to the Altai mountain region, the Russian part of which includes seven provinces [Atlas Altajskogo kraya, 1978]. The research was conducted on the territory of six of them: Northwestern, Northern, Northeastern, Central, Southeastern and Eastern. The following is a brief characterization of the natural conditions of the studied region, based on the available literature [Kuminova, 1960; Nikolaev, Samoylova, 1978; Ogureeva, 1980; Landscape map..., 2001; Tsybulin, 2009] and reflecting the specificity of environmental conditions determining the peculiarities of the spatial distribution of *F. uralensis*.

The characteristic regional features of all provinces of the northern part of Altai include the predominance of low mountains with a wide distribution of forests and/or meadow steppes (Table 1). According to the moisture level of the territory, the share of forests is highest in the east and west. The composition of forest-forming species exhibits a regular transition from widespread aspen-fir («dark») forests of taiga type in the Northeastern Altai to mixed larch and birch forests in the Northern and, partly, Northwestern Altai. As the share of forest landscapes decreases, the area of forest-steppe communities increases, while meadow steppes and steppe meadows, often with the participation of shrubs, also become widespread. It should be noted that the steppes of the foothills differ from the steppe areas of the West Siberian Plain in the richness and thickness of the grass cover [Kuminova, 1960]. The latter is due to high moisture content near mountain ranges and is equally true for meadow-steppe foothills and low mountains. Tundra high-altitude mountains are least represented in the northern provinces of Altai.

The Central Altai province is characterised by the presence of extensive intermontane basins with their bottoms lying at 700 to 1000 m a.s.l. The main mass of true steppes of the Central Altai is confined to the bottoms, southern sides of basins and southern slopes of residual hills located inside the intermontane basins, as well as to the broad terraces of the Katun valley, although on the territory of the province their total area is small and does not exceed 2 % (Table 1). The exposed areas of steppes are often ploughed and their remaining small fragments are used as hayfields and pastures. In addition to the steppe landscapes proper, areas with steppe vegetation are part of forest-steppe communities, which are a combination of larch (often with an admixture of birch) forests with dry sod-grass steppes and are confined to southern slopes. In addition, high-altitude mountains tundra and glacial-nival landscapes are widespread in this part of the Altai.

The Southeastern Altai province is characterized by harsh climatic conditions and serves as a kind of transitional link between the Central Altai and Mongolia, combining in its appearance some features of both neighbouring regions. There are also large intermontane basins here, but their bottoms lie much higher than in the Central Altai (from 1500 to 2000 m a.s.l.). The shortage of atmospheric moisture characteristic of this territory, combined with strong soil freezing due to the lack of a permanent snow cover, leads to the preservation of permafrost and the formation of a specific vegetation cover with the predominance of decertified steppes and solonchaks. In the areas bordering the Central Altai, fine

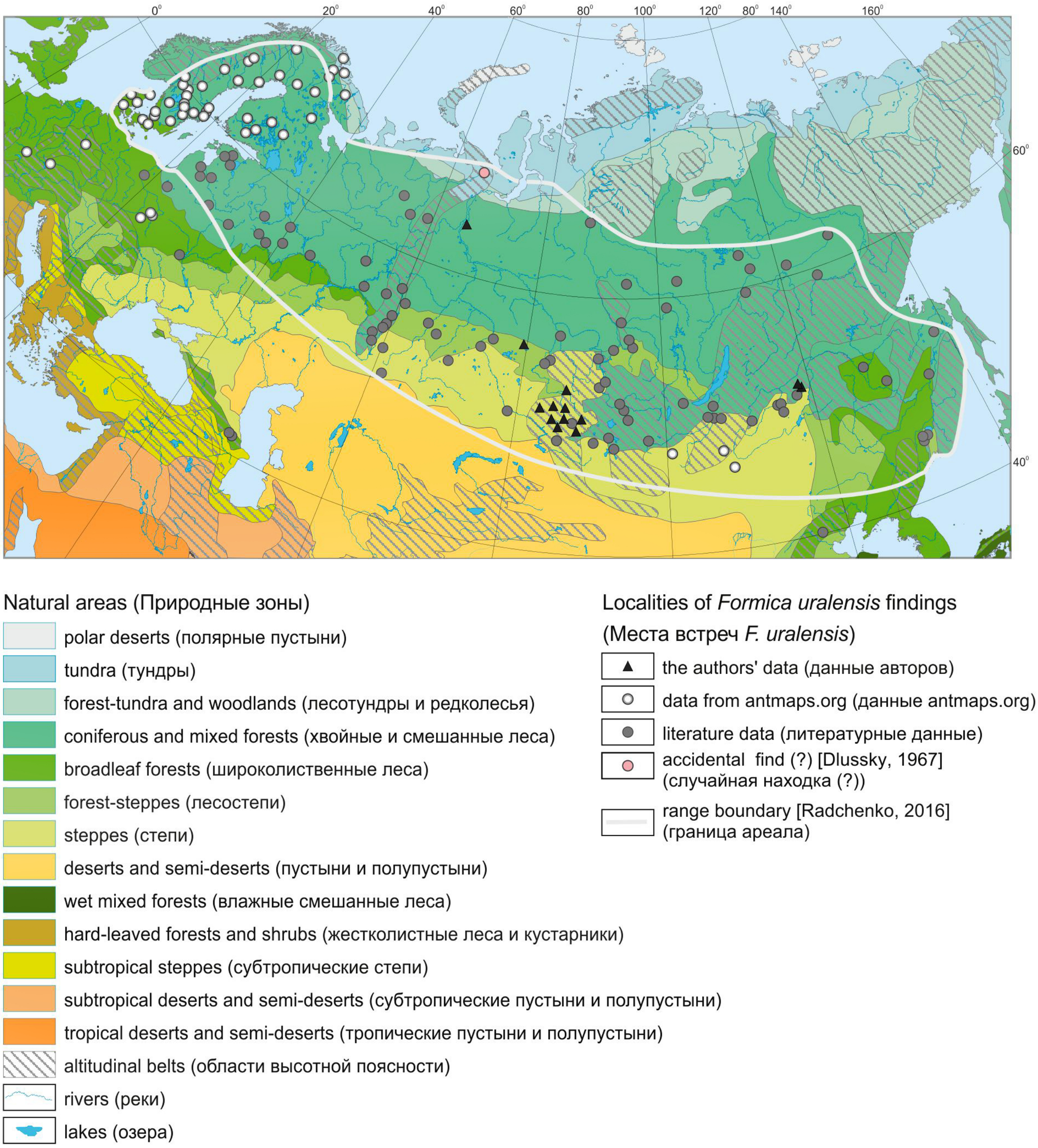


Fig. 1. Distribution of *Formica uralensis* in the Palearctic.
Рис. 1. Распределение *Formica uralensis* в Палеарктике.

Table 1. Diversity and share of landscapes in the provinces of the Russian part of the Altai Mountains (% of province area)
Таблица 1. Разнообразие и представленность ландшафтов в разных провинциях российской части Алтайской горной области (% от площади провинции)

Landscapes (type/subtype)	Provinces					
	NE	N	NW	CA	SE	E
Glacial-nival (glaciers, scree)	–	–	0.1	10.0	5.3	–
Tundra	5.0	–	3.4	**15.0**	**52.0**	**30.0**
Tundra-cryophytic-steppe	–	–	–	–	4.0	2.0
Alpine-subalpine sparse-forest-meadow	5.4	1	13.0	**24.0**	6.2	**17.0**
Forests:						
mid-altitude mountain	**23.0**	17.0	**29.0**	**34.0**	3.3	**42.5**
low-altitude mountain	**59.0**	17.0	**18.0**	0.1	–	–
intermontane basins	–	–	–	–	–	1.0
Forest-steppe:						
mid-altitude mountain	0.6	**19.0**	5.0	11.0	3.0	–
low-altitude mountain	2.0	**24.0**	12.0	–	–	–
intermontane basins	–	–	–	0.4	–	–
Meadow-steppe low-altitude mountain	–	**20.0**	**17.0**	–	–	–
Forest-meadow mountain valley	5.0	2.0	2.5	3.5	5.0	6.4
Steppe:						
mountain slope	–	–	–	–	6.0	0.1
mountain valley and intermontane basins	–	–	–	2.0	**15.0**	1.0
Total area, km^2 [Landscape map.., 2001]	18287	11656	14966	34340	16719	12406

Note. Provinces of the Russian part of the Altai mountain region: NE — Northeastern, N — Northern, NW — Northwestern, CA — Central Altai, SE — Southeastern, E — Eastern. The values for the landscapes prevailing by area are marked in bold.

Примечание. Провинции российской части Алтайской горной области: NE — Северо-Восточная, N — Северная, NW — Северо-Западная, CA — Центральноалтайская, SE — Юго-Восточная, E — Восточная. Полужирным шрифтом выделены значения ландшафтов, преобладающих по площади.

sod-grass cereal steppes are widespread, and there are also relatively large fragments of meadow steppes confined to the northern sides of the basins. The absence of a pronounced forest belt in the Southeastern Altai leads to the interpenetration of steppe and tundra associations and the formation of specific cryophyte-steppe landscapes.

The Eastern Altai Province, like the Southeastern Province, is characterized by the general severity of climatic conditions. Its specific features include unusually wide plateau watersheds cut by river valleys (the depth of relief dissection in some places reaches 1400–1600 m). More than 30 % of the province's area is covered by mid-altitude mountains forests. The share of high altitude alpine-subalpine meadow and tundra-type landscapes is also high. The total area of steppe landscapes in the East Altai Province is half of that in the Central Altai (Table 1). At the same time, the presence of dry steppe formations and the average hypsometric elevation of the Eastern Altai Province bring it closer to the Central and Southeastern provinces, which distinguishes these territories from the northern provinces of Altai.

Materials used

The analysis was based on the abundance data (the number of nests per hectare) of *F. uralensis* collected by the authors in 187 habitats in the Northern (1981–1982, 2003, 2011), Northeastern (2002), Northwestern (2005, 2009, 2015), Central (1988–1989, 2006–2008, 2013, 2015, 2019), Eastern (2005, 2019) and Southeastern provinces (2005–2006, 2009, 2013). *F. uralensis* nests were counted on transects 10 m wide and 2 km long.

In three habitats where large *F. uralensis* nest complexes were found, in addition to route surveys, the area occupied by the complex and the total number of nests present were estimated. We calculated the abundance of the *F. uralensis* in these habitats as a weighted average of the data obtained on the routes and during the surveys of the complexes, taking into account the ratio of areas with high (in the complex) and low settlement density.

In addition to our own materials, we used literature data on the abundance of *F. uralensis* in 35 habitats located within the Kurai and Chui Basins of the Southeastern Altai, obtained at the survey sites [Zhigulskaya, 2009, 2011]. Based on preliminary analyses of the data collected by the first and second authors, the abundance calculated from site and route surveys in the same habitats differed significantly. This may be due to differences both in the size of the area surveyed and in a set of random factors in the selection of locations for survey sites, as the influence of random effects in site surveys is higher compared to long route surveys. In order to be able to adequately compare the author's data with the literature data [Zhigulskaya, 2011], a correction coefficient was calculated and used at the preliminary stage of the analysis, which allowed levelling the existing differences. The coefficient was calculated based on the data collected by the first and second authors in a few habitats typologically similar to those indicated in the literature, where *F. uralensis* was found both on the sites and transects.

In total, the analysis included the data on the abundance of *F. uralensis* in 222 habitats roughly corresponding to the landscape tract rank. Additional materials on the presence or absence of *F. uralensis* in 26 habitats (of which 6 are literature sources [Zhigulskaya, 2009, 2011] and 20 are the authors' data outside the main surveys, disregarding the abundance of the ant species studied in both cases) were not included in the analysis. We took them into account when classifying habitats according to the degree of optimality of conditions for *F. uralensis*. The collection locations for materials are shown in Figure 2.

Data analysis

The data were analysed with PAST 4.11 and Jacobi [Polunin et al., 2014, 2019].

The principal component analysis (PCA) method [Kendal, Stewart, 1976; Iberla, 1980] and factor classification were used to analyse the landscape-biotopic distribution of *F. uralensis*. These methods of factor analysis, which are fundamentally similar, complement each other well when analysing the spatial variability of animal communities [Toropov, Shor, 2012].

Cluster analysis, carried out using the «Factor Classification» programme [Trofimov, 1976], involves combining all species abundance data into groups, with the number of groups ultimately determined by the internal irregularity of the sample analysed. Jaccard's coefficient [Jaccard, 1902] for quantitative traits was used as a measure of similarity-difference in the spatial distribution of the species [Naumov, 1964]. The habitat similarity matrix obtained after calculating the coefficients is transformed so that they explained proportion of the variance

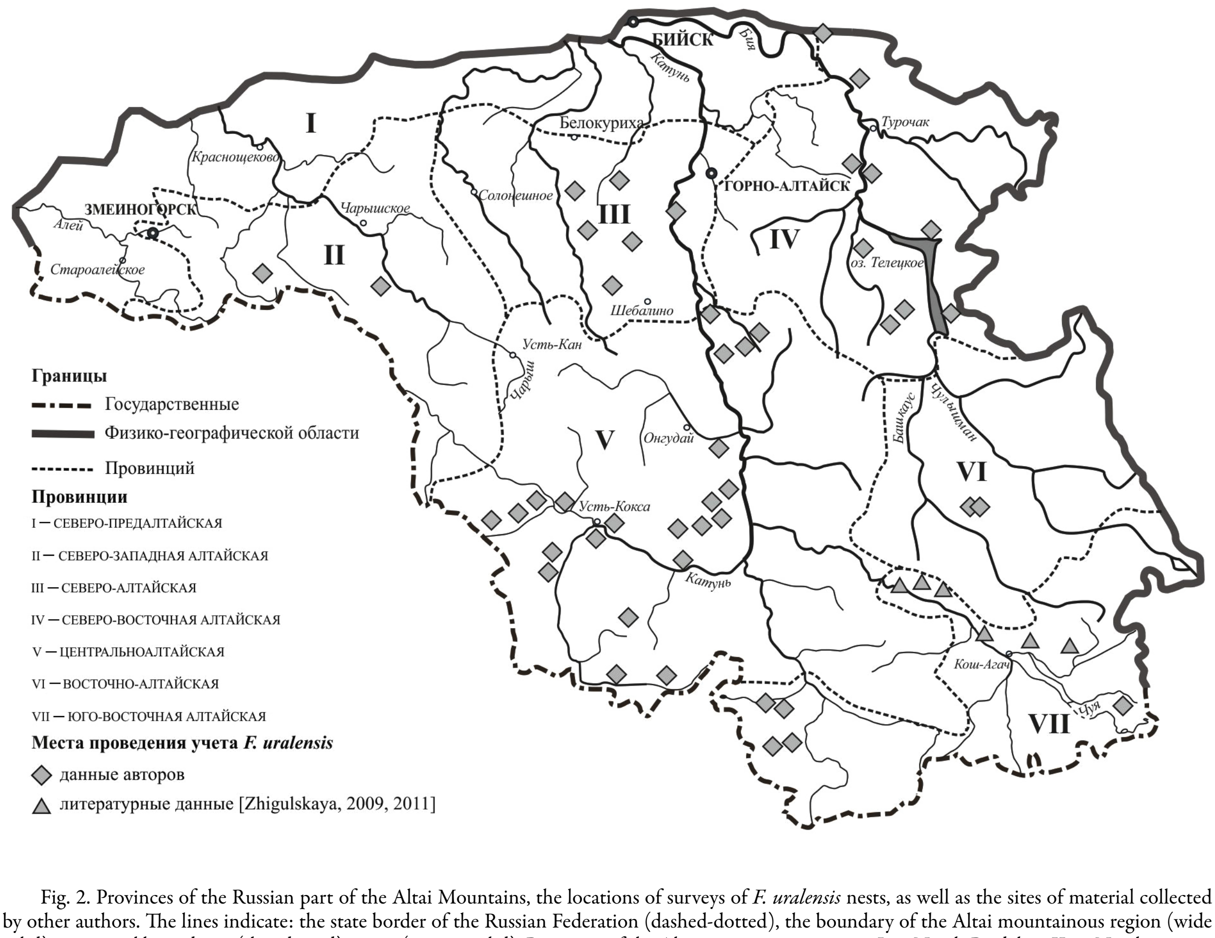


Fig. 2. Provinces of the Russian part of the Altai Mountains, the locations of surveys of *F. uralensis* nests, as well as the sites of material collected by other authors. The lines indicate: the state border of the Russian Federation (dashed-dotted), the boundary of the Altai mountainous region (wide solid), provincial boundaries (thin dotted); rivers (narrow solid). Provinces of the Altai mountainous region: I — North-Predaltai, II — Northwestern, III — Northern Altai, IV — Northeastern, V — Central Altai, VI — Eastern Altai, VII — Southeastern. Sites of the material collection: rhombus — the authors' collections; triangles — literary data [Zhigulskaya, 2009, 2011].

Рис. 2. Провинции российской части Алтайской горной области с указанием мест проведения учётов гнёзд *F. uralensis*, а также точек сбора материала другими авторами. Означения: см. легенду к рисунку.

of the similarity matrix is maximised when combining into groups [Trofimov, 1976; Trofimov, Ravkin, 1980].

When using the factor classification method to study the distribution of a single species, it is often necessary to adjust the calculation method due to the presence of a large number of habitats with zero abundance values [Kislyj et al., 2019]. Since zero values of the abundance result in zero values of the similarity coefficient, this indicates that even biotopically close habitats are absolutely dissimilar. Clustering the null data results in a large number of individual classes, making the results much more difficult to interpret. To avoid such misrepresentation and misinterpretation of the data, a constant in the form of a very low value of 0.00001 was added to all values in the sample (222 habitats). In general, this near-zero change in abundance values play no role, but it enables us to group all habitats with zero abundance of *F. uralensis* into a single cluster, as it serves as an indicator of their 100 % similarity.

In the next stage of the analysis, the result of the factor classification was idealised [Ravkin, Livanov, 2008] according to the insight gained into the causes of changes in species abundance. Detailed analysis of the clustering results showed that, some biotopes were initially accidentally assigned to inappropriate (atypical) clusters, due to formal similarity in the abundance of *F. uralensis*. In such cases, we moved them to groups consisting of typologically similar habitats. For example, the largest group included all habitats known to be unsuitable for *F. uralensis*, where the abundance of this species was zero: tundra and sparse forest-meadow tracts, dense forests with dense undergrowth or moss ground cover, tall grass meadows, high-altitude mountains cold steppes, including solonetz and solonchak steppes, as well as villages and fields. However, this group also included some steppe habitats confined to the Katun valley or slopes in the lower part of mid-altitude mountains, in which *F. uralensis* had not been found for unknown reasons, despite the fact that this species was repeatedly recorded in typologically similar habitats. As the lack of information on *F. uralensis* nests in suitable tracts for the species may be due to a random set of reasons and cannot be formally explained, we transferred such habitats to their respective groups when classifying the data. This relocation certainly leads to a decrease in the proportion of variance explained by the resulting classification, i.e., to a decrease in its informativeness. Subsequent evaluation of the informativeness of the representations obtained allows us to clearly visualise the magnitudes of these «losses». At the same time, the relocation procedure is an important stage of our analysis, which avoids contradictions in explaining the reasons for the non-uniformity of *F. uralensis* abundance.

The results of factor classification are presented in the form of a classification scheme. The graph shows the general direction of variability in the abundance of *F. uralensis* (the main spatial trends) considered in relation to environmental factors; the factor gradients coincide with the main directions of variability in the abundance of this ant species (Fig. 3). These factors are accepted as structure-forming, i.e., external factors determining the features of spatial variability of *F. uralensis* abundance, and their set and relative significance (strength and scope) are treated as the spatial organisation [Ravkin, Livanov, 2008] of *F. uralensis* distribution. In addition to directionality in abundance variability, the graph shows the degree of similarity both between the groups formed during the classification process and the average within-group similarity of the combined variants. Lines in the graph indicate relationships between groups, with the specific similarity value indicated by the number next to the line. The numbers inside the circles correspond to the group number in the classification; the lower numerical indices indicate the average value of similarity of abundance indices for the habitats included in the group. Next to the circle is a brief characteristic of the selected group, which includes a maximally generalized list of habitats included in it and the average abundance values of *F. uralensis*. The arrows on the Figure 3 show the increase in habitat favourability for *F. uralensis* and the main directions of spatial variability in the abundance of this species associated with environmental factors.

The informativeness of classification of habitats according to the degree of optimality of environmental conditions for *F. uralensis*, as well as the strength and scope of impact (manifestation in a small or large number of variants of the analysed sample) of environmental factors associated with the distribution of *F. uralensis*, were assessed using qualitative linear approximation of correlation matrices [Kupershtoh et al., 1978]. Each factor was presented as a set of gradations on a point scale (Table 1 in Supplementary). For four factors (heat availability and moisture supply, type and subtype of vegetation cover and landscape structure reflecting differences at type and sub-type level) gradations are allocated using cartographic data from literature [Atlas Altajskogo kraya, 1978; Nikolaev, Samoylova, 1978; Landscape map.., 2001]. The sum of average daily temperatures above +5 °C is taken as an indicator of heat availability [Atlas Altajskogo kraya, 1978]: 1 — less than 800 °C (tundra highlands); 2 — 800–1200 °C (tundra and subalpine-meadow mid-altitude mountains); 3 — 1201–1600 °C (taiga mid-altitude mountains); 4 — 1601–2000 °C (forest-steppe mid-altitude mountains and forest low-altitude mountains); 5 — 2001–2200 °C (forest-steppe low-altitude mountains and mountain-valley landscapes within low-altitude mountains); 6 — 2201–2400 °C (meadow-steppe low-altitude mountains and foothills). Moisture supply is expressed in terms of average annual precipitation [Atlas Altajskogo kraya, 1978]: 1 — extremely low (less than 200 mm/year — desertified habitats within the Chui Basin of the Southeastern Altai); 2 — very low (200–400 mm/year — dry-steppe valley and intermontane basin habitats within the Southeastern and Central Altai, as well as high-altitude mountain steppes on slopes and sparse forests of the Southeastern Altai); 3 — low (401–600 mm/year — moderately dry steppe habitats within the foothills and mid-altitude mountains of the northern, central and eastern Altai, as well as

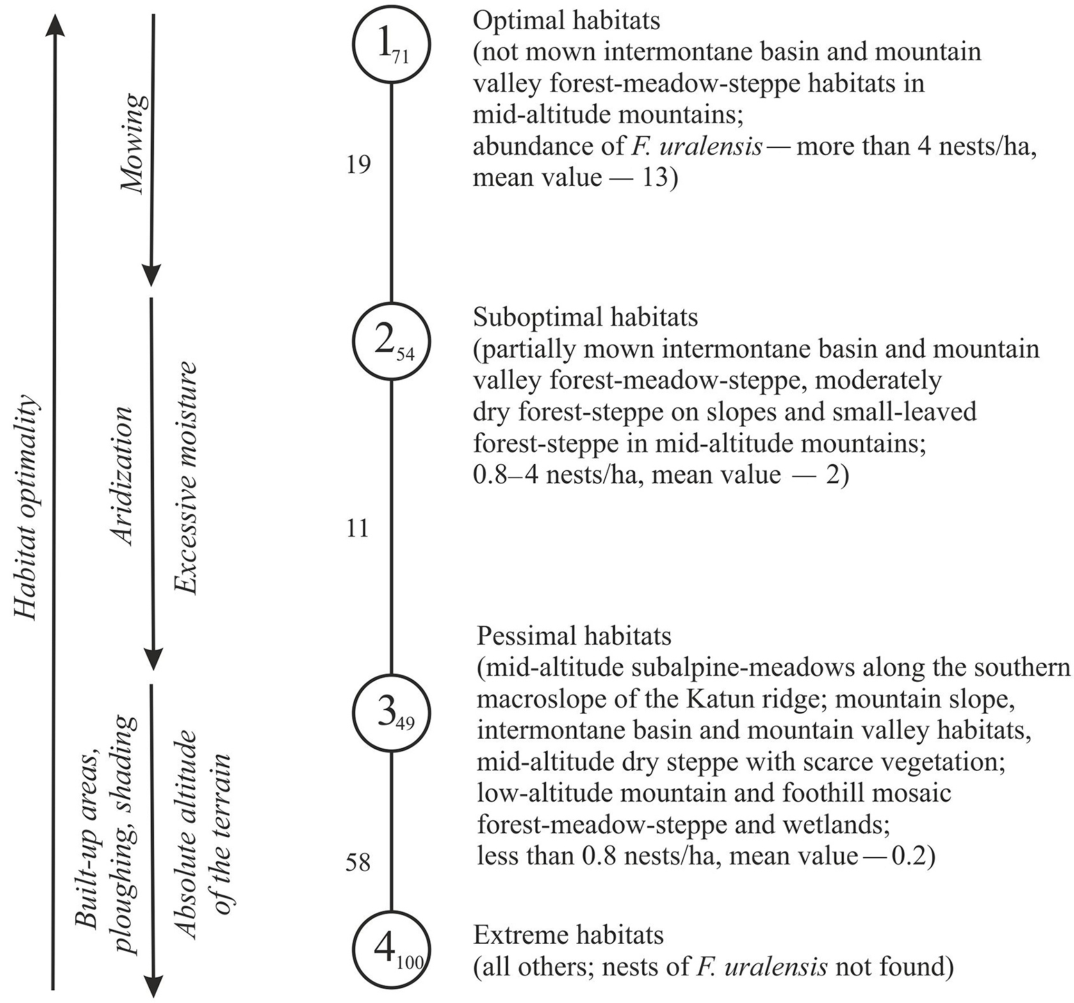


Fig. 3. Spatial-typological changes in favourable environmental conditions for *F. uralensis* according to the abundance of the species in the surveyed landscapes. The lines show links between groups, the figure next to each line is the similarity value. The numbers inside the circles index the groups in the classification, the subscript indicates the average similarity value of the samples (abundance variants for habitats) included in the group. Next to the circle is a brief characteristic of the group, which reflects a maximally generalised list of habitats included in the group and average abundance values of *F. uralensis*. The arrows show the increase of habitat favourability for *F. uralensis* and the main directions of spatial variability of *F. uralensis* abundance associated with environmental factors.

Рис. 3. Пространственно-типологические изменения благоприятности условий среды для обитания *F. uralensis* по обилию вида в обследованных ландшафтах. Линии — связи между группами, цифра рядом с линией — величина сходства. Цифры внутри кружков соответствуют номеру группы в классификации, нижним цифровым индексом указана средняя величина сходства вариантов обилия для местообитаний, вошедших в группу. Рядом с кружком приведена краткая характеристика группы, которая включает максимально обобщённый перечень вошедших в нее местообитаний и средние значения обилия *F. uralensis*. Стрелками показано увеличение благоприятности местообитаний для *F. uralensis* и основные направления пространственной неоднородности обилия этого вида, сопряжённые с факторами среды.

cryophytic steppe habitats of the Southeastern Altai); 4 — medium (601–800 mm/year — foothill meadows; forests (except for «dark» forests) and subalpine sparse forests within the Northwestern, Northern, Central and Eastern Altai; tundras of the Southeastern Altai); 5 — high (801–1000 mm/year — alpine meadow and tundra habitats within all provinces except the Southeastern Altai; «dark» forests of the Northwestern Altai; forests and subalpine sparse forests of the Northeastern Altai). Type and sub-type differences in vegetation cover are reflected using the vegetation map [Atlas Altajskogo kraya, 1978]: 1 — plain marsh (waterlogged habitats within the foothills); 2 — meadow steppe (all steppe meadows and meadow steppes); 3 — steppe (steppe habitats, except deserted variants of communities and cryophytic steppes); 4 — desertified steppe ; 5 — forest steppe (all forest-steppe tracts, including shrub thickets within the forest-steppe belt); 6 — taiga forest (forests dominated by fir, spruce and cedar, as well as those with a ground cover of green mosses); 7 — non-taiga forest (forests dominated by larch and birch, including sparse or park forests, as well as shrub thickets within the forest belt); 8 — mountain marsh (wetland habitats except for foothills); 9 — subalpine meadow (subalpine sparse forests in combination with meadows and thickets of dwarf trees (birch, willow, etc.)); 10 — subalpine meadow (alpine and subalpine meadows); 11 — tundra (tundra and cryophyte-steppe habitats). In addition to the gradations listed above, two more gradations not shown on the vegetation map have been added: 12 — human settlement (all settlements) and 13 — agricultural character of vegetation (fields and fallow lands). To describe the landscape differentiation of the territory, appropriate maps were used [Nikolaev and Samoylova, 1978; Landscape map..., 2001], which enabled us to rank landscapes by altitude (from foothills to highlands) and at the same time by the nature of the prevailing vegetation. A total of 23 gradations were identified (e.g.: 1 — foothill lowland meadow habitats; 2 — foothill lowland marsh habitats; 3 — foothill upland forest steppe; 4 — low-altitude mountains steppe; 5 — low-altitude mountains forest steppe, etc.).

For the other six factors (forest cover, shading, absolute altitude, altitudinal belt, slope exposure and surface inclination), we determined the number of gradations so that to account for the species' response to the environment as revealed by the results of the factor classification. Two gradations were identified for the forest cover: 1 — forests (all forest communities except subalpine sparse forests, as well as sparse and mosaic forests); 2 — other habitats (tundra, meadows, bogs (except forest bogs), steppes and forest-steppe communities, as well as fields and villages). Shading: 1 — high (forests, except subalpine sparse forests, mosaic and sparse forests; dense bushes and forest bogs); 2 — medium (subalpine sparse forests, mosaic, sparse, and park forests, overgrown burnt-up areas and clearings, meadows in combination with shrubs or reforests, other bogs); 3 — no shading (open habitats: tundras, meadows, steppes, fallow lands, fields and villages). Altitude above sea level: 1 — below 300 m a.s.l., 2 — 300–1000 m a.s.l., 3 — 1001–2000 m a.s.l. (for mountain-valley areas within the mid-mountains: 700–2000 m a.s.l.), 4 — above 2000 m a.s.l. Altitudinal belt: 1 — forest-steppe belt, 2 — steppe belt, 3 — forest belt, 4 — subalpine rare forest-meadow belt, 5 — cryophytic-steppe belt, 6 — alpine-tundra belt. Slope exposure: 1 — southern slope, 2 — northern slope, 3 — other slopes and horizontal surfaces. Surface inclination: 1 — gentle surfaces (up to 12 ° — habitats confined to the bottoms of intermontane basins, wide river valleys and mountain plateaus); 2 — sloping (from 13 ° to 20 ° — tracts in the lower parts of long slopes); 3 — steep slopes (more than 20 ° — other mountain-slope habitats).

The share of explained (eliminated) variance of correlation matrices, calculated first separately for each factor and then for their aggregate, served as an indicator of informativeness.

The Table of main characteristics of the habitats studied with each environmental factor represented as a series of gradations on a point scale is given in Appendix (P.20–33).

The present work are registered in ZooBank (www.zoobank.org) under urn:lsid:zoobank.org:pub:6D2689C6-7862-4CB3-B762-A75682DF7B28

Results

Landscape-biotopic distribution

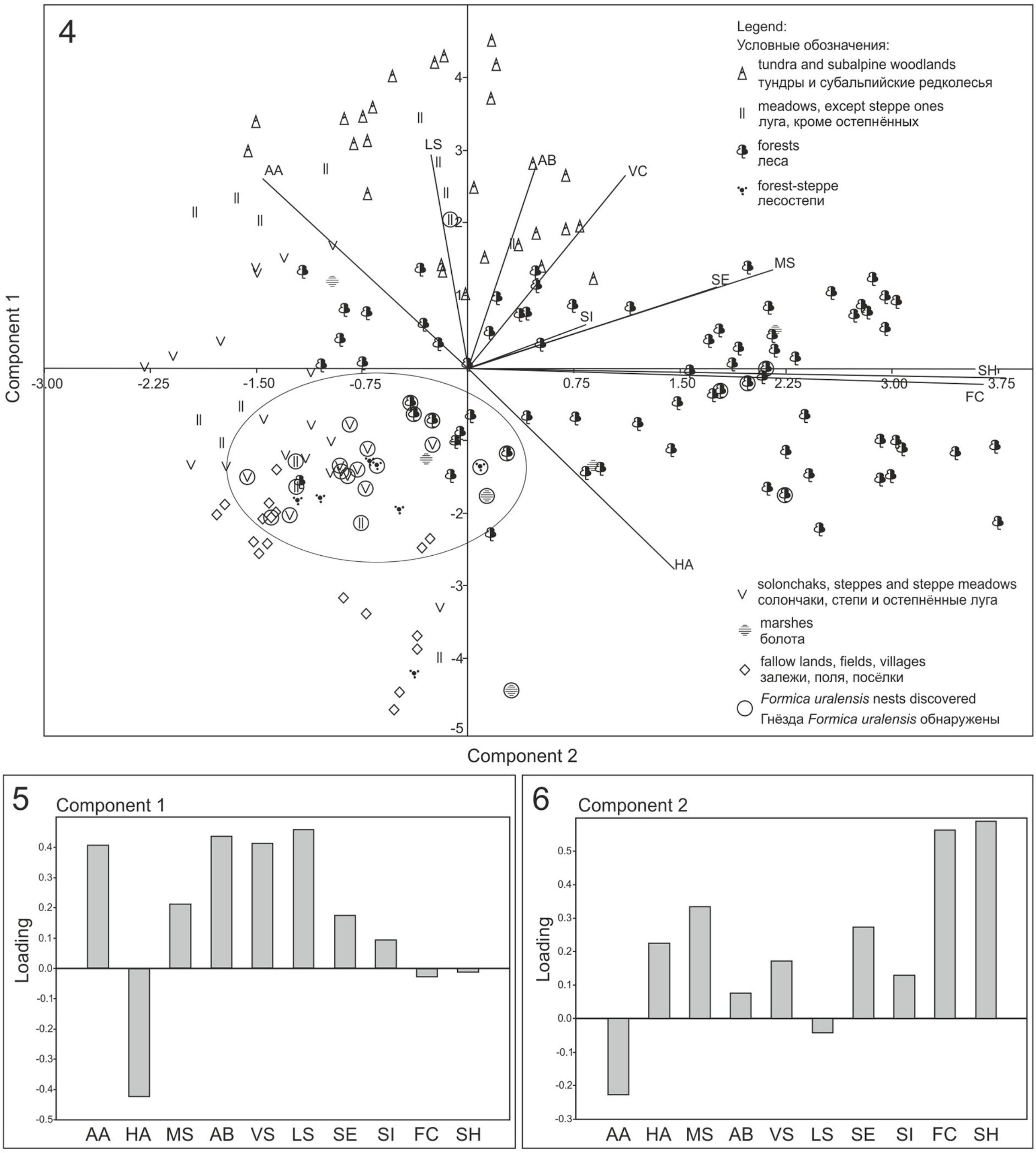
The analysis of generalized data showed that *F. uralensis* was very unevenly distributed over the study area: nests were found only in 52 out of 248 surveyed habitats (21 %). The highest abundance (24 nests/ha) was recorded in forest-steppe habitats of the Central Altai, confined to intermontane basins. In this province, the studied ant species inhabits 28 % of the total number of habitats surveyed, and the largest nest complexes identified during the surveys were also found here. The abundance of *F. uralensis* was significantly lower in the other provinces. The species is rarest in the Northeastern Altai, where it was found only in foothill bogs covered with shrubs (0.4 nests/ha). Its abundance was slightly higher in the Northern Altai, where it inhabited low-altitude mountain flood plains with low grass meadows and waterlogged birch forests (0.4 nests/ha) and steppe meadows with larch-birch forests (0.8 nests/ha), and was also found outside the counts on the edges of aspen-birch and park larch forests and on steppe meadows in the lower part of the mid-altitude mountains. *F. uralensis* is also rare in the Northwestern Altai, where its single nests are found in low-altitude mountain steppe meadows and in sparse larch-birch forests growing along slopes, as well as in perennial grasslands in the Tigirek valley. In the Eastern Altai, both single nests of *F. uralensis* in the Bashkaus valley and a rather large complex of nests of this species in the Yoldu valley (right tributary of the Bashkaus) were recorded. In the Southeastern Altai, single nests of *F. uralensis* were found in steppe areas on the southern slope of the Kurai range, and relatively high abundance was recorded within the Kurai Basin.

In general, *F. uralensis* settlements were recorded at altitudes from 250 to 2370 m above sea level in the surveyed area. Most of the identified habitats of *F. uralensis* are confined to the bottoms and lower part of the sides of intermontane basins or terraced river valleys. Nests of this species are much rarer on mountain slopes.

Features of landscape-biotopical distribution (results of PCA)

The analysis showed that more than 50 % of the total variability of abundance indices is described by the first and second principal components (PC-1 — 38.0 %, PC-2 — 23.5 %). The influence of factors prevailing in the third component (PC-3) explains 13 % of the variability of abundance and is less important for *F. uralensis*. The contribution of the other seven components individually is insignificant, and in total amounts to 23 %. The general location of the abundance variants of the analysed sample in the component space, as well as the contribution of various factors to the composition of the first three components are shown in the figures (Figs 4–6).

In Figures 4–6, the PC-1 axis reflects the dependence in the distribution of available abundance variants on the

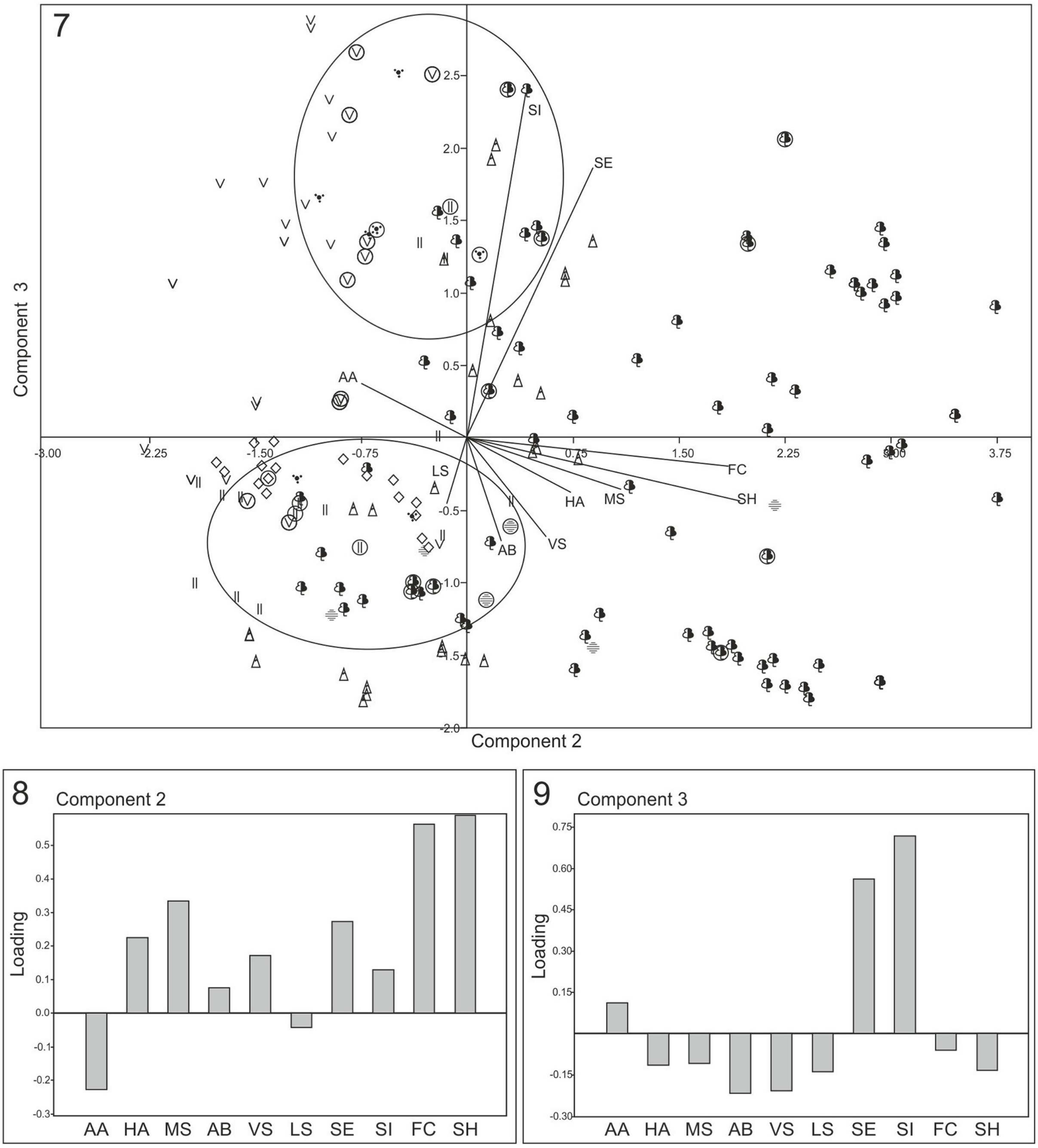


Figs 4–6. Principal component analysis results (PC1 vs. PC2). 4 — the distribution of the surveyed habitats in the space of the first and second principal components; 5 — contribution of environmental factors to the first principal component; 6 — contribution of environmental factors to the second principal component. Factors: AA — absolute altitudes of the terrain; HA — heat availability; MS — moisture supply; AB — altitudinal belt of vegetation; VC — vegetation cover (differences at the level of type and subtype); LS — landscape structure (differences at the level of type and subtype); SE — slope exposure; SI — surface inclination; FC — forest cover; SH — shading.

Рис. 4–6. Результаты анализа главных компонент (PC1 vs. PC2). 4 — расположение обследованных местообитаний в факторном пространстве PC1 vs. PC2; 5 — вклад факторов среды в состав первой главной компоненты; 6 — вклад факторов среды в состав второй главной компоненты. Факторы: AA — абсолютные высоты местности; HA — теплообеспеченность; MS — влагообеспеченность; AB — высотно-поясные различия растительности; VC — растительный покров (различия на уровне типа и подтипа); LS — ландшафтная структура (различия на уровне типа и подтипа); SE — экспозиция склонов; SI — угол наклона поверхности; FC — облесённость; SH — затенение.

absolute altitude of the area and inversely proportional to its heat availability values. Altitude variation largely determines the landscape structure forming on the territory and the type of its vegetation cover, and, accordingly, the manifestation of altitude-belt differences in the appearance of the vegetation cover. Figure 4 clearly shows that the majority of *F. uralensis* nests are confined to steppe and forest-steppe habitats (lower left quadrant of the figure). The distribution of abundance variants according to PC-2 reflects the influence of crown shading, which grows with increasing forest cover of the territory: from subalpine sparse forests to coniferous-deciduous forests of normal density, confined to the northern, most humid provinces of the Altai. The proportion of forest habitats with *F. uralensis* was small. As a rule, these are sparse forests with larch or well-warmed small-leaved (birch) forests within the Central Altai, characterized by poorly expressed undergrowth and steppe grass cover.

The relationship of populated *F. uralensis* habitats with the character of relief, as well as the level of heat availability, which is determined by exposure differences, is clear in Figures 7–9. Two factors, surface inclination and slope exposure, are the main contributors to PC-3 (Fig. 7). Along the PC-3 axis, two rather separate



Figs 7–9. Principal component analysis results (PC2 vs. PC3). 7 — the distribution of the surveyed habitats in the space of the second and third principal components; 8 — contribution of environmental factors to the second principal component; 9 — contribution of environmental factors to the third principal component. Designation of factors as in Figures 4–6.

Рис. 7–9. Результаты анализа главных компонент (PC2 vs. PC3). 7 — расположение обследованных местообитаний в факторном пространстве PC2 vs. PC3; 8 — вклад факторов среды в состав второй главной компоненты; 9 — вклад факторов среды в состав третьей главной компоненты. Обозначение факторов как на рисунках 4–6.

groups of *F. uralensis* habitats are distinguished. The first of them, located in the lower left corner of the figure, corresponds to the upland intermontane basin forest-meadow-steppe and foothill to low-altitude mountain wetland habitats, and the second — in the upper part of the figure — to the mountain-slope steppe and forest-steppe habitats.

Classification of habitats according to the degree of optimality of conditions for *F. uralensis*

When the data were analysed using factor classification software, similar results were obtained. The classification scheme developed on the basis of the analysis of generalized data is an idealized result of clustering the data on *F. uralensis* abundance in 222 habitats. Six clusters were identified at the first stage of data processing. In the subsequent detailed analysis, typologically similar habitats were combined. As a result, four gradations were identified according to the favourableness of environmental conditions for *F. uralensis* habitat.

1. Optimal habitats (high abundance: over 4 nests/ha, average 13). This group includes non-floodplain steppe grazing meadows of intermontane basins of the Central Altai and moderately dry steppes of the northern sides of the Kurai Basin of the Southeastern Altai (1500–1600 m a.s.l.). Edges of floodplain birch-spruce forests with admixture of larch and low-grass sparse larch forests with admixture of spruce, confined to the bottoms of intermontane basins and/or wide river valleys of the Central Altai. Sparse larch-cedar forests of the Eastern Altai.

2. Suboptimal habitats (moderate abundance: 0.8 to 4 nests/ha, average 2). This group includes: intermontane basin non-floodplain steppe-meadow (used for mowing), mid-altitude mountain forest-steppe and mountain-valley forest-meadow-steppe complexes represented by various variants of larch forests in combination with moderately dry steppes, fragments of steppe meadows and shrubs; dry stony steppes in the lower part of the terraced Katun valley (near the mouth of the Edigan River) and on the northern slopes of the terraces. Small-leaved forests of the Central Altai; the edges of larch forests with some spruce on the northern sides of hollows (up to 1500 m a.s.l.); perennial fallow lands within the forest-steppe mid-altitude mountains.

3. Pessimal habitats (low abundance: less than 0.8 nests/ha, average 0.2). This group includes: dry stony steppes, including mountain-slope steppes at altitudes from 1000 to 2700 m a.s.l., intermontane basin steppes and mountain-valley steppes with scarce vegetation (except for stony steppes in the lower part of the terraced Katun valley and on the northern slopes of terraces, as well as solonchak and desertified steppes); subalpine meadows of the southern macroslope of the Katun ridge, as well as intermontane steppe meadows (used for mowing) in the place of reclaimed bogs and in floodplain valleys of the Central Altai; low-altitude mountain steppe meadows and mosaic steppe-meadow-forest habitats, as well as perennial fallow in their place; park larch (not high herbaceous) forests of the high altitude (1500 m a.s.l.) intermontane basins of the Southeastern Altai and forest mid-altitude mountain basins of the Northern Altai, foothill and low-altitude mountain bogs covered by shrubs.

4. Extreme habitats (*F. uralensis* nests were not found). This category of habitats includes: rocky screes and cliffs of subnival high-altitude mountains, as well as tundras; steppes: mountain-slope steppes at altitudes from 2700 m and above, as well as within the high-altitude mountain plateaus of the Southeastern Altai; solonchak and desertified steppes of intermontane basins and terraced valleys (in the middle reaches of the Katun River); meadows: floodplain mountain-valley and intermontane basin meadows within the highlands and upper part of mid-altitude mountains(from 1700 m), alpine and subalpine meadows (except for those distributed on the southern macroslope of the Katun ridge), high-grass forests, as well as foothill meadows within forest-meadow-steppe landscapes; subalpine sparse forests, forests of normal density (except for intermontane basin forests), as well as sparse forests without larch and high-grass larch forests; burnt-up areas, clearings, stream-side willow forests, shrub thickets, bogs (except those located within forest-steppe foothills and low-altitude mountains); fields, fallow lands (except perennial within forest-steppe lowlands and middle mountains), villages and recreational areas of large settlements.

The above classification in generalized form reflects the features of landscape-biotopic distribution of *F. uralensis*, consistent with the results obtained by the principal component analysis and reduced to the presence of a relationship between the abundance of *F. uralensis* and the steppe vegetation cover. The latter, in turn, is caused by the heat and moisture supply changing as absolute altitudes increase and relief changes (slope exposure, the presence of extensive intermontane basins and terraced river valleys).

Organization of spatial distribution

The general direction of *F. uralensis* abundance variability, the degree of similarity between the selected groups in accordance with the habitat classification described above, and the average similarity of abundance variants of the studied species for the habitats grouped together are schematically shown in Figure 3. The differences in favourability for *F. uralensis* in optimal and suboptimal habitats from all other habitats are most noticeable. The number of habitats in the first two groups is very limited and constitutes only 9 % of all biotopes surveyed, while the vast majority of habitats (80 %) are classified as extreme. Significant similarity between pessimal (low abundance of *F. uralensis*) and extreme (*F. uralensis* absent) habitats is largely explained by the averaging of values after idealization of the results of formal partitioning during substantive interpretation of the data.

Differences in the relative importance of environmental factors influencing the spatial distribution of

F. uralensis depend largely on two parameters simultaneously: the strength and scope of their influence. For example, anthropogenic transformation of landscapes (construction and ploughing) has a significant impact on the abundance of *F. uralensis*, but its scope will be small, as it applies only to a limited number of variants in the available sample (8 %). Using the method of qualitative linear approximation of correlation matrices, we assessed the strength and scope of the relationship between environmental factors and abundance (Table 2). Calculations showed that the spatial distribution of *F. uralensis* across habitats within the surveyed part of Altai coincides to the greatest extent with variability in vegetation cover considered at the level of vegetation type and subtype (19 %), as well as with heat availability (18 %). Such factors as water availability (14 %) and landscape differentiation at type and subtype levels (12 %) are slightly less informative. The variation of *F. uralensis* abundance correlates much less with altitudinal and belt differences in vegetation and the absolute altitude of the terrain (7 and 6 % of the recorded variance respectively). Shading, surface inclination, slope exposure and forest cover were the least informative factors according to the results of our assessment, which indicates that their influence on *F. uralensis* distribution is local.

The increment of the explained variance in the cumulative approximation adds 11 % of the explained variance to the informativeness of the ideas about the relationship between landscape-biotopic distribution of *F. uralensis* and the type and subtype of vegetation cover due to heat availability. In addition, moisture supply and landscape differentiation of the territory add 3 and 2 % to the explained variance, respectively, while each of the following factors gives an increment of informativeness at most 1 % of the explained variance of the similarity matrix. Classification modes (by habitat optimality) account for 61 % of the variance of the similarity matrix and give an increment of 20 %. The multiple assessment of the relationship with all identified environmental factors and their combinations is 71 %, which serves as an indicator of a relatively high level of informativeness of our analysis.

Discussion

Despite the long history of studying *F. uralensis*, totalling more than 100 years, the data available so far did not allow us to get a clear idea of the biotopic preferences of *F. uralensis*. On the one hand, this was due to the insufficient study of the territories inhabited by this ant species, on the other hand, due to the specificity of its spatial distribution and relatively rare occurrence in most of its range.

The question of the reasons for the peculiar specificity of the ecology of *F. uralensis* in various parts of its range was raised by researchers at the beginning of the last century [Kuznetsov-Ugamskij, 1928; Bisgaard, 1944; Dlussky, 1967; Rosengren, 1969], but has remained unanswered until now. Since *F. uralensis* has a transpalaearctic distribution [Dlussky, 1967; Zakharov, Dlussky, 2013], it is impossible to analyse its ecological preferences within its entire range in the foreseeable future. We tried to solve this problem in a different way by analysing in detail the landscape-biotopic distribution of *F. uralensis* in the Russian part of Altai. In this relatively small mountain region, a very wide range of diverse landscapes is represented: from foothills and low-altitude mountain steppe to high-altitude mountain tundra, which provides a unique opportunity to study the ecological preferences of various species, including *F. uralensis*. The presence of all types of habitats of the studied ant in Altai allows us to consider this territory as a model, approximately representing the whole range of diverse habitat conditions of *F. uralensis* throughout its range, a kind of «areal in miniature».

The analysis showed that optimal conditions for *F. uralensis* habitat are formed mainly in intermontane basin habitats of the Central and, partly, Southeastern Altai (Kurai Basin), lying at 700 to 1500 m a.s.l. and characterized by moderate anthropogenic load. In

Table 2. Assessment of the strength and scope of the relationship between environmental factors and abundance of *F. uralensis* in the Russian part of Altai

Таблица 2. Оценка силы и общности связи факторов среды и обилия *F. uralensis* в российской части Алтая

Factor, regimes	Explained variance, %	
	Individual assessment	Increase in informativeness
Type and subtype of vegetation cover (VC)	19.0	19.0
Heat availability (HA)	18.0	30.0
Moisture supply (MS)	14.0	33.0
Landscape structure (differences at type and sub-type level) (LS)	12.0	35.0
Altitudinal belt of vegetation (AB)	7.0	36.0
Absolute altitudes of the terrain (AA)	6.0	37.0
Shading (SH)	1.5	37.5
Surface inclination (SI)	1.0	38.0
Slope exposure (SE)	0.8	39.5
Forest cover (FC)	0.4	40.0
Regimes by classification (optimality of environmental conditions)	61	71

addition to intermontane basin habitats, some of the mountain-valley tracts within the Central and Eastern Altai, represented by vast flattened areas with sparse larch forests along river beds and steppe grass cover, can also be considered optimal habitats. According to literature data [Atlas Altajskogo kraya, 1978], the heat availability of the listed habitats, estimated as the total number of average daily temperatures above 10 °C, ranges from 800 to 1600 °C (1200 °C on average). Moisture supply, expressed in average annual precipitation, ranges from 400 to 600 mm per year.

The habitats classified as suboptimal are also confined to the Central and only partly Northern Altai (steppe meadows in the lower part of forest-steppe mid-altitude mountain areas) and are located in approximately the same heat and moisture ranges as the optimal ones. At the same time, most of them experience a significant anthropogenic load (annual mowing, intensive grazing and overgrazing, ploughing), which leads to degradation of natural grass cover, depletion of food, at least carbohydrate, resources necessary to support high numbers of ant colonies, as well as to direct destruction of *F. uralensis* nests. It should be noted that only reconnaissance studies have been carried out in the Eastern Altai, so the assignment of some of the biotopes surveyed here to optimal habitats reflects only the fact of finding a complex of *F. uralensis* nests in this area. Additional studies are needed to assess the degree of optimality of habitats for *F. uralensis* within this province more precisely.

Pessimal («poorly suitable for *F. uralensis*» habitat) and extreme («unsuitable for *F. uralensis*» habitat) conditions are formed as a result of the combined action of diverse environmental factors and are present in all surveyed provinces. Thus, intermontane floodplain meadows, which, in addition to anthropogenic pressure (regular mowing), are subject to annual and quite long-term flooding, can be classified as pessimal habitats. Dry steppes in the Katun valley and forest-steppe complexes of the low-altitude mountains and lower part of the mid-altitude mountains are also poorly suitable for the ant under study. Dry steppes experience moisture deficiency as they are located in the 'rain shadow' of the Terektin ridge, which leads to their xerophytization and extreme impoverishment. Forest steppes up to 700 m a.s.l., on the contrary, lie in the area with sufficient atmospheric moisture (annual precipitation exceeds 600 mm), which leads to the development of a lush grass cover. The reasons for the low abundance of *F. uralensis* here remain unclear and require a separate detailed study. *F. uralensis* is also almost completely absent in the subalpine meadow belt. The only exception is the subalpine meadows on the southern macroslope of the Katun ridge, characterized by distinctive animal communities [Tsybulin, 2009; Bochkareva, Livanov, 2013] due to the warming effect of air masses moving from the adjacent territories of Kazakhstan.

Most of the habitats classified as extreme are characterized by low heat availability, which may be due to either hypsometric elevation of the terrain or shading by tree crowns, shrubs and/or high grasses. For some biotopes, low heat availability is combined with high moisture content (tundras, subalpine meadows and sparse forests, taiga forests), while the other part is represented by cold biotopes with extreme moisture deficiency (desertified steppes of the Chui Basin of the Southeastern Altai). In addition, anthropogenically disturbed habitats such as fields, villages and recreational areas in the vicinity of large human settlements can be considered as extreme.

Information on *F. uralensis* findings (including data on species abundance) in other parts of its range confirms the ideas about optimal habitat conditions for this species obtained during our study for the Russian part of Altai (Fig. 1). Thus, the northern boundary of the range of *F. uralensis*, apparently, passes along the border of the forest zone and only within the Kola Peninsula, washed by the warm sea current, shifts northwards, covering the tundra zone. It should be noted that in the forest zone *F. uralensis* is rare [Kvamme, 1982; Omelchenko, 1996; Fedoseeva, 2003; Stankiewicz et al., 2005; Punttila, Kilpeläinen, 2009; Adakhovskij, 2024] and becomes common only within the forest-steppe and steppe zones [Omelchenko, 1996; Gridina, 2003], as well as mountain territories located in the forest-steppe zone [Pleshanov, 1966; Dmitrienko, 1979; Zhigulskaya, 2011]. The claimed finding of *F. uralensis* in the tundra zone in the Polar Urals [Dlussky, 1967], i.e., far beyond the Kola Peninsula, which is influenced by the warm Gulf Stream current, seems erroneous or accidental and requires confirmation. In the south, the distribution of *F. uralensis* is bounded by deserts, where this species does not enter: the southernmost finds occur in intrazonal mountain areas — the Caucasus [Dubovikoff, 2006; Z.M. Yusupov, personal communication] and northern China [Radchenko, 2016].

In general, our findings confirmed the validity of both hypotheses. On the one hand, the abundance of *F. uralensis* in mountain-valley habitats indicates that this species has physiological adaptations to nest flooding, which occurs occasionally during spring floods in the mountains. In turn, this explains the ability of *F. uralensis* to inhabit bogs where the groundwater level is subject to seasonal and random fluctuations due to climatic factors [Mikhailov et al., 2013]. At the same time, our results indirectly support the assumption that due to climate change and the widespread expansion of forests in the postglacial period, *F. uralensis* could have been displaced within the modern forest zone to bogs as reserves with relatively low vegetation. In addition, it is possible that we are dealing with two cryptic species of ants, which do not have a clear gap between their ranges, but have a clear divergence in ecological preferences (steppe and wetland habitats). However, verification of this hypothesis requires a detailed study using molecular genetic methods of analysis.

In Altai, as throughout its range, *F. uralensis* occupies a wide range of habitats, from bogs to steppes, and abundance in the latter habitat type is much higher, whereas in bogs this species occurs only in the most forested Northern and Northeastern provinces and does not form large nest complexes. The most favoured habitats include warm forest-steppe tracts with sparse stands and low grass cover. This provides optimal habitat conditions for this species in terms of temperature, humidity and light. In addition, it should be noted that the presence of spruce trees in the stand is of significant importance in creating conditions optimal for *F. uralensis*. Apparently, this is closely related to the carbohydrate component of the ants' diet, namely, to the formation of stable trophobiotic relationships with obligatory myrmecophilous aphids of the genus *Cinara* living on coniferous plants. However, this issue requires a separate detailed study.

Conclusions

1. The landscape-biotopic distribution of *F. uralensis* in the Russian Altai is extremely non-uniform, with the species occurring most often within the Central Altai province, where its abundance in some habitats can reach 24 nests/ha, and very large nest complexes are also present.

2. The number of habitats favourable for *F. uralensis* in the studied area turned out to be very limited — only 10 % of the total number of biotopes surveyed. Pessimal habitats, with low abundance of *F. uralensis*, accounted for 11 %. Extreme habitats accounted for 79 %.

3. The ideas about the optimality of conditions for *F. uralensis*, revealed in the process of clustering data on its abundance using the method of factor classification and principal component analysis, are generally similar and are reduced to differences in the hydrothermal regime, which determine the formation of the type of vegetation cover, as well as the differentiation of landscapes at the type and subtype levels. To a much lesser extent, the habitat distribution of *F. uralensis* in the surveyed part of Altai coincides with the altitudinal and belt differences of vegetation and the absolute altitudes of the area.

4. The preferred habitats include forest-steppe tracts located within intermontane basins and broad river valleys at 700 to 1500 m a.s.l. with summer heat availability from 800 to 1600 °C and moisture availability from 400 to 600 mm per year, as well as moderate anthropogenic load (without building, ploughing and annual mowing).

5. Unlike red wood ants (*Formica rufa* group), *F. uralensis* is able to successfully survive in conditions of overwatering and cope with the problem of permanent (in swamps) or temporary (in river floodplains) waterlogging of nests, which indicates the presence of specific physiological and possibly behavioural adaptations. Due to this advantage, *F. uralensis* becomes dominant in such habitats. Under the conditions of temporary (though long-term) water logging in floodplain habitats in Altai, *F. uralensis* even forms large complexes of anthills, which may include up to 400 or more nests. However, our results do not exclude the possibility of the existence of two cryptic species with distinct specific ecological preferences, but this issue requires a separate detailed study using molecular genetic methods.

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Appendix to the article: S.V. Chesnokova, L.V. Omelchenko, T.A. Novgorodova. Landscape-biotopic distribution of *Formica uralensis* Ruzsky, 1895 (Hymenoptera: Formicidae) in the Russian part of Altai (Euroasian Entomological Journal. 2025. Vol.24. No.1. P.38–52).

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Table 1. The main characteristics of the habitats studied. Each environmental factor is represented as a series of gradations on a point scale

Таблица 1. Основные характеристики исследованных местообитаний. Каждый фактор окружающей среды представлен в виде ряда градаций по балльной шкале

Habitats	*Formica uralensis*	Factors									
		AA	HA	MS	AB	VC	LS	SE	SI	FC	SH
Northwestern Altai (Северо-Западный Алтай)											
Altai Territory, Krasnoshchekovsky district, Tigirek village 51.15°N, 83.03°E, 480 m*, small villages, 20.05.2009 (ChS)	–	2	4	4	1	12	5	3	1	2	1
Altai Territory, Krasnoshchekovsky district, Tigirek village 51.13°N, 83.02°E, 600 m, «dark» coniferous taiga («dark» aspen-fir taiga), 21.05.2009 (ChS)	–	2	4	4	3	6	6	2	1	1	3
Altai Territory, Krasnoshchekovsky district, Tigirek village 51.15°N, 83.04°E, 480 m, valley shrubs, 22.05.2009 (ChS)	–	2	4	4	1	7	13	3	1	2	3
# Altai Territory, Krasnoshchekovsky district, Tigirek village, 51.15°N, 83.02°E, 510 m, steppe meadows on slopes, 19.05.2009 (ChS)	+	2	4	4	1	2	5	1	2	2	1
# Altai Territory, Krasnoshchekovsky district, Tigirek village 51.14°N, 83.00°E, 490 m, fallow meadows, 20.05.2009 (ChS)	+	2	4	4	1	13	5	3	1	2	1
Altai Territory, Krasnoshchekovsky district, Tigirek village 51.14°N, 83.04°E, 550 m, shrubs on slopes, 21.05.2009 (ChS)	–	2	4	4	3	7	6	1	1	2	3
Altai Territory, Krasnoshchekovsky district, Tigirek village 51.14°N, 83.05°E, 490 m, valley birch forests, 22.05.2009 (ChS)	–	2	4	4	3	7	15	3	1	1	3
Altai Territory, Krasnoshchekovsky district, Tigirek village 51.15°N, 83.02°E, 550-600 m, larch-birch forests on slopes, 23.05.2009 (ChS)	+	2	4	4	1	5	5	1	3	1	2
Altai Republic, Ust-Kansky district, Ust-Kumir village, 51.01°N, 84.31°E, 776 m, sparse fir-cedar-birch forests, 8–13.07.2015 (NT)	–	2	4	3	3	6	15	3	1	2	2
Northern Altai (Северный Алтай)											
Altai Territory, Altai district, Sarasa village, 51.91°N, 85.37°E, 220 m, meadow steppes and steppe meadows, 20.08.2003 (OL, ChS), # 14.07.2011 (NT)	–	1	5	4	2	2	4	3	1	2	1
Altai Territory, Altai district, Altayskoye village, 51.93°N, 85.38°E, 300–400 m, grain fields, 21.08.2003 (OL, ChS), # 13.07.2011 (NT)	–	2	5	4	2	13	4	3	1	2	1
Altai Territory, Altai district, Sarasa village, 51.87°N, 85.36°E, 250 m, large villages, 19.08.2003 (OL, ChS), # 13.07.2011 (NT)	–	1	5	4	2	12	4	3	1	2	1
# Altai Republic, Maiminsky district, Rybalka village, 286 m, 51.92° N 85.85° E, villages, 20.07.2009, 13–22.07.2011 (NT), 27.07–1.08.2010 (SA)	–	1	5	4	2	12	4	3	1	2	1
Altai Territory, Altai district, Kyrkyla village, 51.75°N, 85.42°E, 600 m, mosaic aspen-birch forests, 19.08.2003 (OL, ChS), # 14.07.2011 (NT)	–	2	4	4	1	5	5	3	1	2	2
# Altai Republic, Shebalinsky district, Ulus-Cherga village, 51.56°N, 85.50°E, 550 m, steppe meadows with larch-birch copses, 11.07.1982 (OL), 16.07.2011 (NT)	+	2	4	3	1	5	5	1	2	2	2
Altai Republic, Shebalinsky district, Cherga village, 51.52°N, 85.58°E, 500 m, waterlogged floodplain valleys with birch forests and shrubs, 05-06.08.2003 (ChS), # 16.07.2011 (NT)	+	2	5	3	1	8	13	3	1	2	2

Table 1. (continuations)
Таблица 1. (продолжение)

Habitats	*Formica uralensis*	Factors									
		AA	HA	MS	AB	VC	LS	SE	SI	FC	SH
Altai Territory, Altai district, Altayskoye village, 51.88°N, 85.28°E, 460 m, pine-birch forests, 20.08.2003 (OL, ChS), # 13.07.2011 (NT)	–	2	5	3	3	7	6	2	1	1	3
Altai Republic, Shebalinsky district, Kamlak village, 51.63°N, 85.73°E, 390 m, birch-pine forests, 18.08.2003 (OL, ChS), # 15.07.2011 (NT)	–	2	5	3	3	7	15	3	1	1	3
Altai Republic, Shebalinsky district, Cherga village, 51.58°N, 85.59°E, 500 m, aspen-birch forests, 11.08.2003 (OL, ChS)	–	2	5	3	3	7	6	2	2	1	3
# Altai Republic, Shebalinsky district, Cherga village, 51.58°N, 85.59°E, 500 m, edges of aspen-birch forests, 20.07.2011 (NT)	+	2	5	3	3	7	6	2	2	1	2
Altai Republic, Shebalinsky district, Ulus-Cherga village, 51.55°N, 85.49°E, 600 m, larch-birch forests, 10.08.2003 (OL, ChS), # 16.07.2011 (NT)	–	2	4	3	3	7	6	2	2	1	3
Altai Republic, Shebalinsky district, Cherga village, 51.57°N, 85.57°E, 470 m, large low-mountain villages, 05.08.2003 (OL, ChS), # 19.07.2011 (NT)	–	2	5	4	1	12	5	3	1	2	1
Altai Republic, Shebalinsky district, Verkh-Kukuya village, 51.46°N, 85.29°E, 950 m, steppe meadows and meadow steppes, 17.08.2003 (OL, ChS), # 17.07.2011 (NT)	+	2	4	4	2	2	8	1	3	2	1
Altai Republic, Shebalinsky district, Verkh-Kukuya village, 51.46°N, 85.27°E, 1010 m, very sparse birch-larch forests, 17.08.2003 (OL, ChS), # 17.07.2011 (NT)	–	3	3	4	1	5	8	1	3	2	2
Altai Republic, Shebalinsky district, Verkh-Kukuya village, 51.46°N, 85.25°E, 900 m, swampy birch forests (sogry), 12.08.2003 (OL, ChS)	–	3	3	4	3	8	16	3	2	1	3
Altai Republic, Shebalinsky district, Verkh-Kukuya village, 51.45°N, 85.30°E, 900 m, fields with meadows and larch-birch forests, 13.08.2003 (OL, ChS), # 17.07.2011 (NT)	–	3	3	4	1	13	13	3	1	2	1
Altai Republic, Shebalinsky district, Verkh-Kukuya village, 51.46°N, 85.30°E, 900 m, small villages, 17.08.2003 (OL, ChS), # 17.07.2011 (NT)	–	3	3	4	1	12	8	3	1	2	1
Altai Republic, Shebalinsky district, Verkh-Kukuya village, 51.46°N, 85.35°E, 1100 m, larch-birch forests, 13.08.2003 (OL, ChS), # 18.07.2011 (NT)	–	3	4	4	3	7	16	2	2	1	3
Altai Republic, Shebalinsky district, Verkh-Kukuya village, 51.46°N, 85.31°E, 1100 m, birch-larch forests, 13.08.2003 (OL, ChS), # 18.07.2011 (NT)	–	3	3	4	3	7	16	2	2	1	3
Altai Republic, Shebalinsky district, Mukhor-Cherga village, 51.43°N, 85.32°E, 1500 m, larch park forests, 10.08.2003 (OL, ChS)	–	3	2	4	1	7	8	3	2	2	2
# Altai Republic, Shebalinsky district, Baragash village, 51.35°N, 85.17°E, 870 m, larch park forests, 18.07.2011 (NT)	+	3	2	4	1	7	8	3	2	2	2
Altai Republic, Shebalinsky district, Ilyinka village, 51.51°N, 85.16°E, 1300 m, spruce-dominated forests, 15.08.2003 (OL, ChS)	–	3	3	4	3	6	16	2	2	1	3
# Altai Republic, Shebalinsky district, Ilyinka villagethe vicinity of Mount Gladkikh, 51.45°N, 85.12°E, 1109 m, spruce-dominated forests, 19.07.2011 (NT)	–	3	3	4	3	6	16	2	2	1	3
Altai Republic, Shebalinsky district, Mukhor-Cherga village, 51.33°N, 85.33°E, 1500 m, larch-cedar forests, 09.08.2003 (OL, ChS), # 22.07.2011 (NT)	–	3	2	4	3	6	16	2	2	1	3
Altai Republic, Shebalinsky district, Mukhor-Cherga village, 51.33°N, 85.33°E, 1500 m, clearings in larch-cedar forests, 03.08.2003 (OL, ChS), # 22.07.2011 (NT)	–	3	2	4	3	6	16	2	2	2	2
Altai Republic, Shebalinsky district, Ilyinka village, 51.48°N, 85.16°E, 1308–1570 m, larch-cedar sparse forests with high-grass subalpine meadows, 15.08.2003 (OL, ChS), # 19.07.2011 (NT)	–	3	2	4	4	9	18	3	1	2	2

Table 1. (continuations)
Таблица 1. (продолжение)

Habitats	*Formica uralensis*	Factors									
		AA	HA	MS	AB	VC	LS	SE	SI	FC	SH
Altai Republic, Shebalinsky district, Mukhor-Cherga village, 51.33°N, 85.32°E, 1500-1767 m, larch-cedar sparse forests with low-grass subalpine meadows, 12.08.1981 (OL), # 22.07.2011 (NT)	–	3	2	4	4	9	18	2	1	2	2
Altai Republic, Shebalinsky district, Mukhor-Cherga village, 51.33°N, 85.31°E, 1860 m, rocky-meadow tundra, 08.08.2003 (OL, ChS), # 22.07.2011 (NT)	–	3	2	4	6	11	19	3	1	2	1
Northeastern Altai (Северо-Восточный Алтай)											
Altai Territory, Solton district, Nizhnyaya Neninka village, 52.73°N, 86.39°E, 220 m, foothill villages, 07.06.2002 (ChS), # 16–18.06.2004 (NT)	–	1	6	3	1	12	1	3	1	2	1
Altai Territory, Solton district, Nizhnyaya Neninka village, 52.70°N, 86.34°E, 220 m, fields, 10.06.2002 (ChS), # 17.06.2004 (NT)	–	1	6	3	1	13	3	3	1	2	1
Altai Territory, Solton district, Nizhnyaya Neninka village, 52.73°N, 86.35°E, 220 m, meadows with willows, 06.06.2002 (ChS), # 16.06.2004 (NT)	–	1	6	3	1	5	1	3	1	2	2
Altai Territory, Solton district, Nizhnyaya Neninka village, 52.70°N, 86.34°E, 220 m, meadows with copses, 09.06.2002 (ChS), # 17.06.2004 (NT)	–	1	6	3	1	5	3	3	1	2	2
Altai Territory, Solton district, Nizhnyaya Neninka village, 52.76°N, 86.42°E, 220 m, bushy swamps, 05-06.06.2002 (ChS), # 17.06.2004 (NT)	+	1	6	3	1	1	2	3	1	2	2
Altai Territory, Solton district, Saidyp village, 52.59°N, 86.58°E, 270 m, birch-aspen forests, 13–14.06.2002 (ChS), # 18.06.2004 (NT)	–	1	6	4	3	7	6	2	1	1	3
Altai Territory, Solton district, Saidyp village, 52.55°N, 86.57°E, 300 m, birch-pine forests, 15–16.06.2002 (ChS), # 18.06.2004 (NT)	–	2	6	3	3	7	6	3	1	1	3
#Altai Territory, Solton district, Saidyp village, 52.57°N, 86.57°E, 250 m, foothill villages, 18.06.2004 (NT)	–	1	6	4	1	12	3	3	1	2	1
Altai Republic, Turochak district, Kebezen village, 52.96°N, 87.08°E, 400 m, pine-birch forests, 30.05–17.06. 2002 (ChS), # 20.06.2004 (NT)	–	2	5	5	3	7	6	3	1	1	3
Altai Republic, Turochak district, Kebezen village, 51.92°N, 87.07°E, 450 m, sparse pine-birch forests, 30.06.2002 (ChS), # 19.06.2004 (NT)	–	2	5	5	3	7	6	3	1	2	2
Altai Republic, Turochak district, Verkh-Biysk village, 50.03°N, 87.05°E, 430 m, birch-aspen forests, 02.07.2002 (ChS), # 19.06.2004 (NT)	–	2	5	5	3	7	6	1	2	1	3
Altai Republic, Turochak district, Kebezen village, 51.89°N, 87.10°E, 450 m, pine forests, 24–28.06.2002 (ChS), # 19.06.2004 (NT).	–	2	5	5	3	7	6	3	1	1	3
Altai Republic, Turochak district, Kebezen village, Sarykoksha River floodplain, 51.90°N, 87.03°E, 400 m, floodplain willows, 27.06.2002 (ChS), # 21.06.2004 (NT)	–	2	5	5	3	7	15	3	1	2	2
Altai Republic, Turochak district, Kebezen village, 51.90°N, 87.13°E, 460 m, meadows on fallow lands, 1.07.2002 (ChS)	–	2	5	5	3	13	6	3	1	2	1
Altai Republic, Turochak district, Kebezen village, 51.90°N, 87.13°E, 460 m, pine-fir-birch forests, 26.06.2002 (ChS), # 21.06.2004 (NT)	–	2	5	5	3	7	6	3	1	1	3
Altai Republic, Turochak district, Kebezen village, 51.89°N, 87.15°E, 465 m, afforested swamps, 29.06.2002 (ChS), # 20.06.2004 (NT)	–	2	5	5	3	8	6	3	1	2	2
Altai Republic, Turochak district, Kebezen village, 51.90°N, 87.09°E, 500 m, «dark» aspen-fir taiga, 24–25.06.2002 (ChS), # 21.06.2004 (NT)	–	2	5	5	3	6	6	2	2	1	3
Altai Republic, Turochak district, Kebezen village, 51.91°N, 87.10°E, 400 m, low mountain villages, 21–25.06.2002 (ChS), # 20.06.2004 (NT)	–	2	5	5	3	12	6	3	1	2	1

Table 1. (continuations)
Таблица 1. (продолжение)

Habitats	*Formica uralensis*	Factors									
		AA	HA	MS	AB	VC	LS	SE	SI	FC	SH
Altai Republic, Turochak district, Suuchak tract, lower reaches of the Pyzha River, 51.74°N, 87.14°E, 520 m, birch-aspen forests along burnt areas, 10.09.2002 (ChS), # 22.06.2004 (NT)	–	2	4	5	3	7	6	1	2	2	2
# Altai Republic, Turochak district, Artybash village, 51.80°N, 87.28°E, 430 m, fir-cedar forests, 18–19.06.2003, 26.08.2003, 7–8.08.2007, 17–22.08.2008, 14–20.00.2009, 2–7.07.2010, 24–27.08.2019 (NT)	–	2	5	5	3	6	6	3	2	1	2
# Altai Republic, Turochak district, Iogach village, 51.78°N, 87.24°E, 430 m, Biya river floodplain, mixed grass meadow, 25.06.2003 (NT)	–	2	5	5	3	6	14	3	1	2	1
Altai Republic, Turochak district, Yailu village, 51.78°N, 87.62°E, 600 m, pine-birch forests, 28.08.2002 (ChS), # 10.08.2004 (NT)	–	2	5	5	3	7	6	1	2	1	3
Altai Republic, Turochak district, southern end of Lake Teletskoye, Bele cordon, 51.42°N, 87.80°E, 570 m, larch-birch forests, 1–2.09.2002 (ChS), # 10.08.2004 (NT)	–	2	5	5	3	7	6	1	3	1	2
Altai Republic, Turochak district, middle reaches of the Pyzha river, cordon Obogo, 51.52°N, 87.29°E, 1010 m, birch-aspen forests, 18.08.2002 (ChS), # 20.06.2003 (NT)	–	3	3	5	3	7	16	1	3	1	3
Altai Republic, Turochak district, middle reaches of the Pyzha river, cordon Obogo, 51.52°N, 87.28°E, 900 m, valley birch-spruce forests, 17.08.2002 (ChS), # 20–27.06.2003 (NT)	–	3	3	5	3	6	15	3	1	1	3
Altai Republic, Turochak district, the Kochesh River (right tributary of the Pyzha River), 51.51°N, 87.32°E, 1070 m, fir-cedar taiga, 23.08.2002 (ChS), # 20–23.06.2003 (NT)	–	3	3	5	3	6	16	2	1	1	3
Altai Republic, Turochak district, the Kochesh River (right tributary of the Pyzha River), 51.52°N, 87.31°E, 1050 m, overgrown clearcuts in the fir-cedar taiga, 21.08.2002 (ChS), # 20.06.2003 (NT)	–	3	3	5	3	6	16	2	1	2	2
Altai Republic, Turochak district, , the Kochesh River (right tributary of the Pyzha River), 51.53°N, 87.40°E, 1200 m, spruce-fir-cedar taiga, 15.08.2002 (ChS), # 26.06.2003 (NT)	–	3	3	5	3	6	16	2	1	1	3
Altai Republic, Turochak district, northern macro slope of Mount Archa, 51.52°N, 87.44°E, 1400–1600 m, cedar taiga, 10.08.2002 (ChS), # 21.06.2003 (NT)	–	3	3	5	3	6	16	2	2	1	3
Altai Republic, Turochak district, Mount Archa, 51.53°N, 87.43°E, 1820 m, sparse forests with meadows and dwarf trees, 11.08.2002 (ChS), # 25.06.2003 (NT).	–	3	2	5	4	9	17	3	1	2	2
Altai Republic, Turochak district, Mount Evrechala, 51.46°N, 87.43°E, 2010 m, sparse forests with meadows and dwarf trees on rocks, 12.08.2002 (ChS), # 22.06.2003 (NT)	–	4	2	5	4	9	17	2	2	2	2
Altai Republic, Turochak district, Mount Evrechala, 51.46°N, 87.43°E, 2020 m, rocky tundra, 12.08.2002 (ChS), # 22.06.2003 (NT)	–	4	2	5	6	11	19	2	2	2	1
Altai Republic, Turochak district, Mount Archa, 51.53°N, 87.44°E, 1880 m, tundra with dwarf trees, 9.08.2002 (ChS), # 8.08.2004 (NT)	–	3	2	5	6	11	19	3	1	2	1
Central Altai (Центральный Алтай)											
Altai Republic, Ongudaysky district, village Bolshoy Yaloman, 50.36°N, 86.23°E, 2200 m, rocky scree and cliffs, 1.07.2008 (ChS)	–	4	1	5	6	11	23	1	3	2	1
Altai Republic, Ust-Koksinsky district, spurs of the Kholzun ridge, 50.22°N, 84.92°E, 2100 m, rocky tundra, 28.07.2006 (ChS)	–	4	1	5	6	11	23	2	3	2	1
Altai Republic, Ongudaysky district, village Bolshoy Yaloman, 50.37°N, 86.31°E, 2050 m, tundra stony dryad-forb with dwarf birch, 29.06.2008 (ChS)	–	4	1	5	6	11	23	2	3	2	1

Table 1. (continuations)
Таблица 1. (продолжение)

Habitats	*Formica uralensis*	Factors									
		AA	HA	MS	AB	VC	LS	SE	SI	FC	SH
Altai Republic, Ust-Koksinsky district, spurs of the Kholzun ridge, 50.24°N, 84.97°E, 2000 m, meadow tundra, 2.08.2007 (ChS)	–	3	2	4	6	11	19	3	2	2	1
Altai Republic, Ust-Koksinsky district, Katunsky ridge, southern macroslope, 49.62°N, 85.85°E, 2250 m, meadow tundra with rocky screes and remnants, 19.08.2008 (ChS)	–	4	2	5	6	11	23	3	1	2	1
Altai Republic, Ust-Koksinsky district, Katunsky ridge, southern macroslope, 49.63°N, 85.85°E, 2250 m, moss-lichen tundra, 19.08.2008 (ChS)	–	4	1	5	6	11	23	2	1	2	1
Altai Republic, Ust-Koksinsky district, Katunsky ridge, southern macroslope, 49.63°N, 85.85°E, 2250 m, tundra with dwarf trees and rocky screes, 19.08.2008 (ChS)	–	4	1	5	6	11	23	2	1	2	1
Altai Republic, Ust-Koksinsky district, Katun Ridge, Multinskiye Lakes, 49.98°N, 85.85°E, 2250 m, dwarf-herbaceous tundra, 29.08.2008 (ChS)	–	4	1	5	6	11	23	1	3	2	1
Altai Republic, Ongudaysky district, village Bolshoy Yaloman, 50.36°N, 86.32°E, 2050 m, tundra with mixed grasses and dwarf trees, 30.06.2008 (ChS)	–	4	1	5	6	11	23	3	1	2	1
Altai Republic, Ongudaysky district, village Bolshoy Yaloman, 50.38°N, 86.34°E, 2000 m, waterlogged tundra with shrubs, 30.06.2008 (ChS)	–	3	1	5	6	11	19	3	2	2	1
Altai Republic, Ust-Koksinsky district, spurs of the Kholzun ridge, 50.25°N, 84.97°E, 1900 m, subalpine meadows, 1.08.2007 (ChS)	–	3	1	4	4	10	18	2	2	2	1
Altai Republic, Ust-Koksinsky district, spurs of the Kholzun ridge, 50.24°N, 84.95°E, 1900 m, cedar-larch sparse forests, 5–7.08.2007 (ChS)	–	3	2	4	4	9	17	1	2	2	2
Altai Republic, Ust-Koksinsky district, spurs of the Kholzun ridge, 50.25°N, 84.98°E, 1900 m, cedar-larch sparse forests with meadows and dwarf trees, 6–7.08.2007 (ChS)	–	3	2	4	4	9	17	3	1	2	2
Altai Republic, Ust-Koksinsky district, spurs of the Kholzun ridge, 50.24°N, 84.95°E, 1800 m, mid-mountain bogs, 4.08.2007 (ChS)	–	3	2	4	4	8	17	3	1	2	1
Altai Republic, Ongudaysky district, village Bolshoy Yaloman, 50.37°N, 86.27°E, 2060 m, cedar sparse forests on rocky southern slopes, 1.08.2008 (ChS)	–	4	2	4	4	9	20	1	2	2	2
Altai Republic, Ongudaysky district, village Bolshoy Yaloman, 50.36°N, 86.28°E, 2100 m, larch-cedar with dwarf trees sparse forests along scree slopes, 29–30.08.2008 (ChS)	–	4	2	4	4	9	20	1	2	2	2
Altai Republic, Ust-Koksinsky district, Katun Ridge, Multinskiye Lakes, 49.98°N, 85.85°E, 1800-2000 m, steeply sloping tall grass cedar-larch sparse forests, 26.08.2008 (ChS)	–	3	4	4	4	9	17	1	3	2	2
Altai Republic, Ongudaysky district, village Bolshoy Yaloman, 50.38°N, 86.33°E, 1950 m, larch-cedar sparse forests with low grass meadows, 27.06.2008 (ChS)	–	3	2	4	4	9	17	3	1	2	2
Altai Republic, Ust-Koksinsky district, Katun Ridge, Multinskiye Lakes, 49.98°N, 85.84°E, 1750 m, spruce-larch-cedar tall grass sparse forests, 28.08.2008 (ChS)	–	3	3	4	4	9	17	1	2	2	2
Altai Republic, Ust-Koksinsky district, Katun Ridge, Multinskiye Lakes, 49.96°N, 85.85°E, 1700 m, overgrown burnt areas in spruce-cedar sparse forests, 28.08.2008 (ChS)	–	3	3	4	4	6	20	2	1	2	2
Altai Republic, Ongudaysky district, village Bolshoy Yaloman, 50.37°N, 86.28°E, 1960 m, burnt areas in larch-cedar sparse forests, 2.07.2008 (ChS)	–	3	2	4	4	9	17	2	2	2	2
Altai Republic, Ust-Koksinsky district, Katunsky ridge, southern macroslope, 49.62°N, 85.86°E, 2200 m, tall grass alpine meadows, 20–21.08.2008 (ChS)	–	4	2	4	6	10	21	1	3	2	1

Table 1. (continuations)
Таблица 1. (продолжение)

Habitats	*Formica uralensis*	Factors									
		AA	HA	MS	AB	VC	LS	SE	SI	FC	SH
Altai Republic, Ust-Koksinsky district, Katunsky ridge, southern macroslope, 49.61°N, 85.86°E, 1900 m, subalpine meadows, 17–21.08.2008 (ChS)	+	3	2	4	4	10	18	1	3	2	1
Altai Republic, Ust-Koksinsky district, Katunsky ridge, southern macroslope, 49.60°N, 85.85°E, 1500 m, thickets of shrubs with tall grass meadows, 15–21.08.2008 (ChS)	–	3	2	4	3	7	15	1	2	2	2
Altai Republic, Ust-Koksinsky district, Katunsky ridge, southern macroslope, 49.60°N, 85.86°E, 1450 m, high grass mountain meadows with shrubs, 16–21.08.2008 (ChS)	–	3	2	4	3	7	14	1	1	2	1
Altai Republic, Ust-Koksinsky district, Katun Ridge, Multinskiye Lakes, 49.98°N, 85.83°E, 1650 m, waterlogged spruce-cedar sparse forests, 27.08.2008 (ChS)	–	3	3	4	4	9	17	3	1	2	2
Altai Republic, Ust-Koksinsky district, spurs of the Kholzun ridge, 50.23°N, 84.94°E, 1870 m, cedar forests, 03.08.2007 (ChS)	–	3	3	4	3	6	16	2	2	1	3
Altai Republic, Ongudaysky district, village Bolshoy Yaloman, 50.39°N, 86.32°E, 1850 m, cedar forests, 28.06.2008 (ChS)	–	3	3	4	3	6	16	2	2	1	3
Altai Republic, Ust-Koksinsky district, Amur village, 50.32°N, 85.00°E, 1650 m, cedar-spruce-larch forests, 23.08.2006 (ChS)	–	3	3	4	3	6	16	2	2	1	3
Altai Republic, Ust-Koksinsky district, Amur village, 50.33°N, 85.00°E, 1550 m, sparse larch high-grass forests, 16.08.2006 (ChS)	–	3	3	4	3	7	16	1	2	2	2
Altai Republic, Ust-Koksinsky district, Amur village, 50.35°N, 85.00°E, 1400 m, birch-larch-cedar-spruce green-moss forests, 4.08.2006 (ChS)	–	3	3	4	3	6	16	2	2	1	3
Altai Republic, Ust-Koksinsky district, Amur village, 50.39°N, 85.12°E, 1100 m, edges of larch-birch-spruce moss-grass forests, 20.07.2007 (ChS)	+	3	4	3	3	6	16	2	2	1	2
Altai Republic, Ust-Koksinsky district, Amur village, 50.40°N, 85.11°E, 1100 m, birch-spruce-larch forests on the northern slopes of the mountain remnants, 31.07.2008 (ChS)	+	3	4	3	3	7	9	2	2	1	2
Altai Republic, Ust-Koksinsky district, Ust-Koksa village, 50.26°N, 85.59°E, 1010 m, larch-birch forests on slopes, 22–24.08.2007 (ChS)	–	3	4	3	3	7	16	1	2	1	3
Altai Republic, Ongudaysky district, Kupchegen village, Chike-Taman Pass, 50.64°N, 86.32°E, 1200 m, larch-birch forests, 22.07.2008 (ChS)	–	3	3	3	3	7	16	1	2	1	3
Altai Republic, Ongudaysky district, village Bolshoy Yaloman, 50.45°N, 86.38°E, 1000 m, larch-pine-cedar-spruce riverside forests, 26.06.2008 (ChS)	–	3	4	3	3	6	16	3	1	1	3
Altai Republic, Chemalsky district, village Edigan, 51.11°N, 86.26°E, 1050 m, larch-birch forests, 7.1988 (OL)	+	3	4	3	3	7	16	1	1	1	3
# Altai Republic, Chemalsky district, Edigan village, 51.14°N, 86.34°E, 1010 m, fir-birch forests, 07.1988 (OL)	+	3	4	3	3	7	16	2	2	1	3
Altai Republic, Ust-Koksinsky district, village Yustik, 50.34°N, 85.29°E, 1150 m, burnt areas in larch-birch-spruce forests, 16.07.2007 (ChS)	–	3	4	3	3	6	16	2	2	2	1
Altai Republic, Ongudaysky district, village Bolshoy Yaloman, 50.45°N, 86.38°E, 1100 m, overgrown burnt areas in spruce-cedar-larch forests, 30.06–2.07.2008 (ChS)	–	3	3	3	3	7	16	2	2	2	2
Altai Republic, Ust-Koksinsky district, Amur village, 50.33°N, 85.00°E, 1280 m, tall grass meadows, 16.08.2006 (ChS)	–	3	3	4	3	7	16	3	1	2	1
Altai Republic, Ust-Koksinsky district, Amur village, 50.38°N, 85.10°E, 1080 m, herbaceous meadows on clearings used for grazing, 22.07.2007 (ChS)	+	3	4	3	1	5	9	3	1	2	1

Table 1. (continuations)
Таблица 1. (продолжение)

Habitats	*Formica uralensis*	Factors									
		AA	HA	MS	AB	VC	LS	SE	SI	FC	SH
Altai Republic, Ust-Koksinsky district, Amur village, 50.39°N, 85.09°E, 1055 m, streamside willow forests, 13–21.07.2007 (ChS)	–	3	4	3	3	7	9	3	1	2	2
Altai Republic, Ust-Koksinsky district, Katun Ridge, Multinskiye Lakes, 49.93°N, 85.85°E, 1750 m, mountain-valley spruce-cedar low herbaceous forests, 28.08.2008 (ChS)	–	3	2	4	3	6	15	3	1	1	3
Altai Republic, Ust-Koksinsky district, Katunsky ridge, southern macroslope, 49.60°N, 85.86°E, 1350 m, spruce-birch tall grass forests, 21.08.2008 (ChS)	–	3	3	4	3	7	16	3	1	1	3
Altai Republic, Ust-Koksinsky district, Katunsky ridge, southern macroslope, 49.60°N, 85.75°E, 1300 m, birch-spruce low grass forests, 21.08.2008 (ChS)	–	3	3	4	3	6	15	3	1	1	3
Altai Republic, Ust-Koksinsky district, Amur village, 50.40°N, 85.09°E, 1050 m, streamside larch-birch-spruce forests, 20.08.2006 (ChS), 11–13.07.2019 (ChS, NT).	+	3	4	3	3	7	9	3	1	2	2
Altai Republic, Ust-Koksinsky district, village Yustik, 50.36°N, 85.24°E, 1070 m, park larch forests with spruce admixture, 20.08.2006 (ChS)	+	3	4	3	3	5	13	3	1	2	2
Altai Republic, Ust-Koksinsky district, Ust-Koksa village, 50.26°N, 85.62°E, 970 m, birch valley forests, 10.08.2007 (ChS)	+	3	4	3	3	7	15	3	1	1	3
Altai Republic, Ongudaysky district, village Bolshoy Yaloman, 50.46°N, 86.38°E, 1850 m, birch and spruce forests with meadows for mowing, 22.06.2008 (ChS)	+	3	4	3	3	5	15	3	1	2	2
Altai Republic, Ongudaysky district, Malyi Yaloman village, 50.45°N, 86.55°E, 830 m, birch forests in floodplain valleys, 5–6.07.2008 (ChS)	–	3	4	3	3	7	15	3	1	1	3
Altai Republic, Chemalsky district, village Yelanda, 51.30°N, 86.04°E, 850 m, riverside ribbon pine forests, 25.06.1989 (OL)	–	3	6	2	3	7	15	3	1	1	3
Altai Republic, Chemalsky district, Chemal village, 51.33°N, 86.02°E, 450 m, riverside pine forests (massifs), 12.07.1989 (OL)	–	2	6	3	3	7	15	3	1	1	3
Altai Republic, Chemalsky district, Edigan village, 51.10°N, 86.20°E, 450 m, floodplain meadows with birch forests and shrubs, 07.1988 (OL)	+	2	5	3	1	5	13	3	1	2	1
Altai Republic, Ust-Koksinsky district, Amur village, 50.32°N, 85.00°E, 1450 m, sparse larch forests with tall grass meadows and areas of stony steppes, 18.08.2006 (ChS)	–	3	3	3	1	5	8	1	2	2	2
Altai Republic, Ust-Koksinsky district, Ust-Koksa village, 50.28°N, 85.60°E, 1010 m, larch sparse forests with hawthorn thickets, 12.08.2007 (ChS)	–	3	4	3	1	5	8	1	1	2	2
Altai Republic, Chemalsky district, Edigan village, 51.10°N, 86.27°E, 1100 m, park larch-high herbaceous forests on steppe slopes, 29.07.1988 (OL)	–	3	4	3	1	7	16	1	2	1	2
Altai Republic, Ust-Koksinsky district, village Yustik, 50.36°N, 85.25°E, 1080 m, meadows used for for mowing on old clearings, 17.07.2007 (ChS)	+	3	4	3	1	5	13	3	1	2	1
Altai Republic, Ust-Koksinsky district, village Yustik, 50.34°N, 85.27°E, 1150 m, shrub steppes on slopes, 18.07.2007 (ChS)	–	3	4	3	1	5	8	1	2	2	1
Altai Republic, Ust-Koksinsky district, Ust-Koksa village, 50.28°N, 85.61°E, 1100 m, stony steppes with sparse larch forests, 11.08.2007 (ChS)	–	3	4	3	1	5	8	1	2	2	1
Altai Republic, Chemalsky district, Kuyus village, 51.03°N, 86.24°E, 1100 m, stony steppes on slopes with rocky outcrops, 7.1988 (OL)	+	3	4	2	2	3	7	1	3	2	1
Altai Republic, Ongudaysky district, village Bolshoy Yaloman, 50.46°N, 86.37°E, 1090 m, sparse spruce-cedar-larch forests, 27.06.2008 (ChS)	+	3	4	3	1	5	8	1	3	2	2

Table 1. (continuations)
Таблица 1. (продолжение)

Habitats	*Formica uralensis*	Factors									
		AA	HA	MS	AB	VC	LS	SE	SI	FC	SH
# Altai Republic, Ongudaysky district, village Bolshoy Yaloman, 50.45°N, 86.37°E, 1100 m, spruce-cedar-larch forests on steppe slopes, 30.06.2008 (ChS)	+	3	4	3	1	5	8	3	3	2	2
Altai Republic, Ongudaysky district, village Bolshoy Yaloman, 50.51°N, 86.54°E, 1100 m, shrubs on slopes with sparse larch forests, 20.07.2008 (ChS)	–	3	4	3	1	6	16	1	2	2	2
Altai Republic, Chemalsky district, Kuyus village, 51.02°N, 86.25°E, 1020 m, shrubs on forested slopes, 30.07.1988 (OL)	+	3	4	3	1	5	8	1	2	2	1
# Altai Republic, Ust-Koksinsky district, Ust-Koksa village, 50.27°N, 85.70°E, 900 m, hayfields and fallow lands, 24.08.2007 (ChS)	+	3	4	3	1	13	9	3	1	2	1
Altai Republic, Ust-Koksinsky district, Ust-Koksa village, 50.27°N, 85.63°E, 1005 m, large villages of intermontane basins, 24.08.2007 (ChS)	–	3	4	3	1	12	9	3	1	2	1
Altai Republic, Ongudaysky district, village Bolshoy Yaloman, 50.51°N, 86.54°E, 1070 m, mixed grass-wormwood steppes, 17.07.2008 (ChS)	+	3	4	2	2	3	7	2	1	2	1
Altai Republic, Ongudaysky district, village Bolshoy Yaloman, 50.54°N, 86.55°E, 1070 m, depleted herbaceous stony steppes, 21.07.2008 (ChS)	–	3	4	2	1	3	7	1	2	2	1
Altai Republic, Ongudaysky district, Kupchegen village, 50.64°N, 86.35°E, 1100 m, shrub steppes on slopes, 23.07.2008 (ChS)	–	3	4	3	2	3	8	1	2	2	1
Altai Republic, Ongudaysky district, Kupchegen village, 50.64°N, 86.33°E, 1040 m, meadow steppes, 22–23.07.2008 (ChS)	+	3	4	3	2	3	8	1	1	2	1
Altai Republic, Ust-Koksinsky district, Amur village, 50.40°N, 85.11°E, 1065 m, medium-sized settlements of intermountain basins, 15.07.2006 (ChS)	–	3	4	3	2	12	9	3	1	2	1
Altai Republic, Ust-Koksinsky district, Amur village, 50.40°N, 85.11°E, 1075 m, degraded moderately dry steppes, 19.07.2006 (ChS)	+	3	4	3	2	3	10	1	2	2	1
Altai Republic, Ust-Koksinsky district, Abay village, 50.42°N, 85.08°E, 1075 m, bushy lowland swamp, 24.07.2007 (ChS)	–	3	4	3	1	8	9	3	1	2	2
Altai Republic, Ust-Koksinsky district, Amur village, 50.41°N, 85.10°E, 1000 m, valley thickets of shrubs, 25.07.2007 (ChS)	–	3	4	3	1	5	9	3	1	2	1
Altai Republic, Ust-Koksinsky district, Amur village, 50.42°N, 85.08°E, 1070 m, meadows used for mowing on the site of swamps, 25–26.07.2008 (ChS)	+	3	4	3	1	5	9	3	1	2	1
Altai Republic, Ust-Koksinsky district, Amur village, 50.39°N, 85.18°E, 1070 m, floodplain meadows with willows used for mowing, 21.08.2007 (ChS)	+	3	4	3	1	5	13	3	1	2	1
Altai Republic, Ongudaysky district, village Bolshoy Yaloman, 50.47°N, 86.38°E, 1040 m, perennial fallows, 21–24.06.2008 (ChS)	+	3	4	3	2	13	7	3	1	2	1
Altai Republic, Ongudaysky district, Inya village, 50.50°N, 86.62°E, 750 m, forb-grass fallows, 18.07.2008 (ChS)	–	3	4	2	2	13	12	3	1	2	1
Altai Republic, Ongudaysky district, Inya village, 50.50°N, 86.62°E, 780 m, large-boulder grass-grass impoverished steppes, 19.07.2008 (ChS)	–	3	4	2	2	3	12	3	1	2	1
Altai Republic, Ongudaysky district, Malyi Yaloman village, 50.52°N, 86.54°E, 770 m, deserted steppes on the slopes of river terraces, 18.07.2008 (ChS)	–	3	4	2	2	4	12	1	2	2	1
Altai Republic, Ongudaysky district, Malyi Yaloman village, 50.50°N, 86.61°E, 850 m, fine-scree lichen-grass-wormwood steppes, 20.07.2008 (ChS)	+	3	4	2	2	3	12	3	1	2	1
Altai Republic, Chemalsky district, Edigan village, 51.11°N, 86.15°E, 620 m, forb-wormwood stony steppes, 30.07.1988 (OL)	+	2	4	2	2	3	12	3	1	2	1
Altai Republic, Chemalsky district, Kuyus village, 51.02°N, 86.23°E, 580 m, stony steppes with rocky outcrops, 07.1988 (OL)	–	2	4	2	2	3	7	1	3	2	1

Table 1. (continuations)
Таблица 1. (продолжение)

Habitats	*Formica uralensis*	Factors									
		AA	HA	MS	AB	VC	LS	SE	SI	FC	SH
Altai Republic, Chemalsky district, Yelanda village, 51.24°N, 86.07°E, 500 m, herbaceous-sedge steppes, 07.1989 (OL)	–	2	4	2	2	3	12	3	1	2	1
Altai Republic, Chemalsky district, Yelanda village, 51.20°N, 86.09°E, 650 m, mixed grass-feather grass steppes on alluvial fans,07.1989 (OL)	+	2	4	2	2	3	12	1	2	2	1
Altai Republic, Chemalsky district, Kuyus village, 51.12°N, 86.16°E, 500 m, fields of oats, 22.08.2003 (OL, ChS)	–	2	4	2	2	13	12	3	1	2	1
Altai Republic, Ust-Koksinsky district, Amur village, 50.40°N, 85.06°E, 1055 m, fields of oats, 4–11.08.2006 (ChS)	–	3	4	3	2	13	10	3	1	2	1
Altai Republic, Ongudaysky district, Malyi Yaloman village, 50.50°N, 86.57°E, 700 m, small villages of the steppe valleys, 16–18.07.2008 (ChS)	–	3	4	2	2	12	12	3	1	2	1
Altai Republic, Ongudaysky district, Inya village, 50.46°N, 86.63°E, 770 m, middle-size villages of the steppe valleys, 17–18.07.2008 (ChS)	–	3	4	2	2	12	12	3	1	2	1
Altai Republic, Chemalsky district, Kuyus village, 51.03°N, 86.23°E, 580 m, small villages of the steppe valleys, 22.08.2003 (OL, ChS)	–	2	4	2	2	12	12	3	1	2	1
Altai Republic, Ust-Koksinsky district, village Yustik, 50.38°N, 85.24°E, 1100 m, steppe meadows in the lower part of slopes, 15.07.2007 (ChS)	+	3	4	3	2	3	9	1	1	2	1
Altai Republic, Ongudaysky district, village Bolshoy Yaloman, 50.46°N, 86.37°E, 1100 m, dry stony steppes with cedar-larch forest spots, 21.06.2008 (ChS)	+	3	4	3	1	5	8	1	2	2	2
Altai Republic, Ust-Koksinsky district, Multa village, 6,5 km SE, 50.12°N, 86.02°E, 1026 m, edges of larch-cedar-birch forests, 11–15.07.2013 (NT)	–	3	4	4	3	7	16	3	1	2	2
Altai Republic, Ust-Koksinsky district, Multa village, 50.15°N, 85.97°E, 962 m, herbaceous forest meadows, 11.07.2013 (NT)	–	3	4	4	3	7	16	3	1	2	1
Altai Republic, Ust-Koksinsky district, Multa village, 50.15°N, 85.97°E, 962 m, edges of cedar-spruce-birch forests, 11.07.2013 (NT)	–	3	4	4	3	7	16	3	1	2	2
Altai Republic, Ust-Koksinsky district, Multa village, 13km S, 50.07°N, 85.95°E, 2272 m, highland tundra, 13.07.2013 (NT)	–	4	2	5	6	11	23	3	1	2	1
Altai Republic, Ust-Koksinsky district, Multa village, 50.07°N, 85.93°E, 2029 m, sparse fir-cedar-birch forests, 13.07.2013 (NT)	–	4	2	5	3	7	16	3	1	2	2
Altai Republic, Ust-Koksinsky district, estuary of the Kaitanak River, 50.12°N, 85.47°E, 1028 m, valley cedar-fir-birch forests, 13–17.07.2015 (NT)	–	3	4	4	3	7	15	3	1	1	3
Altai Republic, Ust-Koksinsky district, Kaitanak Pass, 50.15°N, 85.35°E, 1635 m, subalpine-meadow sparse forests, 15.07.2015 (NT)	–	3	2	5	4	9	18	3	2	2	2
Altai Republic, Ust-Koksinsky district, Krasnaya Mountain, 50.07°N, 85.22°E, 1930 m, larch-spruce-cedar forests, 15.07.2019 (NT)	–	3	2	5	3	6	16	2	2	1	3
Altai Republic, Ust-Koksinsky district, Krasnaya Mountain, 50.07°N, 85.22°E, 2023 m, high-mountain subalpine-meadow sparse forests, 16.07.2015 (NT)	–	4	2	5	4	9	20	2	1	2	2
Altai Republic, Ust-Koksinsky district, Krasnaya Mountain, 50.07°N, 85.22°E, 2130 m, subalpine meadows, 15.07.2019 (NT)	–	4	2	5	4	10	21	2	1	2	1
Altai Republic, Ust-Koksinsky district, Krasnaya Mountain, 50.09°N, 85.22°E, 1864 m, middle subalpine-meadow sparse forests, 17.07.2019 (NT)	–	3	2	5	4	9	17	2	1	2	2
Southeastern Altai (Юго-Восточный Алтай)											
# Altai Republic, Kosh-Agach district, Kurai village, 2300 m, feather grass-forb rocky mountain slope steppes [Zhigulskaya, 2011]	+	4	2	3	2	3	22	1	3	2	1

Table 1. (continuations)
Таблица 1. (продолжение)

Habitats	*Formica uralensis*	Factors									
		AA	HA	MS	AB	VC	LS	SE	SI	FC	SH
Altai Republic, Kosh-Agach district, Kurai village, 2200 m, grass-forb rocky mountain slope steppes [Zhigulskaya, 2011]	–	4	2	3	2	3	22	1	3	2	1
Altai Republic, Kosh-Agach district, Kurai village, 1900 m, feather grass-forb-sedge rocky mountain slope steppes [Zhigulskaya, 2011]	–	3	2	2	2	3	7	1	3	2	1
# Altai Republic, Kosh-Agach district, Kurai village, 1700 m, feather grass-wormwood-cinquefoil intermountain-basin steppes [Zhigulskaya, 2011]	+	3	3	2	2	3	10	3	1	2	1
Altai Republic, Kosh-Agach district, Kurai village, 1600 m, fine-turf fescue-grass intermountain-basin steppes [Zhigulskaya, 2011]	–	3	3	2	2	3	10	3	1	2	1
# Altai Republic, Kosh-Agach district, Kurai village, 1600 m, small-turf fescue-grass intermountain-basin steppes in hollows [Zhigulskaya, 2011]	+	3	3	2	2	3	10	3	1	2	1
Altai Republic, Kosh-Agach district, Kurai village, 1500 m, fine-turf wormwood-sedge-grass intermountain-basin steppes [Zhigulskaya, 2011]	–	3	3	2	2	3	10	3	1	2	1
Altai Republic, Kosh-Agach district, Kurai village, 3100 m, mountain gravelly tundra [Zhigulskaya, 2011]	–	4	1	4	6	11	23	2	1	2	1
Altai Republic, Kosh-Agach district, Kurai village, 2850 m, mountain moss-lichen tundra [Zhigulskaya, 2011]	–	4	1	4	6	11	23	2	1	2	1
Altai Republic, Kosh-Agach district, Kurai village, 2800 m, mountain meadow kobresia-dryad tundra [Zhigulskaya, 2011]	–	4	1	4	6	11	23	2	1	2	1
Altai Republic, Kosh-Agach district, Kurai village, 2850 m, fragments of alpine steppes within the meadow tundra [Zhigulskaya, 2011]	–	4	1	4	2	3	22	1	2	2	1
Altai Republic, Kosh-Agach district, village Kokorya, 2800 m, cold alpine steppes [Zhigulskaya, 2011]	–	4	1	4	2	3	22	1	1	2	1
Altai Republic, Kosh-Agach district, village Kokorya, 2700 m, cold alpine steppes [Zhigulskaya, 2011]	–	4	1	4	2	3	22	1	2	2	1
Altai Republic, Kosh-Agach district, village Kokorya, 2600 m, cold alpine steppes [Zhigulskaya, 2011]	–	4	1	4	2	3	22	1	2	2	1
Altai Republic, Kosh-Agach district, Kurai village, 2800 m, subalpine meadow grass-forb steppes [Zhigulskaya, 2011]	–	4	1	4	2	3	21	2	2	2	1
# Altai Republic, Kosh-Agach district, Kurai village, 2700 m, subalpine meadow grass-forb steppes [Zhigulskaya, 2011]	+	4	1	4	2	3	21	2	2	2	1
Altai Republic, Kosh-Agach district, Kurai village, 2600 m, subalpine meadow grass-forb steppes [Zhigulskaya, 2011]	–	4	1	4	2	3	21	1	1	2	1
Altai Republic, Kosh-Agach district, Kurai village, 2600 m, subalpine grass-forb meadows [Zhigulskaya, 2011]	–	4	1	4	4	10	21	1	1	2	1
Altai Republic, Kosh-Agach district, Kurai village, 2500 m, subalpine grass-forb meadows [Zhigulskaya, 2011]	–	4	1	4	4	10	21	1	1	2	1
Altai Republic, Kosh-Agach district, Kurai village, 2400 m, subalpine grass-forb meadows [Zhigulskaya, 2011]	–	4	1	4	4	10	21	1	1	2	1
# Altai Republic, Kosh-Agach district, left bank of the Chuya River, northern macro-slope of the North Chuya Ridge, 1900 m, park larch forests [Zhigulskaya, 2011]	+	3	3	2	1	5	9	2	2	2	2
Altai Republic, Kosh-Agach district, left bank of the Chuya River, northern macro-slope of the North Chuya Ridge, 1800 m, meadow grass-forb-sedge steppes [Zhigulskaya, 2011]	+	3	3	2	2	3	10	2	2	2	1
# Altai Republic, Kosh-Agach district, left bank of the Chuya River, northern macro-slope of the North Chuya Ridge, 1600 m, feather grass and mixed grass steppes on slopes [Zhigulskaya, 2011]	+	3	3	2	2	3	10	2	2	2	1

Table 1. (continuations)
Таблица 1. (продолжение)

Habitats	*Formica uralensis*	Factors									
		AA	HA	MS	AB	VC	LS	SE	SI	FC	SH
Altai Republic, Kosh-Agach district, left bank of the Chuya River, northern macro-slope of the North Chuya Ridge, 1500 m, fescue-forb steppes [Zhigulskaya, 2011]	+	3	3	2	2	3	10	2	2	2	1
# Altai Republic, Kosh-Agach district, left bank of the Chuya River, northern macro-slope of the North Chuya Ridge, 1500 m, fescue-forb steppes of the northern slopes [Zhigulskaya, 2011]	+	3	3	2	2	3	10	2	2	2	1
Altai Republic, Kosh-Agach district, Kosh-Agach village, 2100 m, Chui Basin, steppe meadows on the western slopes [Zhigulskaya, 2009]	–	4	2	1	2	3	22	3	2	2	1
Altai Republic, Kosh-Agach district, Kosh-Agach village, 2100 m, Chui Basin, desert steppes on the southern slopes [Zhigulskaya, 2009]	–	4	2	1	2	4	11	1	2	2	1
Altai Republic, Kosh-Agach district, Kosh-Agach village, 1800-1900 m, Chui Basin, desertified feather grass intermountain-basin steppes [Zhigulskaya, 2009]	–	3	3	1	2	4	11	3	1	2	1
Altai Republic, Kosh-Agach district, Kosh-Agach village, 1700-1750 m, Chui Basin, desertified sedge intermountain-basin steppes [Zhigulskaya, 2009]	–	3	3	1	2	4	11	3	1	2	1
Altai Republic, Kosh-Agach district, Kosh-Agach village, 1700 m, Chui Basin, dry achnatherum inter-mountain-basin steppes [Zhigulskaya, 2009]	–	3	3	1	2	4	11	3	1	2	1
Altai Republic, Kosh-Agach district, Kosh-Agach village, 1700 m, Chui Basin, humid achnatherum intermountain-basin steppes [Zhigulskaya, 2009]	–	3	3	1	2	4	11	3	1	2	1
Altai Republic, Kosh-Agach district, Kosh-Agach village, 1700 m, Chui Basin, couch grass intermountain-basin steppes [Zhigulskaya, 2009]	–	3	3	1	2	4	11	3	1	2	1
Altai Republic, Kosh-Agach district, Kosh-Agach village, 1650 m, Chui Basin, salt marshes with Saltwort [Zhigulskaya, 2009]	–	3	3	1	2	4	11	3	1	2	1
Altai Republic, Kosh-Agach district, Kosh-Agach village, 1650 m, Chui Basin, floodplain salt marsh iris-forb meadows [Zhigulskaya, 2009]	–	3	3	1	2	4	11	3	1	2	1
Altai Republic, Kosh-Agach district, Kosh-Agach village, 1650 m, Chui Basin, floodplain salt marsh grassy hilly meadows [Zhigulskaya, 2009]	–	3	3	1	2	4	11	3	1	2	1
Altai Republic, Kosh-Agach district, Kosh-Agach village, 1650 m, Chui Basin, floodplain salt marsh sedge meadows with rare willow [Zhigulskaya, 2009]	–	3	3	1	2	4	11	3	1	2	1
Altai Republic, Kosh-Agach district, the Yustyd River basin, Chui Basin, 2600 m, highland desert fine- turf stony steppes [Zhigulskaya, 2009]	–	4	1	2	2	4	22	1	2	2	1
Altai Republic, Kosh-Agach district, the Yustyd River basin, 2600 m, highland desertified fine-turf slightly gravelly steppes [Zhigulskaya, 2009]	–	4	1	2	2	4	22	3	2	2	1
Altai Republic, Kosh-Agach district, the Yustyd River basin, 2300 m, highland desertified grass-worm-wood scree steppes [Zhigulskaya, 2009]	–	4	1	2	2	4	22	3	2	2	1
Altai Republic, Kosh-Agach district, the Yustyd River basin, 2300 m, high-mountain desertified grass-wormwood steppes without crushed stones [Zhigulskaya, 2009]	–	4	1	2	2	4	22	3	2	2	1
Altai Republic, Kosh-Agach district, the Yustyd River basin, 2200 m, high-mountain desert steppes, steppe floodplain pebbles [Zhigulskaya, 2009]	–	4	1	2	2	4	22	3	1	2	1
Altai Republic, Kosh-Agach district, the Yustyd River basin, 1650 m, mountain slope and valley forests and meadows [Zhigulskaya, 2009]	–	3	3	1	1	5	8	3	1	2	2
Altai Republic, Kosh-Agach district, Ukok plateau, Muzdy-Bulak Lake, 49.28°N, 86.65°E, 2420–2900 m, high mountain steppes, 26.06.2005–2.07.2005 (NT)	–	4	1	3	5	11	22	3	1	2	1

Table 1. (continuations)
Таблица 1. (продолжение)

Habitats	*Formica uralensis*	Factors									
		AA	HA	MS	AB	VC	LS	SE	SI	FC	SH
Altai Republic, Kosh-Agach district, Ukok plateau, valley of the Zhumaly river, 49.41°N, 88.04°E, 2400 m, subalpine meadows with dwarf trees, 4.07.2005, 23.07.2006 (NT)	–	4	1	3	4	10	21	3	1	2	1
Altai Republic, Kosh-Agach district, floodplain of the Chuya river at the confluence of the Kuiktanar river, 50.15°N, 88.28°E, 1765 m, floodplain valley meadows, 6.07.2005 (NT)	–	3	3	2	2	3	14	3	1	2	1
Altai Republic, Kosh-Agach district, South Chuisky Ridge, southern macroslope, lower reaches of the Tara River, 49.65°N, 88.22°E, 2180 m, cedar-larch forests, 30.06.2006 (NT)	–	4	2	2	3	6	16	1	1	1	3
Altai Republic, Kosh-Agach district, Dzhazator village, 17 km SE, 49.65°N, 87.65°E, 1790 m, cedar-larch forests, 5.07.2006 (NT)	–	3	2	2	3	6	16	2	1	1	3
# Altai Republic, Kosh-Agach district, Dzhazator River Valley, 49°39'44.13"N 87°39'13.94"E, 1646 m, edges of cedar-larch forests, 5.07.2006 (NT)	+	3	2	2	3	6	16	3	2	2	2
Altai Republic, Kosh-Agach district, Ukok plateau, 8 km NW from Mount Maitobe, 49.57°N, 87.72°E, 2420 m, dwarf tree tundra with subalpine meadows, 6–11.07.2006 [HT]	–	4	1	3	4	10	22	3	1	2	1
Altai Republic, Kosh-Agach district, Ukok plateau, Ak-Kol river floodplain, 2 km before the confluence with the Ak-Alakha river, 49.42°N, 87.62°E, 2162 m, cryophytic steppe meadows of floodplain valleys, 12.07.2006 (NT)	–	4	1	3	5	11	22	3	1	2	1
Altai Republic, Kosh-Agach district, Ukok plateau, floodplain of the Ak-Alakha River at the confluence of the Ak-Kol River, 49.42°N, 87.62°E, 2162 m, cryophytic steppe meadows of floodplain valleys, 12.07.2006 (NT)	–	4	1	3	5	11	22	3	1	2	1
Altai Republic, Kosh-Agach district, Ukok plateau, floodplain of the Kara-Bulak River, 49.42°N, 87.62°E, 2162 m, cryophytic steppe meadows of floodplain valleys, 14.07.2006 (NT)	–	4	1	3	5	11	22	3	1	2	1
Altai Republic, Kosh-Agach district, Ukok plateau, Kaldzhin-Kul and Kaldzhin-Kul-Bass Lakes, 49.32°N, 87.43°E, 2400 m, high mountain dwarf tundra, 18.07.2006 (NT)	–	4	1	3	6	11	23	3	1	2	1
Altai Republic, Kosh-Agach district, Ukok plateau, Kaldzhin-Kul Lake, 4–6 km C3, 49.32°N, 87.43°E, 2900 m, rocky steppes, 17.07.2006 (NT)	–	4	1	3	5	11	22	3	1	2	1
Altai Republic, Kosh-Agach district, confluence of the rivers Dzhazator and Akbul, 49.66°N, 88.02°E, 2075 m, steppe edges of cedar-larch forests, 12.07.2009 (NT)	–	4	2	2	5	6	16	3	1	2	2
Altai Republic, Kosh-Agach district, confluence of the rivers Dzhazator and Chipty-Kol, 49.66°N, 88.02°E, 1988 m steppe edges of cedar-larch forests, 12.07.2009 (NT)	–	3	2	2	5	6	16	3	1	2	2
Altai Republic, Kosh-Agach district, confluence of the rivers Dzhazator and Arzhan, 49.65°N, 87.9°E, 1894 m, meadow edges of cedar-larch forests, 12.07.2009 (NT)	–	3	2	2	3	6	16	2	1	2	2
Altai Republic, Kosh-Agach district, valley of Dzhazator River, 49.63°N, 87.87°E, 1804 m, sparse valley forests, 12.07.2009 (NT)	–	3	2	2	3	5	16	3	1	2	2
Altai Republic, Kosh-Agach district, confluence of the rivers Dzhazator and Ku-Karagay, 49.63°N, 87.8°E, 1762 m, floodplain meadows, 12.07.2009 (NT)	–	3	2	2	2	3	14	3	1	2	1
Altai Republic, Kosh-Agach district, confluence of the rivers Dzhazator and Tangyt, 49.63°N, 87.72°E, 1709 m, floodplain meadows, 12.07.2009 (NT)	–	3	2	3	2	3	14	3	1	2	1

Table 1. (continuations)
Таблица 1. (продолжение)

Habitats	*Formica uralensis*	Factors									
		AA	HA	MS	AB	VC	LS	SE	SI	FC	SH
Altai Republic, Kosh-Agach district, верховья р. Нарын-Гол, оз. Кок-коль, 49.82°N, 87.54°E, 2520 m, low grass alpine and subalpine meadows with dwarf trees, 15–17.07.2009 (NT)	–	4	1	2	4	10	21	3	1	2	1
# Altai Republic, Kosh-Agach district, Kurai village, southern slope of the Kurai ridge, 50.28°N, 87.85°E, 2369 м, rocky steppes on the southern slopes, 17.07.2013 (NT)	+	4	1	2	2	3	22	1	2	2	1
Altai Republic, Kosh-Agach district, Kurai village, southern slope of the Kurai ridge, 50.28°N, 87.85°E, 2111 m, steppes on the slopes, 18.07.2013 (NT)	–	4	3	2	2	3	22	1	2	2	1
Altai Republic, Kosh-Agach district, Kurai village, southern slope of the Kurai ridge, 50.28°N, 87.85°E, 2251 m, wormwood-cereal rocky steppes on the slopes, 18.07.2013 (NT)	–	4	3	2	2	3	22	1	2	2	1
Altai Republic, Kosh-Agach district, Kurai village, 50.25°N, 87.88°E, 1546 m, rocky steppes on the slopes, 20.07.2013 (NT)	–	3	3	2	2	3	7	1	2	2	1
Altai Republic, Kosh-Agach district, northern macroslope of the North-Chuisky ridge, Aktru valley, 50.13°N, 87.8°E, 1718 m, cedar-larch forests, 21.07.2013 (NT)	–	3	2	3	3	7	16	2	1	1	3
Eastern Altai (Восточный Алтай)											
Altai Republic, Ulagansky district, 25 km SE from the Ulagan village, 50.54°N, 88.10°E, 1500 m, larch-cedar forests on the upper river terrace, 10.06.2005 (NT)	–	3	3	3	3	6	16	3	1	1	3
# Altai Republic, Ulagansky district, 50.41°N, 88.39°E, 1700–1900 m, fescue-wormwood steppes with bushes of *Dasiphora fruticosa* on the slopes, 10–14.06.2005 (NT)	+	3	3	3	1	5	8	3	2	2	1
# Altai Republic, Ulagansky district, the confluence of the Yoldu and Bashakaus rivers, 50.41°N, 88.39°E, 1700–1900 m, larch-cedar forests on the upper river terrace, 10–12.06.2005 (NT)	+	3	3	3	3	6	15	3	2	1	3
Altai Republic, Ulagansky district, upper reaches of the Yoldu river, 50.50°N, 88.57°E, 2020 m, alpine meadows with dwarf birch trees on the lower river terrace, 20.06.2005 (NT)	–	4	2	3	4	10	21	3	1	2	1
Altai Republic, Ulagansky district, upper reaches of the Yoldu river, 50.50°N, 88.57°E, 2000 m, larch-cedar forests, 14–18.06.2005 (NT)	–	3	2	3	3	6	16	2	2	1	3
Altai Republic, Ulagansky district, upper reaches of the Yoldu river, 50.50°N, 88.57°E, 2100 m, alpine meadows with dwarf trees, 20.06.2005 (NT)	–	4	2	3	4	10	20	3	1	2	1
Altai Republic, Ulagansky district, middle reaches of the Yoldu river, 50.47°N, 88.53°E, 1740 m, sparse larch-cedar forests, 7–10.07.2019 (NT)	+	3	3	3	3	6	16	2	1	2	2

Note. * — here and later in the table, the absolute altitude of the terrain is given in metres above sea level. # — the places of the material collection carried out by the authors outside of the main surveys. Absolute altitudes of the terrain (AA): 1 — below 300 m a.s.l., 2 — 300–1000 m a.s.l., 3 — 1001–2000 m a.s.l. (for mountain-valley areas within the mid-mountains: 700–2000 m a.s.l.), 4 — over 2000 m a.s.l.). Altitudinal-zonal vegetation belts (AB): 1 — forest-steppe, 2 — steppe, 3 — forest, 4 — subalpine sparse forest-meadow, 5 — cryophyte-steppe, 6 — alpine-tundra. Degree of forestation (FC): 1 — forests, 2 — other habitats, including open and mosaic forests, as well as subalpine woodlands. Heat availability expressed as the sum of average daily temperatures above +5 °C (HA): 1 — less than 800 °C, 2 — 800–1200 °C, 3 — 1201–1600 °C, 4 — 1601–2000 °C, 5 — 2001–2200 °C, 6 — 2201–2400 °C. Landscape differentiation of the territory (LS): 1 — foothill lowland meadow habitats, 2 — foothill lowland marsh habitats, 3 — foothill upland forest steppe, 4 — low-altitude mountains steppe, 5 — low-altitude mountains forest steppe, 6 — low mountain forest, 7 — mid-mountain steppe, 8 — mid-mountain forest-steppe, 9 — intermountain-basin forest-steppe, 10 — intermountain-basin steppe, 11 — intermountain-basin semi-desert, 12 — mountain-valley steppe, 13 — mountain-valley forest-meadow-steppe, 14 — mountain-valley meadow, 15 — mountain-valley forest, 16 — mid-mountain forest, 17 — mid-mountain subalpine-sparse forest, 18 — mid-mountain alpine-subalpine meadow, 19 — mid-mountain tundra, 20 — highland subalpine-sparse forest, 21 — high mountain alpine-subalpine meadow, 22 — high mountain tundra-cryophyte steppe, 23 — high mountain tundra landscapes. Moisture supply is expressed in terms of average annual precipitation (MS): 1 — less than 200 mm/year, 2 — 200–400, 3 — 401–600, 4 — 601–800, 5 — 801–1000 mm/year. Slope exposure (SE): 1 — southern slope, 2 — northern slope, 3 — other slopes and horizontal surfaces. Shading (SH): 1 — high, 2 — medium, 3 — no shading. Surface inclination (SI): 1 — up to 12°, 2 — 13°–20°, 3 — more than 20°. Vegetation cover (VC): 1 — plain marsh, 2 — meadow steppe, 3 — steppe, 4 — desertified steppe, 5 — forest steppe, 6 — taiga forest; 7 — non-taiga forest, 8 — mountain marsh, 9 — subalpine meadow, 10 — subalpine meadow (alpine and subalpine meadows), 11 — tundra (tundra and cryophyte-steppe habitats), 12 — human settlement (all settlements), 13 — agricultural character of vegetation (fields and fallow lands). For own collections, the collectors of the material are indicated in parentheses: NT — T.A. Novgorodova, OL — L.V. Omelchenko, SA — A.V. Stekol'shchikov, ChS — S.V. Chesnokova.

Примечание. * — Здесь и далее в таблице приведена абсолютная высота местности в метрах над уровнем моря. # — Места сбора материала, проведенного авторами вне учетов. Абсолютные высоты местности (AA): 1 — ниже 300 м над уровнем моря (н.у.м.), 2 — 300–1000 м н.у.м., 3 — 1001–2000 м н.у.м. (для горно-долинных в пределах среднегорий: 700–2000 м н.у.м.), 4 — свыше 2000 м н.у.м.). Высотно-зональные пояса растительности (AB): 1 — лесостепной, 2 — степной, 3 — лесной, 4 — субальпийский редколесно-луговой, 5 — криофитно-степной, 6 — альпийско-тундровый. Степень облесённости (FC): 1 — леса, 2 — остальные местообитания, включая разреженные и мозаичные леса, а также субальпийские редколесья. Теплообеспеченность, выраженная в сумме средних суточных температур выше +5 °C (HA): 1 — менее 800 °C, 2 — 800–1200 °C, 3 — 1201–1600 °C, 4 — 1601–2000 °C, 5 — 2001–2200 °C, 6 — 2201–2400 °C. Ландшафтная дифференциация территории (LS): 1 — предгорные низинные луговые, 2 — предгорные низинные болотные, 3 — предгорные возвышенные лесостепные, 4 — низкогорные степные, 5 — низкогорные лесостепные, 6 — низкогорные лесные, 7 — среднегорные степные, 8 — среднегорные лесостепные, 9 — межгорно-котловинные лесостепные, 10 — межгорно-котловинные степные, 11 — межгорно-котловинные полупустынные, 12 — горно-долинные степные, 13 — горно-долинные лесо-лугово-степные, 14 — горно-долинные луговые, 15 — горно-долинные лесные, 16 — среднегорные лесные, 17 — среднегорные субальпийско-редколесные, 18 — среднегорные альпийско-субальпийские луговые, 19 — среднегорные тундровые, 20 — высокогорные субальпийско-редколесные, 21 — высокогорные альпийско-субальпийские луговые, 22 — высокогорные тундрово-криофитностепные, 23 — высокогорные тундровые ландшафты. Влагообеспеченность, выраженная среднегодовым количеством осадков (MS): 1 — менее 200 мм/год, 2 — 200–400, 3 — 401–600, 4 — 601–800, 5 — 801–1000 мм/год. Экспозиция склонов (SE): 1 — южный склон, 2 — северный склон, 3 — прочие склоны и горизонтальные поверхности. Затенение (SH): 1 — высокое, 2 — среднее, 3 — затенение отсутствует. Угол наклона поверхности (SI): 1 — до 12°, 2 —13°– 20°, 3 — более 20°. Растительный покров (VC): 1 — равнинно-болотный, 2 — лугово-степной, 3 — степной, 4 — опустыненно-степной, 5 — лесостепной, 6 — таёжно-лесной; 7 — нетаёжно-лесной, 8 — горно-болотный, 9 — субальпийско-редколесный, 10 — субальпийско-луговой, 11 — тундровый, 12 — поселковый (рудеральный), 13 — аграрный характер растительности. Для собственных сборов в круглых скобках указаны сборщики материала: NT — Т.А. Новгородова, OL — Л.В. Омельченко, SA — А.В. Стекольщиков, ChS — С.В. Чеснокова.

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