

Ecological Structure of the West Siberian Forest-Steppe Spider Community (Arachnida, Araneae) and Its Comparison with the Ground-Beetle (Coleoptera, Carabidae) Community

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Abstract—An investigation of the spatiotemporal management of the aboveground spider community has been carried out at the continuous habitat gradient profile from the forest outlier center to the meadowland center in the southern part of the forest-steppe zone of Novosibirsk oblast in 2007–2008. We apply two sampling methods which complete each other: pitfall trapping and hand separation of soil samples. Eighty-three species of spiders from 14 families are determined. Spiders are most abundant in the early summer and less abundant in the middle of summer. Representatives of different families are of maximum abundance in different sites: Lycosidae and Gnaphosidae mainly in the forest and Philodromidae in the solonetz meadow. The distribution of diversity and abundance of spiders and ground beetles throughout the habitat gradient are generally similar. This is contradictory to the spatial interactions of these two groups in Arctic and extreme ecosystems. Niche distinguishing between ground beetles and spider species is not only topical. It includes the usage of different strata of vegetation, various seasonal activity, and trophic specialization.

Keywords: predatory soil-dwelling arthropods, spatial distribution, seasonal dynamics, types of geographical ranges, dominant species

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INTRODUCTION

Spiders (Arachnida, Araneae) and ground beetles (Coleoptera, Carabidae) are the main groups of aboveground predatory invertebrates. They control the food webs in the soils of most ecosystems of the temperate zone thanks to their high species diversity and abundance. There are a lot of separate studies of the structure of ground-beetle or spider ecological communities. However, simultaneous studies of the structure of both taxocenes are rare.

Most of these works appear no earlier than the 1990s (Alderweireldt, Desender, 1990; Kromp, Steinberger, 1992) and are devoted to the study of the reactions of spider and ground-beetle communities to various environmental factors by tracking parameters changes of species biodiversity: species richness, abundance, diversity indices, etc.

The impact of environmental factors on these communities were analyzed, for example, by U. Irmeler et al. (Irmeler et al., 2002). They studied the effect of the flows and the distance from the sea using the example of two contrasting geographical locations: on the shores of the North Sea with pronounced flows and on the Baltic Sea without them. With a rising distance from the water, the species richness of both taxocenes increases, but ground

beetles clearly differentiate habitats compared with spiders. A similar study was carried out for the impact of river floods on the ground-beetle and spider communities in Germany (Bonn et al., 2002). I. Mate et al. (Máthé et al., 2003) have shown the invert indices of number and species richness of ground beetles compared with spiders in different bogs habitats in Romania. In the works of V.G. Mordkovich and I.I. Lyubechanskii, contrasting trends of the spatial distribution of ground beetles and spiders in habitats along different gradients of natural and anthropogenic origin in the northern taiga (Lyubechanskii, 2012; Mordkovich et al., 2014) and on the shores of a salt lake in the forest steppe (Mordkovich et al., 2015) were marked.

The indicator role of spiders and ground beetles and the human impact on their communities are also often studied. S.D. Uzenbaev (1987) studied the population of predatory arthropods in undisturbed and dried bogs in Karelia. He noticed opposite changes in the diversity indices of both taxocenes, nonsynchronous seasonal population dynamics, and a different role of ground beetles and spiders in pests control. In Finland (Alaruikka et al., 2002) no effect of urbanization gradient on either taxocenes has been shown. The urbanization gradient existence itself with respect to the soil animals were also discussed in this study.

L. Cole et al. (Cole et al., 2005) noted a strong association of diversity parameters of spider and ground-beetle assemblages to the type of vegetation and the intensity of agriculture in Scotland and the relative indicative value of these two groups. Spider communities seem to them more vulnerable and, therefore, are better indicators, but ground beetles are more convenient, because determining them to species is easier. J. Pearce and colleagues (Pearce et al., 2006) have shown little impact of the cutting-edge effects on forest communities of ground beetles and spiders in Canada.

Quite a lot of works are devoted to the reaction of the community of invertebrates to wildfires. K. Niwa and R. Peck (Niwa, Peck, 2002) examined the impact of forest fires in Oregon (United States) on the assembly of ground beetles and spiders: they found no differences in general diversity indices of both groups studied in the burned areas of different ages. Only a weak correlation between the time that passed from the fire and the abundance was found; however, there were differences for certain species of ground beetles and families of spiders. F. Samu et al. (Samu et al., 2010) found a higher rate of recovery of spider assemblages than ground beetles in the first years after a fire in Hungary. M. Moretti et al. (Moretti et al., 2006) showed an average recovery rate of species composition of terrestrial predatory invertebrates after forest fires in Switzerland (compared to the high-speed recovery of flying insect communities and low-speed recovery of litter saprophages). A higher rate of post-fire recovery of ground-beetle community when compared with spiders was found in the West Siberian northern taiga (Mordkovich et al., 2006 (2008)).

There are experimental evidences of interactions between ground beetles and spiders. A. Lang (Lang, 2003) has shown a trophic niche of ground beetles and wolf spiders (Lycosidae) overlapping and a cocumulative reduction in the number of herbivorous aphids on isolated sites of a wheat field in his work. T. Bilde and S. Toft (Bilde, Toft, 1998) noted a lower degree of "accumulated hunger" of spiders compared to ground beetles collected at the same time in nature: this may indicate a more advanced physiological and ecological adaptations of spiders to a lack of prey.

In general, this small review shows the considerable plasticity and relatively high elasticity of both taxocenes, which causes a rapid response to the changes of environmental factors. The reactions are similar in many respects, especially for the rough effects. At the same time, ground beetles and spiders often show opposite trends in their response to the same environmental factor, especially in a stable environment and a smooth change on the estimated impacts.

This work is a part of the systematic study of soil-zoological component of the West Siberian forest-steppe biocoenoses started more than half a century ago (Mordkovich, 1964; Mordkovich, Volkovintser, 1974; Mordkovich, 1976). At the field test site used in the

present study, stationary studies of soil and aboveground arthropods, in particular, ground beetles, were held in 2007–2008 (Lyubechanskii, 2009; Lyubechanskii, Bepalov, 2011). In these works, along with the structure of the ground-beetle community, soils and plant associations of this profile are characterized.

The objectives of this study are as follows:

1. To study the spatial and temporal structure of aboveground spider community in the forest steppe of the south of Western Siberia using two complementary methods of collection: soil samples (pits) and traps;
2. To evaluate its spatial heterogeneity with a gradual transition from forest to grass landscapes.
3. To compare the structure of the spider community with the structure of ground-beetle populations that has been already identified for this profile.

MODEL REGION, MATERIALS, AND METHODS

The study was conducted in the southern forest steppe of Western Siberia (Novosibirsk oblast, Karauskii raion, near the settlement of Troitskoe; N 53°42.8', E 77°42.5'). A straight profile about 180 m long passing through typical habitats from the center of the birch-forest outlier to the middle of the meadowland was selected at the watershed area. Within this profile, six sample plots with distances of 30–40 m between them were chosen in 2007 to explore the biotopical association of invertebrate species. In 2008, the number of sample plots was increased to 19 and the distance between them was reduced to 10 m, in order to study the spatial heterogeneity of soil-dwelling arthropod distribution on a large scale. Ten soil traps (cup diameter 6.5 cm with fixing liquid, 3% solution of acetic acid) were set at each sample plot. Brief descriptions of the habitats in which the censuses were conducted and their compliance with each other are given in Table 1. Detailed descriptions of the habitats are given in the works (Lyubechanskii, 2009; Lyubechanskii, Bepalov, 2011).

In 2007, censuses of aboveground soil invertebrates were carried out during three short periods: from May 28 to June 3, from July 14 to 19, and from August 27 to 31; and in 2008 they were carried out during two long periods, from May 28 to June 21 and from July 5 to 21 (eight census periods for 5 days). This census arrangement made it possible to cover the seasonal change of species in 2007 and to study the dynamics of activity during the period of the highest number in 2008.

There were more than 1000 trap days in 2007, and about 3900 in 2008. Also in 2007, within specified time periods, soil pits censuses were conducted: more than 60 soil samples with an area of 0.125(1/8) m² and a depth of 15 cm; 20 at each time period, with a 3- to 4-fold replications in each of six sample plots were

Table 1. Brief characteristic of examined habitats and their compliance with each other in 2007 and 2008

Brief characteristic of the habitat	Number of the sample plot	
	2007	2008
Birch–aspen forest outlier	1	1–3
Park birch forest of the edge of the forest outlier	2	4–6
Woodreed–hog’s-fennel meadow of the edge of the forest outlier	3	7–11
Meadow solonetz	4	12–13
Steppificated meadow	5	14–17
Single birch with the herb layer under its crown	6	18–19

sorted by hand. Altogether, in 2 years, about 5000 spiders were collected by all methods.

In the analysis of diversity indices, in addition to adult spiders identified to the species level, immature individuals identified to the genus level and considered “quasi-species” (QS) were taken into account. QS accounting allows a more accurate assessment of the ecological role of different spider families because juveniles are in the majority in the local communities, lead lives similar to adult spiders, and are censused using the same methods (unlike beetles; for them, larvae and adults often live in different environments, in the soil layer and on the soil surface).

A zoogeographical analysis of fauna of the spider population in separate habitats of the study area helps explain the ecological trends of their spatial distribution on the landscape elements. For example, the abundance of “southern” species in a particular locality may indicate its warm and dry microclimate. In the areographic analysis we used the typology of habitats developed for ground beetles (Dudko, Lyubechanskii, 2002) and later modified for spiders (Mordkovich et al., 2015). The geographical range of each species has a latitudinal and longitudinal component. The following groups were marked out based on the latitudinal component: boreal, subboreal humid, subarid, and polyzonal species; based on the longitude: transgolarctic, transpalearctic, and west, central, and east palearctic. The names of areographic groups of species should not be confused with their environmental confinement. They mean only the preferred biome.

The geographical ranges of species of the subboreal zone are divided into two types: humid and subarid. Subboreal humid species are usual in the deciduous forests and steppe; the northern border of their distribution runs through the taiga zone. Subarid species stay mainly on the steppe zone, their northern boundary of distribution reaches the forest steppe, and the southern can be in the desert zone. West, central, and east palearctic

species inhabit respectively panatlantic (Euro–Siberian), central, and panpacific sectors of the palearctic.

Areographical spider groups were identified based on the materials of the world catalog of spiders (World Spider Catalog, V. 17.0, 2016) and our own data. Statistical calculations were carried out in the program PAST V. 2.17 (Hammer et al., 2001).

RESULTS

Structure of the Spider Fauna

One hundred and eighteen quasi-species of spiders from 14 families (83 identified to the species level) were found during the study period on the profile. Species belonging to the families Clubionidae and Hahniidae were found exclusively in soil samples. Species of families Agelenidae, Araneidae, Eutichuridae, Miturgidae, and Titanoecidae were collected only by traps. A comparison of general indicators of species richness is given in Table 2.

According to the trap data, the most species-rich families are Gnaphosidae and Lycosidae (24–34% of species richness). They are followed by Thomisidae and Salticidae (8–10%). According to soil samples, the proportion of families in number of species is more even. The family with the highest level of species richness is Dictynidae (five species), and it is 17% of the total species richness. The next families in the number of species are Linyphiidae and Salticidae (13% each).

The similarity of species composition, identified by the trap-technique in 2007 and 2008, was 0.34. The similarity between the fauna identified in traps and in soil samples in 2007 was 0.20 for quasi-species (Jaccard’s coefficient).

Species Richness Spatial Distribution

Biotores of the forest outlier and forest edge are richer in species of spiders compared with the more dry and open habitats of steppificated meadows and solonetz. The habitat under the crown of a single tree (according to traps) and solonetz (according to soil samples) could come up to the tree habitat in the late summer according to the number of species. In most habitats, the minimum number is in the middle of the summer and there is a rise of its value in the end of summer, which is more conspicuous according to soil samples (Fig. 1). The distribution of the number of species on the profile positions in 2008 has a similar character.

Areographic Analysis

Most spider species that were found in soil samples have very widespread distribution in the latitudinal and longitudinal directions. More than a half of the species are transgolarctic or transpalearctic, and only

Table 2. Indices of species richness and total density of the spider families depending on the sampling technique and the year of sampling

	Species in 2007 (traps)	Species in 2007 (soil samples)	Species in 2008 (traps)	Individuals per 100 trap days in 2007 (traps)	Individuals per m ² in 2007 (soil samples)	Individuals per 100 trap days in 2008 (traps)
Agelenidae	1	0	1	4	0	21.39
Araneidae	3	0	0	5.67	0	0
Clubionidae	0	1	0	0	12	0
Dictynidae	0	5	1	1.67	128	4.5
Eresidae	1	1	1	13.7	12	9.34
Gnaphosidae	12	3	19	165	332	510.01
Hahniidae	0	2	0	0	92	0
Linyphiidae	2	4	2	4	108	3.43
Lycosidae	12	3	14	864	174	2460.51
Eutichuridae	1	0	0	3.67	0	0
Philodromidae	1	2	3	78.1	32	247.04
Salticidae	5	4	4	9.67	84	24.53
Theridiidae	1	2	2	8.35	6	14.1
Thomisidae	5	3	6	19.2	100	144.41
Titanoecidae	2	0	3	12	0	33.68
Miturgidae	1	0	2	0	0	6.67
Determined at the species level	41	23	57			
Quasi-species	61	42	73			
Total dynamic density				1189.03	1080	3479.61

40% are west palearctic. There are no species unique to the central or eastern palearctic sector.

According to the latitudinal component, most species are subboreal humid. A third of species are polyzonal. There are no boreal or subarid species in soil samples, though they were found in a small number by using traps. At the same time, about a kilometer from the studied profile is a salt lake with saline and subarid types of spiders are present on its shores in a significant number (Mordkovich et al., 2015).

The total picture of the situation became clearer when the data are described by the trap technique (Fig. 2). According to the fauna, in general, the picture is similar. A small proportion in the longitudinal component of the habitat have central palearctic species. A proportion of transpalearctic species gradually increases from the center to the edge of the forest outlier and the proportion of transgolarctic species decreases. One to three central palearctic species were met in the open landscapes (forest edge, solonetz, and steppified site). The largest proportion of west and central palearctic species were met on solonetz (position 4).

According to the latitudinal component, the ratio is more stable. The only boreal species is found only in the heart of the forest outlier (position 1). Subarid species

were found only in open landscapes (positions 3–5). Subboreal humid and polyzonal species constitute the basis of fauna in all positions, like in the soil samples, in a ratio of about 1 : 1.5–1 : 2.

Abundance Distribution of Spiders within the Profile Forest Steppe

According to the trap data, during the research period (2007–2008), the population of spiders on the studied habitats was determined by representatives of three families, Lycosidae (71–72%), Gnaphosidae (14–15%), and Philodromidae (7%). The dominance of the first two is maintained throughout the summer. Philodromidae are especially noticeable in early summer (up to 15%); at the end of summer and in 2008, the proportion of family Thomisidae, which is taxonomically close to them, became significant (5%) (Table 2). Subdominant families were found within the profile only in the nonforest positions (3–5).

Spider catchability was greatest in forest habitats in 2007 (positions 1 and 2). During the summer, it tended to decrease. The herbal habitats (3–5) catching efficiency for the entire season was the lowest (Fig. 3a). Data for all summer shows a uniform reduction of total catchability from 1 to 4 position (in the direction from

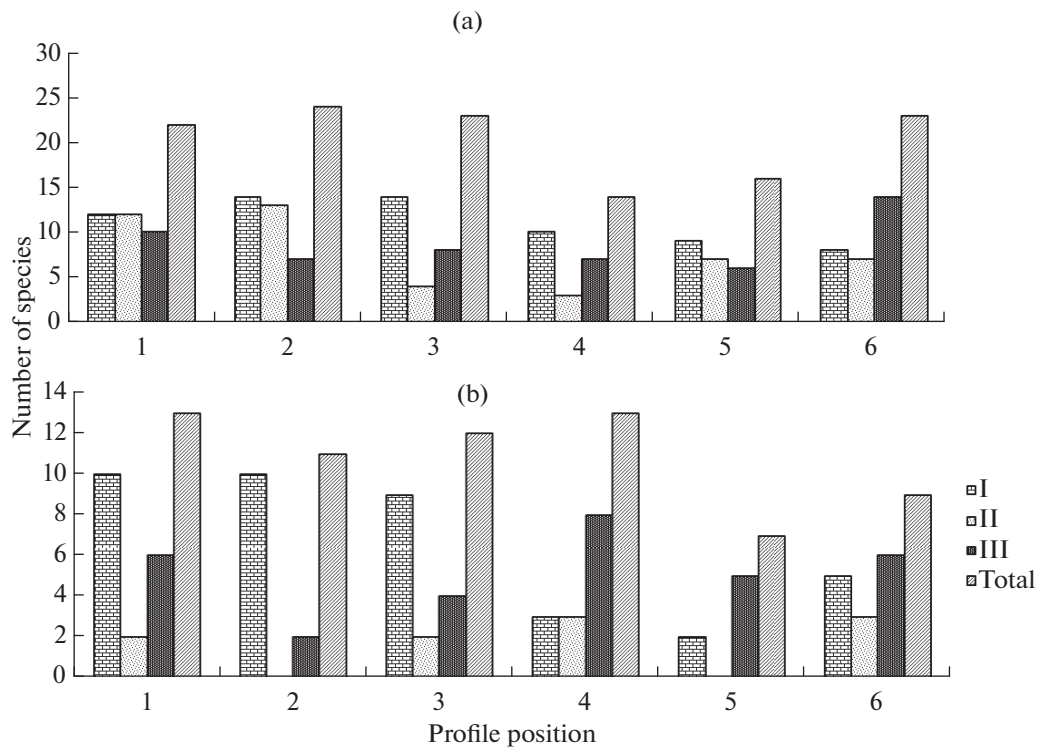


Fig. 1. Distribution of the spider species number within the profile in 2007 (A) based on trap sampling and (B) based on soil samples method. (1) Middle of the forest outlier, (2) the edge of the forest outlier, (3) meadow of the forest outlier, (4) meadow solonetz, (5) steppified meadow, and (6) single birch tree. I, Early summer; II, middle of the summer; and III, end of the summer. Total, total for the season.

the center of the forest outlier to the solonetz). Catchability in meadow positions 5 and 6 began to grow again. In 2008 (Fig. 3b) the total catchability distribution on the sample plots was similar, although on a meadow (positions 14–17) it was higher than near a single tree (position 19).

The structure of spider population defined according to soil samples, similar to the structure of the fauna, looks much more even. There is no predominance of wolf spiders. Gnaphosidae and Lycosidae retain leadership, but change their places (respectively 30 and 16% of the total abundance for the season). Next is family Dictynidae (12%) (Table 2). A similar pattern with traps was observed in the seasonal dynamics: spider density was the highest in the first period and the lowest in the second. In total value there is another peak of density on the profile—on solonetz (position 4). This is due to the species that occur in the middle and end of the summer (Fig. 3c). The greatest species diversity is also observed there at this time of the year (Fig. 1).

A strong positive correlation between the total distribution of species number at the profile positions and the number of spiders according to soil samples ($r = 0.9996$, $p < 0.0001$), but not according to the soil traps ($r = 0.17$, $p = ns$), were observed in 2007. In some peri-

ods of 2007, the correlation was positive, but weak: individual valid values could not be corrected for multiple comparisons using the Benjamini–Hochberg method (Benjamini, Hochberg, 1995). In 2008, the correlation between the total number of species in the position and overall catchability was significantly positive ($r = 0.45$, $p = 0.05$).

The largest number of juveniles according to the traps were found in the middle of the summer. In early summer their catchability at all the positions was lower when compared with adult spiders. In midsummer this ratio reversed, and at the end it returned to the same as in early summer. The most numerous are young spiders of the genera *Alopecosa* (Lycosidae) and *Zelotes* (Gnaphosidae). Juveniles always prevail in the soil samples. However, the maximum number of them is typical for late summer. This is due to the fact that most juveniles in soil samples belong to families Philodromidae and Thomisidae, which reproduce later than Lycosidae and Gnaphosidae (Fig. 4).

Spatial Distribution of the Dominance Species (Table 3)

By dominant species here we mean the species with a significantly higher number than other species (the curve in the coordinates “rank species–abundance”

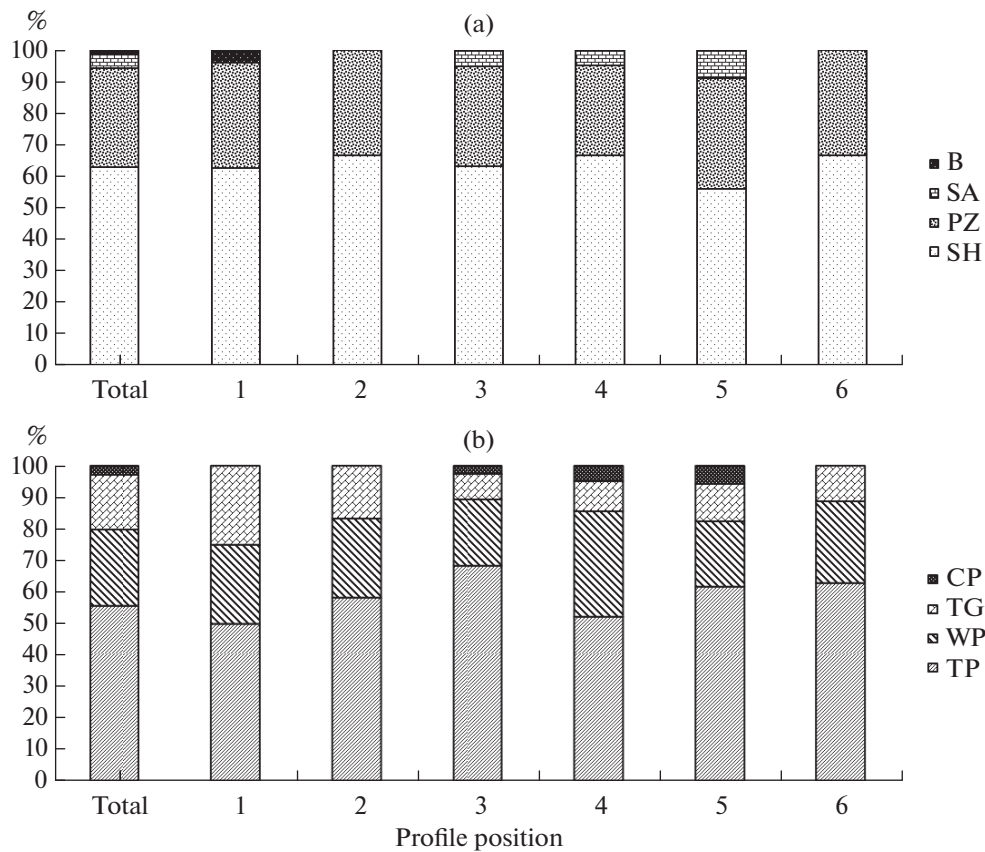


Fig. 2. Ratio of the number of spider species with different types of geographical range in the profile positions according to trap sampling in 2007–2008 based on the latitude on the top and on the longitudinal component of the range on the bottom. B, boreal; SA, subarid; SH, subboreal humid; PZ, polyzonal; TG, transgolarctic; TP, transpaliarctic; WP, west paliarctic; and CP, central paliarctic.

between the last dominant species and the first sub-dominant has a sharp bend).

The codominance of four species with two super-dominant species (*Alopecosa sulzeri* and *Pardosa lugubris*) that inhabit the forest outlier (1 and 2, and the first one is also slightly represented in 6), and the third, *Thanatus arenarius*, which inhabits only open habitats (3–5), were observed at the beginning of the summer 2007. By midsummer juveniles of the genus *Alopecosa* begin to dominate in the community. Only one representative remains a dominant species of the adult stage in the community, *A. aculeata*; several sub-dominants (adults) inhabit almost exclusively a forest position, and *Xerolycosa miniata* is steppificated. By late summer, the number of juveniles decreases; there is a new dominant in the community, *A. solitaria*, that uniformly occupies positions 1, 2, 3, and 6. The remaining four species are subdominants with several times smaller size and a maximum abundance in different parts of the profile: *Trochosa terricola* in position 2, *Zelotes longipes* in 3, *Eresus cinnaberinus* in 3, and *Ozyptila scabricula* in 5.

The change of the dominant species was observed not only during the summer, but also between differ-

ent years of study. In both years the most massive species *A. sulzeri*, *P. lugubris*, *A. aculeata*, and *T. arenarius* dominated according to the trap technique. *A. accentuata* and *A. solitaria* dominated only in 2007; and *Haplodrassus signifer*, *Gnaphosa leporina*, *X. miniata*, *A. cuneata*, and *A. taeniata* dominated only in 2008.

According to the spider species distribution within the profile in 2008, there is one generalist species that occurs equally in both forest and open habitats, avoiding only extreme: the central part of the forest outlier and solonetz. This is *Alopecosa sulzeri* (Fig. 5). Other dominant species were found only in tree (1 to 5) or herbal positions. *A. aculeata*, *A. taeniata*, and *P. lugubris* are forest species. *A. cuneata*, *X. miniata*, *G. leporina*, *H. signifer* and *T. arenarius* are meadow species. *Alopecosa cuneata* are most numerous at the edge of the forest (position 6); *Xerolycosa miniata*, at the positions with the highest herbage (6, 8, and 16); and *Thanatus arenarius* is the basis of the population in the positions 12 to 14 (solonetz). Cluster analysis of the species confinement to certain profile positions give similar results.

According to soil sample data, in the early summer of 2007, *Hahnia ononidum* dominates; the next are

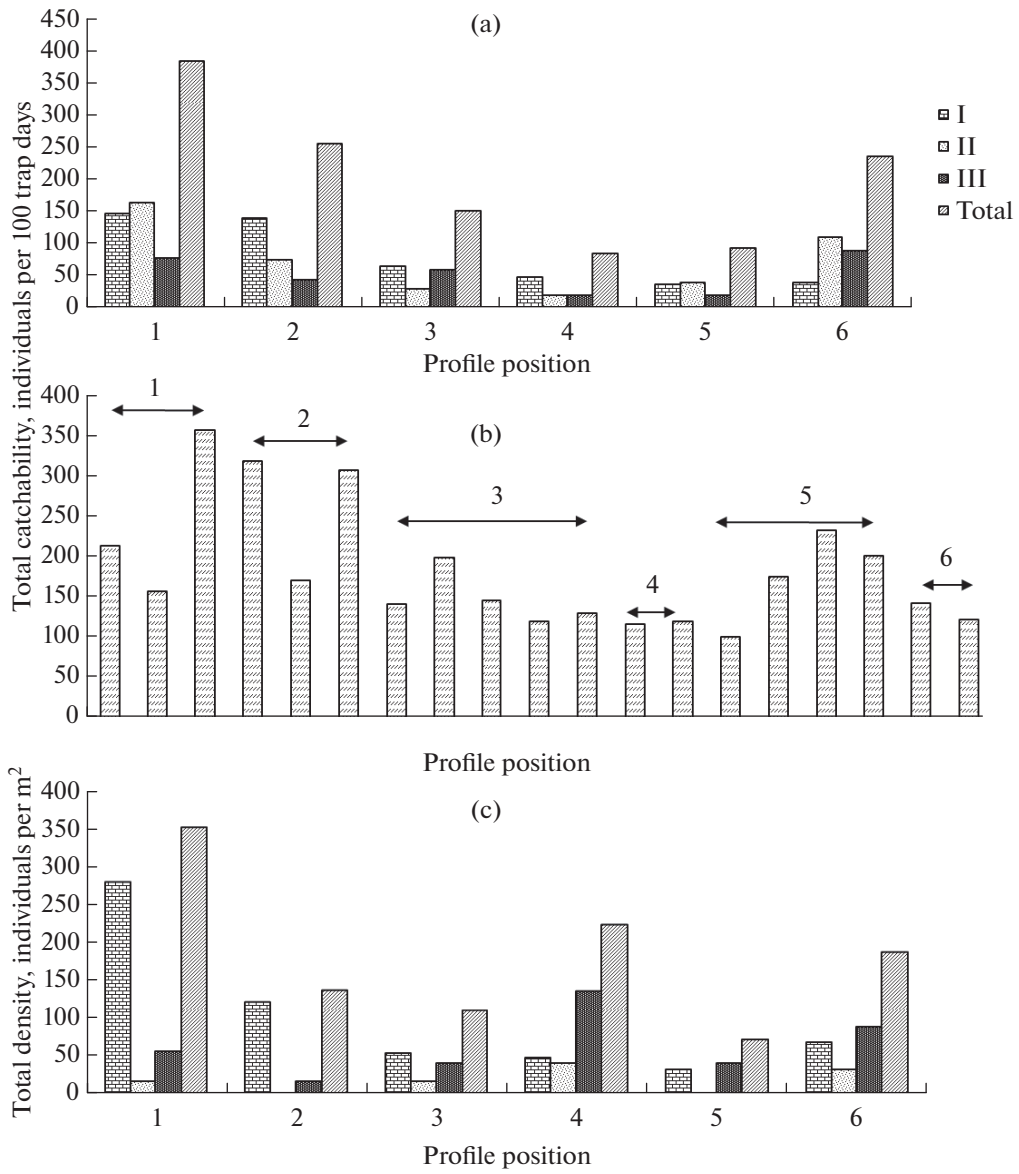


Fig. 3. Distribution of spider number indicators within the profile: (A) according to the trap sampling in 2007, (B) according to the trap sampling in 2008, and (C) according to soil samples in 2007. For legend, see Fig. 1.

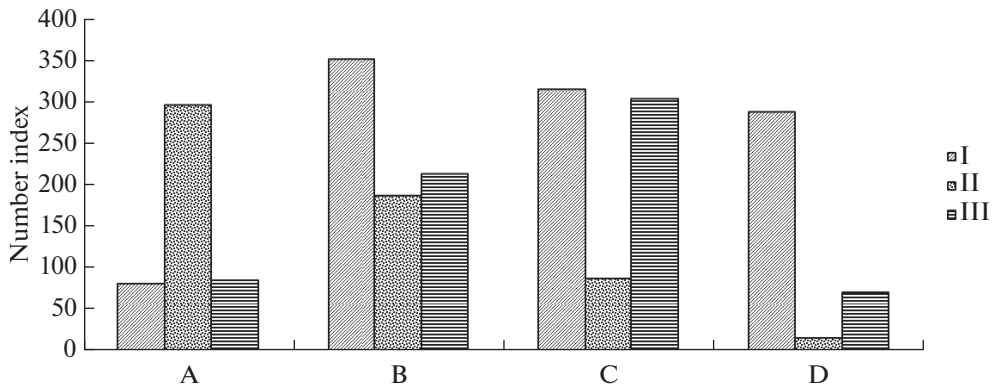


Fig 4. Ratio of juvenile and adult individuals of spiders depending on the time and sampling method in 2007. I, early summer; II, middle of summer; and III, end of summer. (A) juvenile, according to trap sampling, individuals per 100 trap days; (B) adult, according to trap sampling; (C) juvenile according to soil samples, individuals per m²; and (D) adults according to soil samples.

Table 3. Distribution of the dominant species of spiders on the profile positions and their change during the summer 2007. The period of the species domination: I, the beginning of summer; II, the middle of summer; and III, the end of summer. All other symbols are presented as in Table 1

Traps, individuals per 100 trap days	Period	Profile positions						Total
		1	2	3	4	5	6	
<i>Alopecosa</i> sp.	I, II, III	81.01	42.02	47.69	15.67	21.34	116.7	324.43
<i>Alopecosa solitaria</i> (Herman, 1879)	III	46	14	20	2	2	48	132
<i>Pardosa lugubris</i> (Walckenaer, 1802)	I	55.09	47.75	0	0	0	0	102.84
<i>Alopecosa sulzeri</i> (Pavesi, 1873)	I	45.09	40.08	0	0	0	6.68	91.85
<i>Thanatus arenarius</i> L. Koch, 1872	I	0	0	23.38	28.39	20.37	2	74.14
<i>Zelotes</i> sp.	II, III	13.67	20.68	7.34	9.01	1.67	13.34	65.71
<i>Alopecosa aculeata</i> (Clerck, 1757)	II	52	11.69	0	0	0	0	63.69
<i>Alopecosa accentuata</i> (Latreille, 1817)	I	37.07	4	0	0	0	0	41.07
<i>Zelotes longipes</i> (L. Koch, 1866)	III	3.67	0	6	5.67	5.34	4	24.68
<i>Trochosa terricola</i> Thorell, 1856	II, III	9.34	14	0	0	0	0	23.34
<i>Zelotes subterraneus</i> (C. L. Koch, 1833)	II	6	8.68	2	0	0	6	22.68
Lycosidae spp.	II	8	4	2	2	0	0	16
<i>Xerolycosa miniata</i> (C. L. Koch, 1834)	II	0	0	0	0	13.67	2	15.67
<i>Eresus cinnaberinus</i> (Olivier, 1789)	III	0	2	8	3.67	0	0	13.67
<i>Alopecosa taeniata</i> (C. L. Koch, 1835)	II	2	10	0	0	0	0	12
<i>Pardosa</i> sp.	II	6	5.67	0	0	0	0	11.67
<i>Ozyptila scabricula</i> (Westring, 1851)	III	0	0	2	0	6	2	10
Soil samples, individuals per m ²								
<i>Gnaphosa</i> sp.	I, II, III	32	16	12	48	8	40	156
<i>Zelotes</i> sp.	I, II, III	72	8	16	0	0	40	136
<i>Alopecosa</i> sp.	I, II	56	28	24	8	0	16	132
<i>Hahnia ononidum</i> Simon, 1875	I	76	0	0	0	0	0	76
Linyphiidae Gen. sp. 3	III	0	0	0	56	0	0	56
<i>Dictyna arundinacea</i> (Linnaeus, 1758)	I	0	0	8	16	16	0	40
<i>Xysticus</i> sp.	III	0	0	8	0	0	32	40
<i>Evarcha</i> sp.	I	8	20	0	0	8	0	36
<i>Argenna subnigra</i> (O. Pickard-Cambridge, 1861)	I	16	0	0	0	16	0	32

juveniles of the genera *Alopecosa*, *Zelotes*, and *Gnaphosa*. Only then follows *Dictyna arundinacea*. In mid-summer, the number of spiders is very low, and juvenile members of the same genera dominate. At the end of the summer, along with the juvenile members of the already-mentioned genera, there is a new subdominant of the family Linyphiidae. The total number of dominant species in these soil samples is presented in Table 3.

The seasonal dynamics of the spider population were studied for nearly 2 months (from May 28 to July 22) in 2008. Similar to 2007, the overall spider catchability gradually reduced to the middle of summer and the number of juveniles in the same time increased because of the same groups (*Alopecosa* and *Zelotes*) (Fig. 6).

Similarity of the Variance of Spider Population in Different Habitats

Three coefficients of similarity (Jaccard's, Oshiai, and Morishita) were calculated for the quantitative data. The method of clustering of unweighted pair (UPGMA) was used.

In early summer, position 1 and 2 (forest) were the most similar to each other. Sometimes position 6 (a single birch in the meadow) adjacent to the cluster formed by these two positions (Morishita index) (Fig. 7a). Another cluster is formed by positions 3, 4, and 6 (Jaccard's and Oshiai indices) or positions 3, 4, and 5 (Morishita index). In midsummer, the similarity between all positions is reduced. "Forest" (1, 2, 3, 6) and "Meadow" (4, 5) positions (Jaccard's and Oshiai indices) are separately marked on the cluster (Fig. 7b);

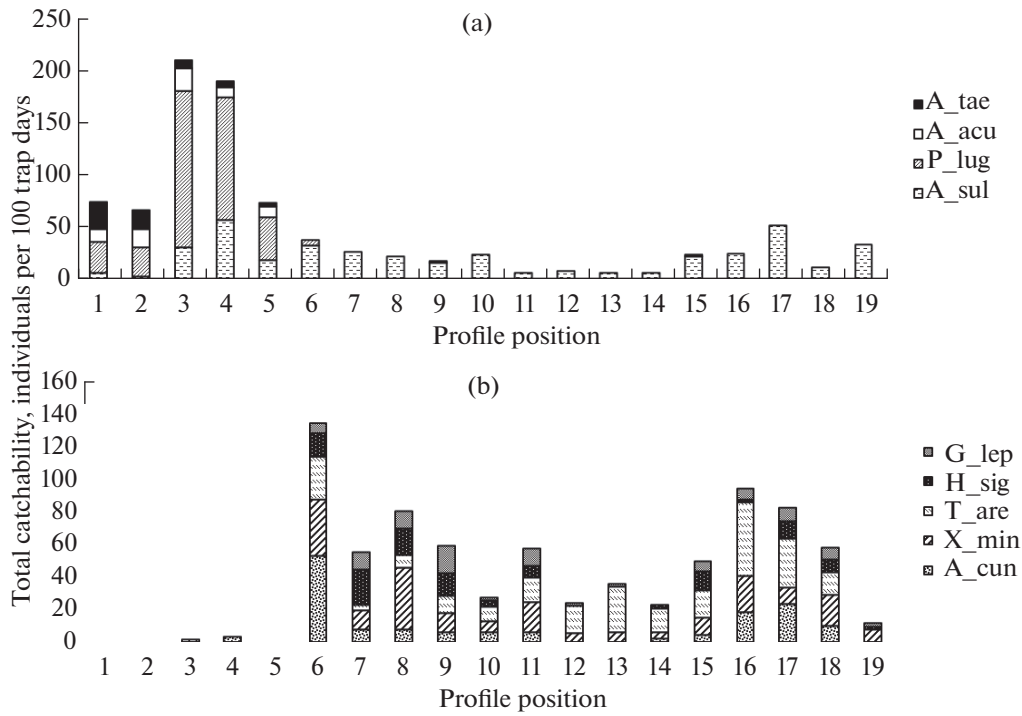


Fig. 5. Distribution of the dominant spider species in 2008, according to trap sampling. (A) forest species (*A_sul*, *Alopecosa sulzeri*; *P_lug*, *Pardosa lugubris*; *A_acu*, *Alopecosa aculeata*; and *A_tae*, *Alopecosa taeniata*) and (B) species of the open (*A_cun*, *Alopecosa cuneata*; *X_min*, *Xerolycosa miniata*; *T_are*, *Thanatus arenarius*; *H_sig*, *Haplodrassus signifer*; and *G_lep*, *Gnaphosa leporina*). (1–19) Profile positions in 2008, see Table 1.

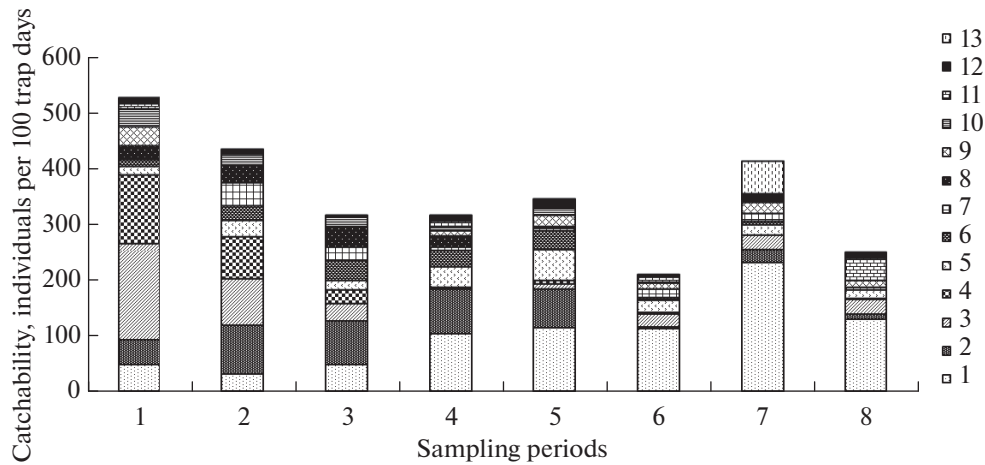


Fig. 6. Seasonal dynamics of the dominant spider species in 2008. 1, *Alopecosa* sp.; 2, *A. sulzeri*; 3, *Pardosa lugubris*; 4, *Thanatus arenarius*; 5, *Xerolycosa miniata*; 6, *A. cuneata*; 7, *Lycosidae* spp.; 8, *Haplodrassus signifer*; 9, *Zelotes* sp.; 10, *Gnaphosa leporina*; 11, *A. aculeata*; 12, *Xerolycosa* sp.; and 13, *A. taeniata*. Horizontally marked sampling periods, (1) 27.05–01.06, (2) 01.06–07.06, (3) 07–12.06, (4) 12–17.06, (5) 17–22.06, (6) 07–12.07, (7) 12–17.07, and (8) 17–22.07.

positions 1, 2, 5 are isolated, and 3, 4, and 6 form a tight cluster (Morishita index). In late summer, the community divided into three factions that were not very similar to each other: forest (1 and 2), herbal community (3, 5, and 6), and solonetz (4). (Jaccard's and Oshiai indices) (Fig. 7c). In the case of using the Morishita index, solonetz (4) and steppified

meadow (5) are almost equally separated from the cluster of other "humid" communities (1, 2, 3, and 6).

Cluster analysis of the spider distribution within the profile according to soil samples give similar results, although it is based on other species. The variance of spider population in habitats form clusters 1–2–5 and 3–4–6 (Fig. 7d).

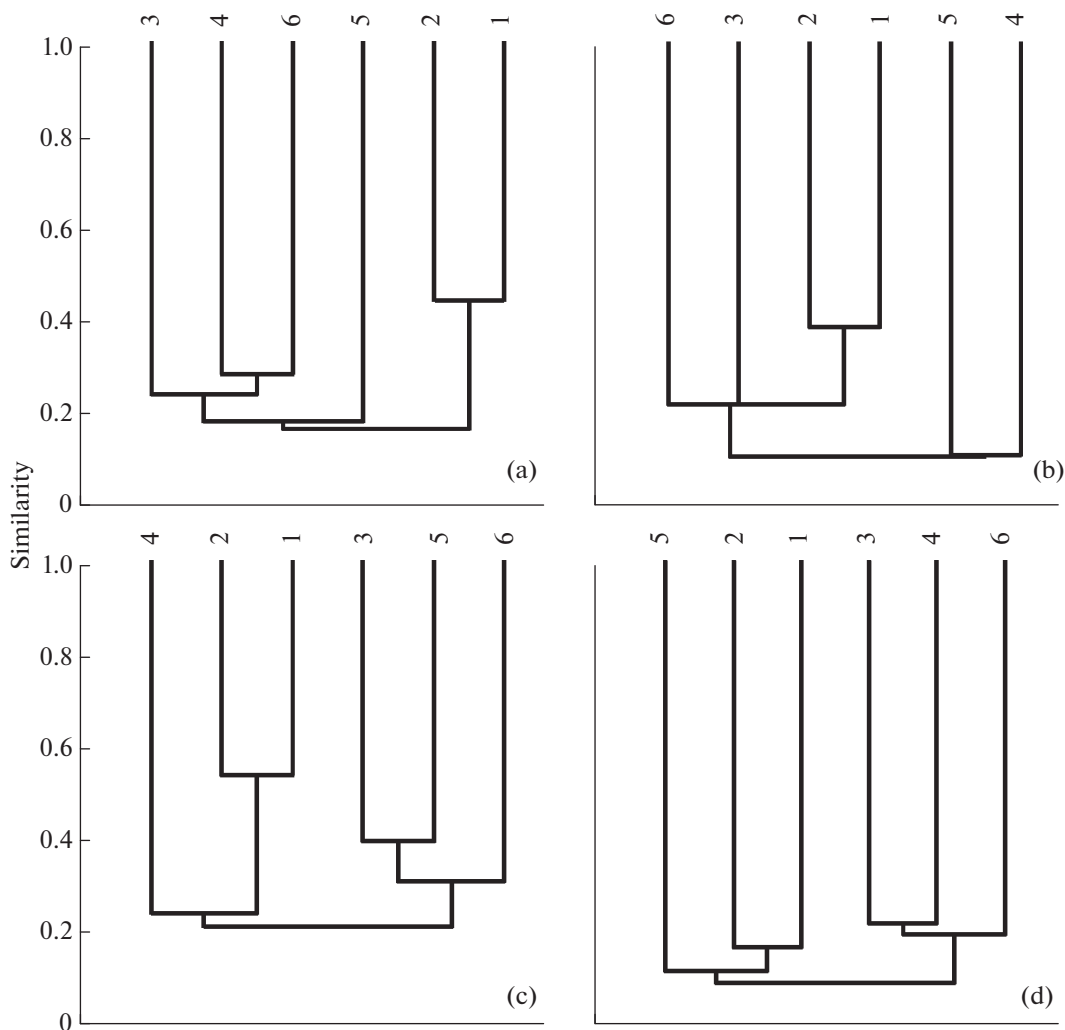


Fig. 7. Similarity of the variances of the spider population in the discrete habitats of the profile in 2007 (Jaccard's index, UPGMA). (A) early summer, (B) middle of the summer, (C) end of the summer, and (D) soil samples of the season.

Positions 1 and 5 (forest) were practically always segregated in 2008 with the operation with different similarity coefficients. The remaining part of the cluster, depending on the indices used, has an unstable structure and weak bootstrap support (50). Positions 6 (the boundary of the forest and meadows) and 19 (single birch) separate from the cluster more often. The remaining positions are mainly grouped on the basis of their spatial proximity to each other (Fig. 8).

DISCUSSION

Comparison of Spatiotemporal Organization of the Spiders and Ground-Beetle Communities

General characteristics of species diversity of spiders and ground beetles are shown in Table 4. The taxocene of spiders in all cases is richer in species than the taxocene of ground beetles. By using different

methods of data collection (soil samples and traps), the faunal composition of one or the other group shows a low similarity. This is due to the large number of topical strategies of the species that composed the taxocene of spiders (roving hunters, ambush spiders, grass inhabitants, etc.) and ground beetles (their various life forms), so different collection methods give different picture of the species composition. The falling into traps is also associated with the mobility of juvenile and adult stages of spiders: juveniles are less mobile than adults, so they are better registered by the soil sample method. By the samplings made in different years, the spider similarity is higher than that of ground beetles, because spiders have one breeding peak in the first half of the summer and different species of ground beetles are active at different times of the warm period: some species of ground beetles were not included in samplings in 2008, when there were no autumn censuses.

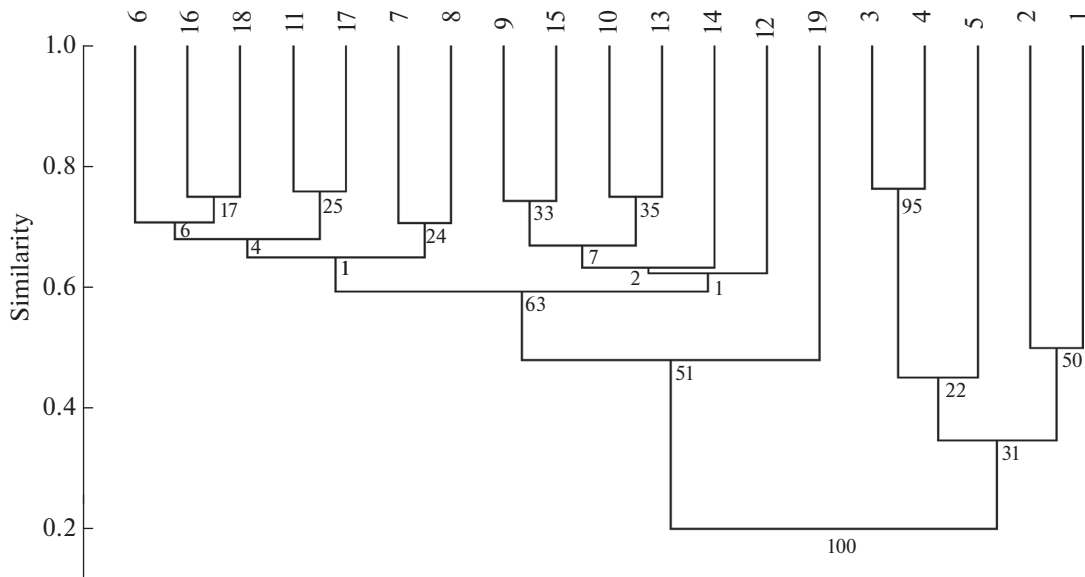


Fig. 8. Similarity of the variances of the spider population in the continuous habitats of the profile in 2008 (Jaccard's index, UPGMA). For legend see Table 1.

The number of species of ground beetles and spiders in the profile positions in each period separately and in the entire season of 2007 did not correlate either according to the traps or according to soil samples. The amount of ground-beetle species in 2007, according to the traps, was highest in position 2. Also, it was high in positions 1 and 5, and was the lowest in position 4 (Lyubechanskii, 2009). For spiders it is maximum in the positions 2 and 3, high in 1 and 6, and lowest in position 4 (Fig. 1a). Therefore, we cannot talk about uncoupling at least species diversity peaks at these two taxocenes.

According to soil samples, the amount of ground-beetle species is maximum in position 3 and minimum in position 4 (Lyubechanskii, 2009). The amount of spider species is maximum in 1 and 4 and minimum in position 5 (Fig. 1b). Thus, the rare species of spiders, as well as slow-moving ambush spiders, concentrate in the most arid position of the profile (4, solonetz), which is minimally visited by ground beetles. Maybe spiders are forced out on relatively unproductive positions by ground beetles as a result of competition, or simply are killed by these predatory beetles.

Indicators of the spider and ground-beetle numbers (Fig. 3) are correlated only in the early summer. There is no correlation between the density of ground beetles and spiders at the beginning of the summer according to the soil samples, but in the middle and the end of summer the correlation is negative (in August, $r = -0.89, p < 0.01$). Catchability of ground beetles and spiders in general for the 2007 season has a positive insignificant correlation. Thus, in 2008, the total distribution of ground beetles and spiders in habitats shows considerable similarity and similar values of total dynamic density ($r = 0.67, p = 0.0016$) (Fig. 9).

The catchability ratio in different positions of the profile retained for the 2007 season for the ground beetles ($p < 0.01$), but not for spiders.

All this suggests that the overall density of ground beetles and spiders depend on the same broad and diverse group of victims, related mainly to soil-dwelling arthropods and geobionts. In midsummer, with an increase in the number of ground beetles and juveniles spiders, the interactions between them become competitive or even predatory.

Rank distributions of the abundances of spiders is very similar to that of ground beetles (Fig. 10, plots 1 and 3). The number of dominants are practically the same, but spiders have a long “tail” of sporadic founded species (73 species compared to 57 of ground beetles). If we only take into the account the spider

Table 4. General characteristics of species diversity of spiders and ground beetles

	Ground beetles	Spiders
Similarity of the species composition by trap sampling and soil sampling, 2007	0.24	0.20
Similarity of the species composition by trap sampling, 2007 and 2008	0.44	0.56
Species by trap sampling, 2007	35	59
Species by trap sampling, 2008	57	73
Identical species for 2007–2008	28	19
Species by soil sample method, 2007	22	42
Identical species with determined by trap sampling in 2007	11	17

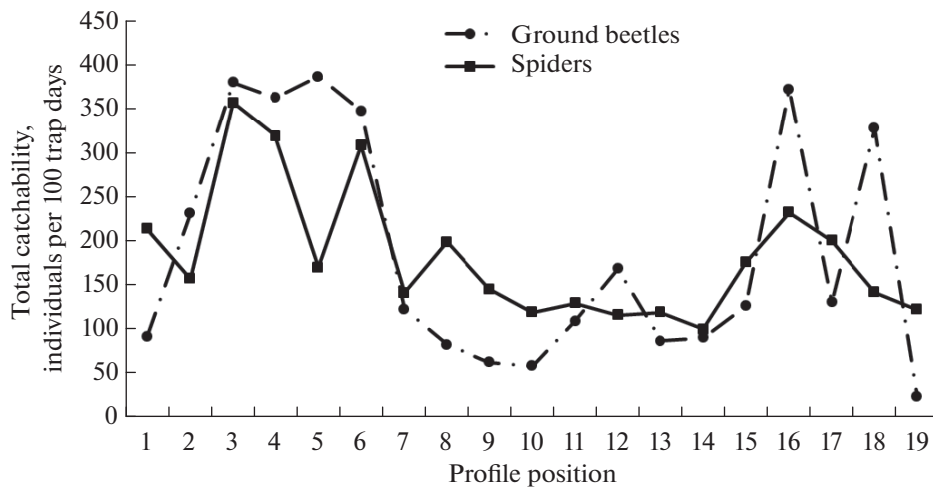


Fig. 9. Distribution of the total dynamic density of the ground beetles and spiders within the profile positions in 2008. Data on ground beetles (Lubechanskii, Bespalov, 2011).

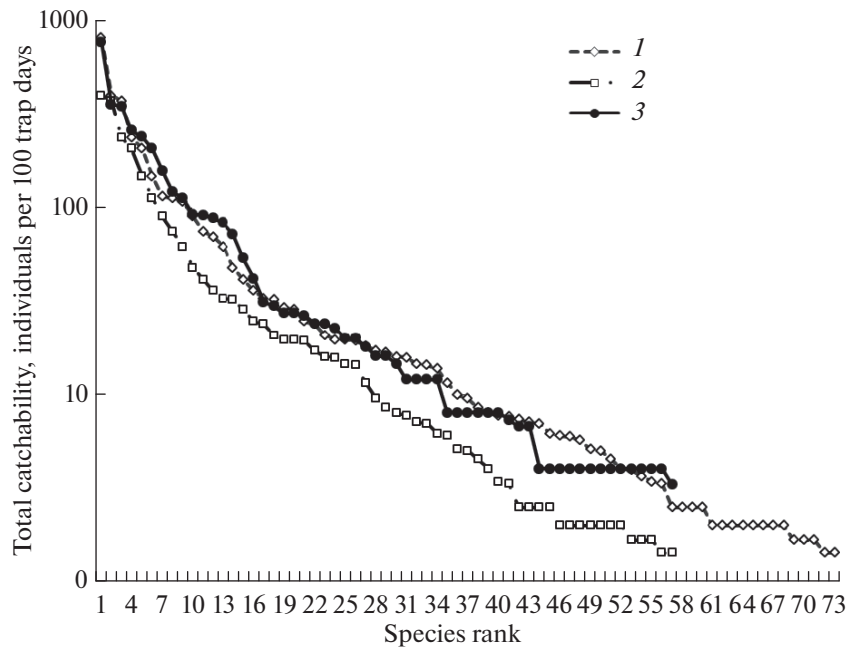


Fig. 10. Distribution of the species abundance of spiders in general (1), of spiders determined to the species level (2), and of ground beetles (3) in 2008.

taxa identified to species level (Fig. 10, plot 2), then the distribution of abundances is more uneven than that of ground beetles. Thus, two spiders species are dominant (generalist, almost indifferent to vegetation type, *Alopecosa sulzeri*, and forest species *Pardosa lugubris*; both roving hunters, and the second is about half the body size of the first), and only one species of ground beetles is dominant (*Poecilus fortipes* (Schaud.)), also a generalist species, but mostly a meadow one). The third and fourth species of high abundance of spiders, ambush spider *Thanatus arenarius*, and roving hunter *Xerolycosa miniata*, inhabit open habitats.

Among the subdominants of ground beetles are meadow species *Calathus erratus* C. Sahlb. and forest species *Pterostichus oblongopunctatus* F. Typical steppe species of ground beetles (botrobiont *Taphoxenus gigas* F.-W. et al.) have a much lower number and few interactions with the spiders that inhabit the solonetz and steppicated site. Taking into account the juvenile spiders, they also have one pronounced dominant, *Alopecosa* sp.

Tree diagrams of the habitat similarities for spider population (Figs. 7, 8) and ground beetles in 2007 and

2008 [For ground beetles, see (Lyubchanskii, 2009; Lyubchanskii, Bepalov, 2011)] essentially do not differ. The same positions are separated for ground beetles and spiders: the difference between forest and open habitats are always noticeable.

In a comparison of the tree diagrams of species similarity by preferred habitats, spider species, like ground-beetle species that inhabit the profile, are clearly divided into forest species and species of open habitats. However, ground-beetle differentiation goes further; it is possible to identify the “forest,” “meadow,” and “steppe” species and generalist species of open spaces (Lyubchanskii, Bepalov, 2011). Spiders do not differentiate profile space with such clarity [compare with (Irmler et al., 2002)], except for only a few specialized species. However, generalist spider *A. sulzeri* only slightly prefers forest, and *Poecilus fortipes* has a pronounced peak of abundance in the meadow habitats.

Comparison of the Areographical Content of Ground Beetles and Spiders

There is a high proportion of boreal subarid species in the ground-beetle fauna of the studied area of forest-steppe landscape (in spider fauna these species are rare). Due to this, the proportion of subboreal humid and polyzonal species is less in ground beetles; however, these species are of high abundance among spiders species. Among ground-beetle species, most are east palearctic species, and among spiders most are transgolarctic. There are no transgolarctic species among ground beetles, but there are about 15% of them among spiders. There are no east palaeartic species among the spiders, but among ground beetles they comprise 5–10% of the species. Central palearctic species in both taxocenes are a small proportion.

Spider species with relatively narrow subarid central palearctic geographical ranges are more common in open habitats and in forest habitats of the profile; on the other hand, a significant part of the fauna is presented by species with very broad transgolarctic ranges. The significantly larger areas of spiders compared with areas of ground beetles does not allow us to easily use spiders for zoogeographical reconstructions and indications of habitat via areographical analysis.

CONCLUSIONS

In the complex, rich ecosystem of the southern forest steppe there is a saturated taxocene of predatory soil-dwelling arthropods, the most numerous of which are spiders and ground beetles. Their species richness reaches several tens of species within transects of almost 200 m long, which is made up of forest and herbaceous ecosystems. The number of spider species was practically one and a half times more than ground-beetle species; the total dynamic density of the representatives of both taxocenes was approximately equal. The distribution of species richness and abundance

indices of spiders and ground beetles in the forest steppe was similar. Dominant species replace each other during the summer. Both groups inhabit the profile entirely, but at the level of individual species of ground beetles and representatives of certain families of spiders there is a clear separation of species confined to forest and herbaceous ecosystems.

Specialization of ground beetles is more pronounced: herbal species types could be divided into field, steppe, and generalists of open spaces (Lyubchanskii, Bepalov, 2011). Spiders do not have such a clear division; however, species of families with relatively slow-moving life forms (ambush spiders) dominate in the most arid and unproductive site of the profile. Unlike the sparsely populated northern ecosystems (Lyubchanskii, 2012; Mordkovich et al., 2014) and extreme conditions of the coast of the salt lake in the forest steppe (Mordkovich et al., 2015), the two examined animal taxocenes practically do not show opposite trends in the spatial distribution and temporal dynamics. We believe that the separation of ecological niches of ground beetles and spiders goes on a finer pattern than the topical one and includes the use of different strata of vegetation, different seasonal activity, and trophic specialization.

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REFERENCES

- Alaruikka, D., Kotze, D.J., Matveinen, K., and Niemela, J., Carabid beetle and spider assemblages along a forested urban-rural gradient in southern Finland, *J. Insect Conserv.*, 2002, vol. 6, no. 4, pp. 195–206.
- Alderweireldt, M. and Desender, K., Microhabitat preference of spiders (Araneae) and carabid beetles (Coleoptera, Carabidae) in maize fields, *Meded. Rijksfac. Landbouwwet., Gent.*, 1990, vol. 55, no. 2, pp. 501–510.
- Benjamini, Y. and Hochberg, Y., Controlling the false discovery rate: a practical and powerful approach to multiple testing, *J. R. Stat. Soc., B: Stat Methodol.*, 1995, vol. 57, no. 1, pp. 289–300.
- Bilde, T. and Toft, S., Quantifying food limitation of arthropod predators in the field, *Oecologia*, 1998, vol. 115, pp. 54–58.
- Bonn, A., Hagen, K., and Reiche, D.W. V., The significance of flood regimes for carabid beetle and spider communities in riparian habitats—a comparison of three major rivers in Germany, *River Res. Appl.*, 2002, vol. 18, no. 1, pp. 43–64.

- Cole, L.J., McCracken, D.I., Downie, I.S., Dennis, P., Foster, G.N., Waterhouse, T., Murphy, K.J., Griffin, A.L., and Kennedy, M.P., Comparing the effects of farming practices on ground beetle (Coleoptera: Carabidae) and spider (Araneae) assemblages of Scottish farmland, *Biodiversity Conserv.*, 2005, vol. 14, no. 2, pp. 441–460.
- Dudko, R.Yu. and Lyubchanskii, I.I., The fauna and zoogeographical characteristic of carabid beetles (Coleoptera, Carabidae) in Novosibirsk oblast, *Eurasian Entomol. J.*, 2002, vol. 1, no. 1, pp. 30–45.
- Hammer, Ø., Harper, D.A.T., and Ryan, P.D., PAST: paleontological statistics software package for education and data analysis, *Palaeontol. Electron.*, 2001, vol. 4, no. 1. http://palaeo-electronica.org/2001_1/past/issue1_01.htm.
- Irmeler, U., Heller, K.A.I., and Meyer, H., Zonation of ground beetles (Coleoptera: Carabidae) and spiders (Araneida) in salt marshes at the North and the Baltic Sea and the impact of the predicted sea level increase, *Biodiversity Conserv.*, 2002, vol. 11, pp. 1129–1147.
- Kromp, B. and Steinberger, K.H., Grassy field margins and arthropod diversity: a case study on ground beetle and spiders in eastern Austria (Coleoptera: Carabidae; Arachnida: Aranei, Opiliones), *Agric. Ecosyst. Environ.*, 1992, vol. 40, pp. 71–93.
- Lang, A., Intraguild interference and biocontrol effects of generalist predators in a winter wheat field, *Oecologia*, 2003, vol. 134, no. 1, pp. 144–153.
- Lyubchanskii, I.I., Carabid beetles community of the typical habitats in southern forest-steppe (West Siberia), *Eurasian Entomol. J.*, 2009, vol. 8, no. 3, pp. 315–318.
- Lyubchanskii, I.I. and Bespalov, A.N., Spatial heterogeneity of a ground beetle (Coleoptera, Carabidae) population along a forest-steppe transect: local level of consideration, *Contemp. Probl. Ecol.*, 2011, vol. 4, no. 4, pp. 388–395.
- Lyubchanskii, I.I., Spider community structure in the natural and disturbed habitats of the West Siberian northern taiga: comparison with Carabidae community, *Russ. Entomol. J.*, 2012, vol. 21, no. 2, pp. 147–155.
- Máthé, I., Urák, I., Balog, A., and Balázs, E., The community structure of the ground dwelling carabid beetles (Coleoptera: Carabidae) and spiders (Arachnida: Araneae) in peat bog “Mohos” (Transylvania, Romania), *Entomol. Rom.*, 2003, vol. 8, pp. 95–102.
- Mordkovich, V.G., Population of herpetobiont beetles (Coleoptera, Carabidae, Silphidae, Tenebrionidae) in microlandscapes of the north of Barabinsk forest-steppe and its transformation caused by human economic activities, *Zool. Zh.*, 1964, vol. 43, no. 5, pp. 680–694.
- Mordkovich, V.G., Dynamics of species composition and abundance of soil-dwelling arthropods as an indicator of succession, in *Struktura, funktsionirovanie i evolyutsiya sistemy biogeotseonozov Baraby. Chast' 2. Biogeotseoticheskii protsessy (Structure, Functions, and Evolution of the Biogeocenoses of Baraba Region, Part 2: Biogeocenotic Processes)*, Kovalev, R.V., Ed., Novosibirsk: Nauka, 1976, pp. 401–416.
- Mordkovich, V.G., Berezina O.G., Lyubchanskii I.I., Andrievskii V.S., and Marchenko I.I. Soil Arthropoda of post-fire successions in northern taiga of West Siberia, *Contemp. Probl. Ecol.*, 2008, vol. 1, no. 1, pp. 96–103.
- Mordkovich, V.G., Dudko, R.Yu., Trilikauskas, L.A., and Lyubchanskii, I.I., Carabid beetles (Coleoptera, Carabidae) and spiders (Aranei) are a part of soil fauna on the shore of a salt lake in South Siberia, Russia, *Eurasian Entomol. J.*, 2015, vol. 14, no. 5, pp. 447–454.
- Mordkovich, V.G., Lyubchanskii, I.I., Berezina, O.G., Marchenko, I.I., and Andrievskii, V.S., *Zoedafon zapadno-sibirskoi severnoi taigi: prostranstvennaya ekologiya naseleniya pochvoobitayushchikh chlenistonogikh estestvennykh i narushennykh mestoobitanii (Zoedaphone of the West Siberian Northern Taiga: Spatial Ecology of the Soil-Dwelling Arthropods of Natural and Disturbed Habitats)*, Moscow: KMK, 2014.
- Mordkovich, V.G. and Volkovintser, V.V., Soil fauna, in *Struktura, funktsionirovanie i evolyutsiya sistemy biogeotseonozov Baraby. Chast' 1. Biogeotseonozy i ikh komponenty (Structure, Functions, and Evolution of the Biogeocenoses of Baraba Region, Part 1: Biogeocenotic Components)*, Kovalev, R.V., Ed., Novosibirsk: Nauka, 1974, pp. 258–279.
- Moretti, M., Duelli, P., and Obrist, M.K., Biodiversity and resilience of arthropod communities after fire disturbance in temperate forests, *Oecologia*, 2006, vol. 149, no. 2, pp. 312–327.
- Niwa, C.G. and Peck, R.W., Influence of prescribed fire on carabid beetle (Carabidae) and spider (Araneae) assemblages in forest litter in southwestern Oregon, *Environ. Entomol.*, 2002, vol. 31, no. 5, pp. 785–796.
- Pearce, J.L., Venier, L.A., Eccles, G., Pedlar, J., and McKenney, D., The use of ground beetles (Coleoptera: Carabidae) and spiders (Araneae) as bioindicators of sustainable forest management: a review, *Ecol. Indic.*, 2006, vol. 6, no. 4, pp. 780–793.
- Samu, F., Kádár, F., Ónodi, G., Kertész, M., Szirányi, A., Szita, É., Fetykó, K., Neidert, D., Botos, E., and Altbäcker, V., Differential ecological responses of two generalist arthropod groups, spiders and carabid beetles (Araneae, Carabidae), to the effects of wildfire, *Comm. Ecol.*, 2010, vol. 11, no. 2, pp. 129–139.
- Uzenbaev, S.D., *Ekologiya khishchnykh chlenistonogikh mezotrofnogo bolota (Ecology of Raptorial Arthropods from the Mesotrophic Mire)*, Petrozavodsk: Karel. Fil., Akad. Nauk SSSR, 1987.
- World Spider Catalog, Natural History Museum, Bern, ver. 17.0, 2016. <http://wsc.nmbe.ch>. Accessed June 17, 2016.

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