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Spatial distribution of spiders (Arachnida: Araneae) in agroecosystems of the European part of Russia

Пространственное размещение пауков (Arachnida: Araneae) в агроэкосистемах европейской части России

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ABSTRACT. Species composition, dominance structure and seasonal dynamics of spatial distribution of spiders were studied in agricultural fields (edges and central zones were considered separately), field margins and bordering strips of adjacent natural habitats in the Moscow area and Krasnodar territory. In total, 286 spider species in 146 genera and 20 families were recorded. The species diversity both in agroecosystems and in adjacent natural habitats was similar, but that of the field centre was noticeably lower. In both sampling sites, the structure of araneocomplexes changed drastically from the field margins towards the centre of the field, whereas it varied insignificantly within the central zone (200–400 m from the edges) of large fields in Krasnodar territory. The dominant spider species occurring in the field margins, unlike those of the croplands, were influenced by the local, natural fauna of the field margins. Species penetrating into the cropland beyond a 100 m zone were capable of occupying the rest of the field regardless of its size.

РЕЗЮМЕ. Изучены видовой состав, структура доминирования и сезонная динамика пространственного размещения пауков на сельскохозяйственных полях (отдельно в краевой и в центральной зонах), их обочинах и пограничных участках естественных биотопов в Московской области и Краснодарском крае. Всего обнаружены 286 видов пауков из 146 родов и 20 семейств. Видовое разнообразие в агроэкосистемах и прилегающих природных биотопах схоже, но заметно ниже в центральной части полей. В обоих регионах структура аранеокомплекса четко различается по многим показателям в краевой и центральной зонах полей, однако на крупных полях Краснодарского края различия не существенны в пределах центральной зоны (200–400 м от края). Набор видов, доминирующих на обочинах полей, в большей степени, чем на посевах, определяется локальной, природной фауной. Виды, проникающие за пределы стометровой зоны от края поля способны освоить и остальную его территорию вне зависимости от ее площади.

KEY WORDS: Araneae, spiders, agroecosystem, agrocoenosis, agrolandscape, Moscow area, Krasnodar territory.
КЛЮЧЕВЫЕ СЛОВА: Araneae, пауки, агроэкосистема, агроценоз, агроландшафт, Московская область, Краснодарский край.

Introduction

Spiders are common in agrocoenoses, making up 20 to 80% of the predatory fauna [Legotay, 1980; Minoranski, 1984; Sterling *et al.*, 1992; Zhang, 1992]. Although being different from most natural associations, cropland spider complexes somewhat resemble meadow communities [Legotay, 1980; Łuczak, 1979] and their diversity varies from tens to more than 300 species [Young & Edwards, 1990; etc.]. For instance, 50 to 120 spider species have been reported from European wheat fields, and this rises to 200 species if field margins are included [Toft, 1989; Zhukovets, 1990; Minoranski, 1984; Topping & Sunderland, 1992; Feber *et al.*, 1998; Toth & Kiss, 1999]. Overall the spider diversity in agrocoenoses is lower than in natural habitats [Nyffeler, 1984]. Species composition and especially that of dominant species was found to be similar across agricultural landscapes of the European temperate zone [Jocque, 1981; Alderweireldt, 1989a; Toft, 1989; Seyfulina & Tschernyshev, 2001], with the Linyphiidae and Lycosidae predominating [Duffey, 1956; Gibson *et al.*, 1992; Downie *et al.*, 2000]. Some 20 spider species are widespread and common for all the European agrocoenoses and are therefore referred to as agrobionts [Łuczak, 1979; etc.]. It is known that the same sampling methods yield a smaller number of spider species from larger agricultural fields [Basedov, 1998].

In addition to the cropland (i.e., the area covered by the crops), each agroecosystem includes field margins, with which it is closely connected; the latter are comparatively narrow strips bordering the agricultural field and are covered with wild, grassy vegetation [Tschernyshev, 2001]. Therefore, three essential zones of an agroecosystem can be identified: (1) field centre (= central zone), i.e., the main sown area; (2) field edge (= edge zone, or edge), i.e., a relatively narrow marginal strip of the cropland (here defined as the 10 m wide edge, see below under 'Material and methods'); and (3) field margin, i.e., an unploughed narrow (several metres), strip of grassy vegetation encircling the field (beyond doubt, this zone is an ecotone [*sensu* Łuczak, 1979; etc.] between the agricultural field and the adjacent natural habitats). It has repeatedly been demonstrated that spider species diversity and richness is higher in the sown area when the field margins are marked [Alderweireldt, 1989a; Bayram & Luff, 1993; Toth & Kiss, 1999; etc.]. Yet, both parameters are significantly higher in the field margin than in the cropland. However, in most cases an increase in spider abundance at the field edges did not result in an increase in abundance for the rest of the field [Alderweireldt, 1989a; Dennis & Fry, 1992; Kromp & Steinberger, 1992; Samu *et al.*, 1999].

The adjacent natural habitats influence the araneofauna of a crop, though the composition of dominant groups (herpetobionts[1] at least) seems to be unaffected [Zhukovets, 1990; etc.]. When the agro- and adjacent natural coenoses represent contrasting habitats (e.g., with a neighbouring forest), the overlap of their faunas is low and makes up several [Łuczak, 1995; Downie *et al.*, 1996] to tens [Duelli *et al.*, 1990; Bedford & Usher, 1994] of metres both inside and outside the cropland. For instance, 68–85% of predators, including spiders, were recorded within a 10 m field edge [Dennis, 1991]. When the cropland and field margins (or the adjacent natural habitats) are similar physiognomically (e.g., grassy habitats), the spider species richness gradually decreases from the field margin to the field centre [Alderweireldt, 1989a].

The present study deals with the spatial–temporal structure of spider communities of two agroecosystems from two distant regions of the European part of Russia, which differ in climatic conditions, agricultural landscapes and practices. The main question to be answered is how penetrable is the field edge for spiders inhabiting the field margin?

Material and methods

Description of sampling sites

The sampling site in Moscow area (MA) was situated in the centre of the Russian Plain on the north-facing slope of the flood plain of the Klyazma River (55°59′N, 37°24′E). The local agricultural fields are of medium size (10–15 ha) and usually surrounded by mixed forests. Experimental plots

[1] Herpetobiont, i.e., a species living at ground level.

Table 1.

Sample sizes of spiders in agroecosystems of Moscow area and Krasnodar territory.

Таблица 1.

Объем учетов пауков в агроэкосистемах Московской области и Краснодарского края.

Zone	Moscow area					Krasnodar territory			
	Sweeping			Pitfall trapping		Sweeping		Pitfall trapping	
	1994	1995	1996	1998	1999	1999	2000	1999	2000
	Number of sweeps and trap/days								
H		no sampling		1 125	400	2 200	1 800	550	750
M	10 350	8 075	3 520	1 500	1 600	2 200	1 800	550	750
E	10 350	8 075	3 740	1 500	1 600	2 200	1 800	550	750
C1		no sampling				2 200	1 800	550	750
C2	2 300	1 900	1 650	750	400	2 200	1 800	550	750
T	23 000	18 050	10 560	4 875	4 000	11 000	9 000	2 750	3 750
	Number of sampled individuals								
H		no data		1 884	664	902	624	947	855
M	1 293	1 165	951	2 527	1 557	664	595	799	944
E	50	372	326	1 550	1 692	275	145	665	272
C1			no data			88	60	714	282
C2	20	55	125	1 018	433	87	45	536	419
T	1 363	1 592	1 402	6 979	4 346	2 016	1 469	3 661	2 772

Abbreviations for agroecosystem zones: C1 — field centre, 200 m away from field border (Krasnodar territory); C2 — ditto, 100–150 m away from field border in Moscow area and 400 m away in Krasnodar territory; E — field edge; H — adjacent natural habitat; M — field margin; T — total estimate for all zones.

Сокращения для зон агроэкосистемы: C1 — центр поля, 200 м от края (только для Краснодарского края); C2 — центр поля, 100–150 м от края (Московская обл.), 400 м от края (Краснодарский край); E — край поля; H — примыкающий биотоп; M — обочина поля; T — суммарно по всем зонам.

were set up in corn (1994), vetch-oat (1995) and winter wheat (1996, 1998, 1999) crops.

The second site was situated in Krasnodar territory (KT), the western part of Ciscaucasia, in the south of the Kuban Plain (45°03′N, 39°18′E). It belongs to the black earth steppe zone, which nowadays is mostly utilized as croplands. Large local fields (up to 100 ha) are separated by forest shelterbelts. Experimental plots were set up in winter wheat crops in 1999 and 2000.

Sampling

Sweeping with an entomological net and pitfall trapping were adopted as the main sampling methods. In total 70 000 sweeps were made, the overall time of trap exposure exceeded 15 000 trap-days (Table 1). Over 25 000 spider specimens were collected. Sweeping was used in 1994–1996 (MA) and 1999–2000 (KT), pitfall trapping in 1998–1999 (MA) and in 1999–2000 (KT).

Sweeping was initiated in young crops and continued until harvest (KT, April–June; MA, May–August) every six, eight and ten days in 1994–1995, 1996 and 1999–2000, respectively. On every sampling date, 71 plots were sampled either with ten single sweeps (in 1996), or with four consecutive series of 25 sweeps on 9–11 distant plots (in the remaining years) (Fig. 1). Pitfall trapping was done every ten days from thawing until the first snow falls (April–October, MA) or from early spring until harvest (March–June, KT). A series of five pitfall traps were set up in each of nine to ten plots and exposed for five days (Fig. 1).

Samples were taken from the field edges, the field centre and the field margins (usually grassy), and during 1998–2000 also from strips of the adjacent natural habitats. The field edge was defined as a 10 m marginal zone of the cropland, neighbouring the field margins. In MA, the field centre was located at 100–150 m from the field border, whereas in KT, it was subdivided into two sub-zones at distances of 200 and 400 m from the field border. The mixed forest (MA in 1998), an oak grove (MA in 1999) and forest shelterbelts (KT) were considered the adjacent natural habitats used for sampling.

It should be noted that the adopted sampling strategy does not provide absolute estimates of arthropod abundance. Sweeping yields data on relative abundance in prototype systems [see Chernov & Rudenskaya, 1970], whereas pitfall trapping estimates only a dynamic population density related rather more to arthropod activity than to their abundance [see Gilyarov, 1987; Topping & Sunderland, 1992]. Both methods are considered informative in comparative studies. Hereinafter, the terms 'spider abundance' and 'spider richness' are applied to the parameters estimated by the adopted sampling methods.

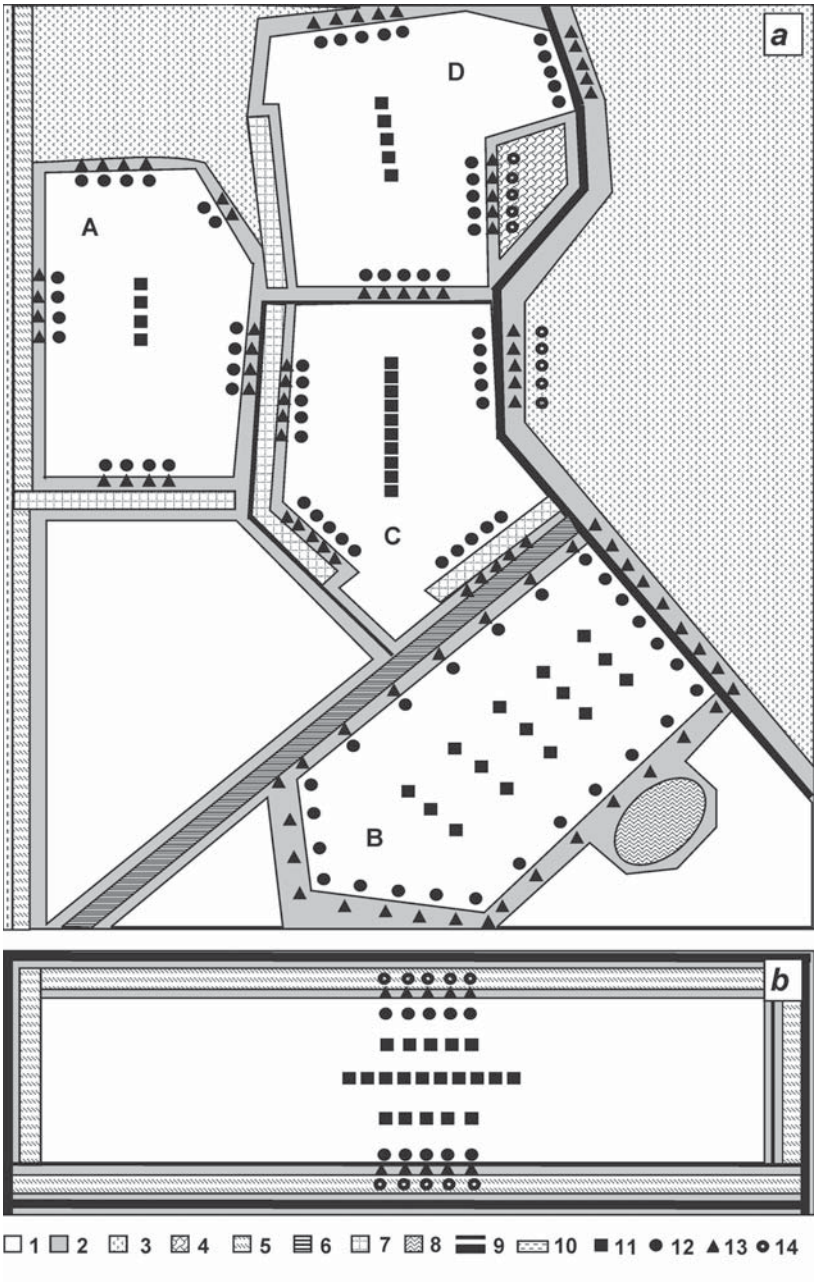

Fig. 1. Sampling plots of study sites in Moscow Area (*a*) and Krasnodar Territory (*b*): A — maize (1994) and vetch-oat fields (1995); B — winter wheat field (1996); C — the same (1998); D — the same (1999), (1 — agricultural fields; 2 — unploughed grassy strips; 3 — mixed forest; 4 — oak grove; 5 — forest shelterbelts; 6 — lime alley; 7 — ditches; 8 — pond; 9 — roads; 10 — highway; 11 — sampling plots, field centre; 12 — the same, field edge; 13 — the same, field margin; 14 — the same, adjacent natural habitats).

Рис.1. Схема расположения учетных площадок на опытных полях в Московской области (*а*) и Краснодарском крае (*б*): А — поле кукурузы (1994 г.) и вико-овсяной смеси (1995 г.); В — поле озимой пшеницы (1996 г.); С — то же (1998 г.); D — то же (1999 г.), (1 — сельскохозяйственные поля; 2 — травяные участки; 3 — смешанный лес; 4 — дубовая роща; 5 — лесополосы; 6 — липовая аллея; 7 — канавы; 8 — пруд; 9 — дороги; 10 — шоссе; 11 — учетные площадки, центр поля; 12 — то же, край поля; 13 — то же, обочина поля; 14 — то же, примыкающие естественные биотопы).

Table 2.

Spider species diversity in agroecosystems of Moscow area and Krasnodar territory.

Таблица 2.

Таксономическое разнообразие пауков в разных зонах агроэкосистем Московской области и Краснодарского края.

Family	Number of species												
	Moscow area						Krasnodar territory						
	Agroecosystem zone				Total		Agroecosystem zone					Total	
	H	M	E	C1	Abs.	%	H	M	E	C2	C3	Abs.	%
Agelenidae	0	0	0	0	0	0	2	2	1	1	0	3	2.2
Anyphaenidae	0	1	0	0	1	0.5	0	0	0	0	0	0	0
Araneidae	0	14	5	6	14	6.8	7	6	6	3	4	8	5.8
Clubionidae	3	8	2	1	10	4.9	5	2	3	0	1	5	3.6
Dictynidae	0	1	2	1	2	1.0	6	2	2	1	1	7	5.0
Dysderidae	0	0	0	0	0	0	1	1	1	0	0	1	0.7
Gnaphosidae	4	6	4	2	7	3.4	7	8	8	6	6	14	10.1
Hahniidae	1	3	1	1	3	1.5	0	0	0	0	0	0	0
Linyphiidae	54	76	38	24	100	48.8	19	22	16	11	8	33	23.7
Liocranidae	1	1	1	1	1	0.5	3	4	4	3	2	4	2.9
Lycosidae	13	13	15	11	16	7.8	7	8	10	9	8	12	8.6
Mimetidae	1	1	0	0	1	0.5	0	1	0	0	0	1	0.7
Oxyopidae	0	0	0	0	0	0	1	0	1	0	1	1	0.7
Philodromidae	0	4	1	3	4	2.0	3	3	5	2	2	5	3.6
Pisauridae	0	1	1	1	1	0.5	1	2	1	1	1	2	1.4
Salticidae	0	10	0	0	10	4.9	10	7	6	2	2	14	10.1
Tetragnathidae	3	8	7	6	8	3.9	3	3	2	2	1	3	2.2
Theridiidae	3	11	8	5	13	6.3	4	3	3	3	2	9	6.5
Thomisidae	4	10	7	6	12	5.8	9	9	11	4	3	15	10.8
Zoridae	1	2	0	0	2	1.0	2	1	0	0	0	2	1.4
All families:	88	170	92	68	205	100	90	84	80	48	42	139	100
including sweeping	–	109	48	32	113	55.1	49	44	40	17	13	74	53.2
including pitfall traps	73	99	64	50	135	65.7	55	53	46	34	31	100	72.0
Total number:						286*							
including sweeping						159							
including pitfall traps						198							

Abbreviations: C1 — field centre, 100–150 m away from field border; C2 — ditto, 200 m away from field border; C3 — ditto, 400 m away from field border; E, H, M — as explained in Table 1.

* = 57 species were reported for both regions.

Сокращения: C1 — центр поля, 100–150 м от края; C2 — центр поля, 200 м от края; C3 — центр поля, 400 м от края; E, H, M — как в таблице 1.

* = 57 из них отмечены в обоих регионах.

Data analysis

A spider species (or a family) was considered dominant if it represented more than 5% of the total. In order to assess species diversity the following indices were used [see Magurran, 1992]: the Margalef index was calculated to express species richness, the Shannon index was calculated to express species richness and uniformity of species abundance, the Berger-Parker index was calculated for the level of species dominance and the reciprocal of the Berger-Parker index, as it is proportional to the increase of diversity. Differences for the independent parameters (i.e., differences from sampling in different plots on the same date) were tested using the Wilcoxon matched pair test; differences for the dependent parameters (i.e., differences from sampling in the same plots at different times) were tested using the Mann-Whitney *U* test; Shannon indices were compared using a *t*-test.

Dominance structure and species diversity were estimated separately for each geographical location and sampling method, with specimen numbers pooled over a season for an agroecosystem zone. Statistical data analysis was performed with MS STATISTICA 5.5, biodiversity statistics were computed with BIODIV 4.1, MS EXCEL 9.0 was used for graphical representation of the data.

Table 3.
Statistical indices of spider species diversity in agroecosystems of Moscow area and Krasnodar territory (abbreviations for agroecosystem zones as in Table 1).

Таблица 3.
Статистические индексы видового разнообразия пауков в агроэкосистемах Московской области и Краснодарского края (Сокращения для зон агроэкосистемы как в таблице 1).

Index	Zone	Mean								
		Moscow area					Krasnodar territory			
		Sweeping			Pitfall trapping		Sweeping		Pitfall trapping	
		1994	1995	1996	1998	1999	1999	2000	1999	2000
Margalef, Dmg	H	no data	8.07	5.823	6.448	5.508	6.166	4.635		
	M	8.579	8.773	12.257	10.753	10.692	5.673	4.379	6.121	5.639
	E	3.822	5.565	4.636	6.51	7.999	7.187	3.975	5.514	4.868
	C1		no data				1.517	2.588	3.415	3.862
	C2	3.474	2.94	4.708	5.439	5.035	1.535	1.971	2.813	3.299
	T	8.949	9.397	12.564	13.306	11.974	9.074	7.09	8.624	7.88
Shannon, H'	H		no data		2.806	1.904	2.5	1.883	1.764	2.194
	M	3.27	3.205	3.527	3.225	3.175	2.581	1.388	2.217	2.365
	E	2.407	2.791	2.563	2.783	2.54	3.135	2.158	2.026	2.347
	C1			no data			1.252	1.819	0.968	1.605
	C2	2.164	2.054	2.571	2.373	2.487	1.044	1.583	0.821	1.584
	T	3.325	3.292	3.439	3.252	3.169	2.935	2.047	2.169	2.619
Berger-Parker, d	H		no data		0.212	0.566	0.292	0.586	0.607	0.314
	M	0.112	0.141	0.124	0.156	0.168	0.259	0.717	0.47	0.229
	E	0.2	0.1664	0.243	0.215	0.266	0.169	0.393	0.347	0.397
	C1			no data			0.593	0.364	0.795	0.487
	C2	0.2	0.3	0.27	0.312	0.235	0.692	0.381	0.834	0.479
	T	0.107	0.109	0.16	0.15	0.145	0.217	0.578	0.363	0.182
Reciprocal of the Berger-Parker index, 1–d	H		no data		0.788	0.434	0.708	0.414	0.393	0.686
	M	0.888	0.859	0.876	0.844	0.832	0.741	0.283	0.53	0.771
	E	0.8	0.8336	0.757	0.785	0.734	0.831	0.607	0.653	0.603
	C1			no data			0.407	0.636	0.205	0.513
	C2	0.8	0.7	0.73	0.688	0.765	0.308	0.619	0.166	0.521
	T	0.893	0.891	0.84	0.85	0.855	0.783	0.422	0.637	0.818

Results

Species diversity

In total, 286 spider species in 146 genera and 20 families were recorded during the study (for a complete list of species see Seyfulina [2004]). Of the 205 species (106 genera and 17 families) encountered in MA, 186 were found in the agroecosystems and 120 of these were confined to the croplands. Of the 139 species (92 genera and 18 families) recorded from KT, 120 were found in the agroecosystems and 91 were restricted to the croplands. Both the total species diversity and that of most families decreased from the field margins toward the field centre (Table 2). In MA there was a significantly higher diversity in the field margins, which was at least as high as that of the adjacent natural habitats, when compared to the cropland (Table 3). In KT, however, no significant differences in species diversity of forest shelterbelts, the field margins and the field edges were found (Table 3). Individual-based rarefaction curves demonstrated that in MA the diversity in the field margins was comparable to that of the mixed forest (Fig. 2a–d), whereas in KT the diversity of the field edges exceeded those of other plots (Fig. 2e–h). The spider species diversity of field edges was found to be virtually equal to that of all adjacent habitats, apart from the mixed forest. In both sampling sites the field centres showed the lowest species diversity, though there were no statistically significant differences between the 200 and 400 m sub-zones of the field centres of large agricultural fields (Table 3; Fig. 2e–h).

Dominance structure

Although family composition of the spider communities changed from the field margins and adjacent habitats toward the field centre (Figs 3, 4), there was a constant, characteristic

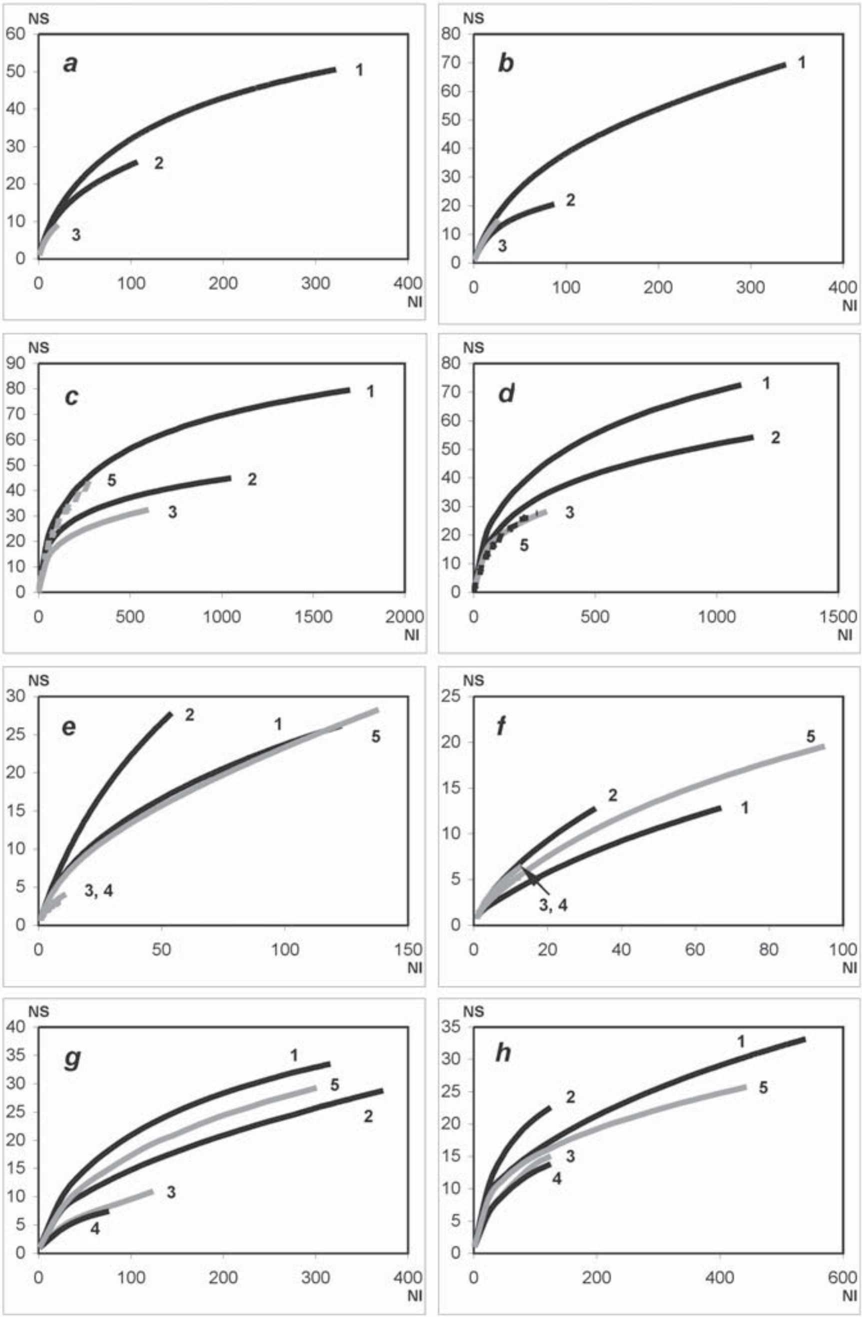

Fig. 2. Individual-based rarefaction curves for agroecosystems of Moscow area (a–d) and Krasnodar territory (e–h): a, b, e, f — sweeping data; c, d, g, h — pitfall trap data; a — 1995; b — 1996; c — 1998; d, e, g — 1999; f, h — 2000; [1 — field margin, 2 — field edge, 3 — field centre, 150–200 m, 4 — field centre, 400 m, 5 — mixed forest (1998), oak grove (1999, MA), forest shelterbelt (1999–2000, KT)].

Рис. 2. Влияние размера выборки на показатели разнообразия в агроэкосистемах Московской области (a–d) и Краснодарского края (e–h): a, b, e, f — по данным кошения; c, d, g, h — по данным почвенных ловушек; a — 1995 г.; b — 1996 г.; c — 1998 г.; d, e, g — 1999 г.; f, h — 2000 г.; [1 — обочина, 2 — край поля, 3 — центр поля, 150–200 м, 4 — центр поля, 400 м, 5 — смешанный лес (1998 г.), дубовая роща (1999 г., МО), лесополоса (1999–2000 гг., КК)].

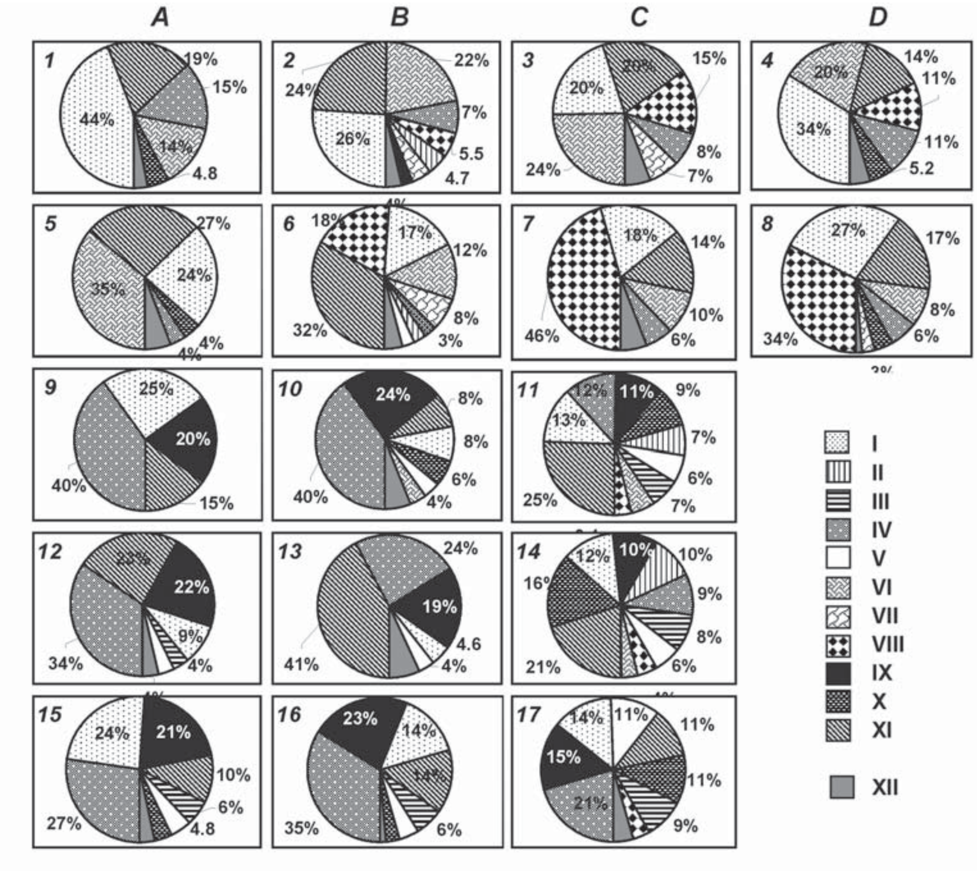

Fig. 3. The ratio between spider families in relative abundance in agroecosystems of Krasnodar territory (1–8) and Moscow area (9–17): A — field centre; B — field edge; C — field margin; D — forest shelterbelt; 1–4 — 1999; 5–8 — 2000; 9–11 — 1994; 12–14 — 1995; 15–16 — 1996; (I — Araneidae, II — Clubionidae, III — Dictynidae, IV — Linyphiidae, V — Lycosidae, VI — Philodromidae, VII — Pisauridae, VIII — Salticidae, IX — Tetragnathidae, X — Theridiidae, XI — Thomisidae, XII — other families).

Рис. 3. Соотношения семейств пауков по относительному обилию в агроэкосистемах Краснодарского края (1–8) и Московской области (9–17): A — центр поля; B — край поля; C — обочина поля; D — лесополоса; 1–4 — 1999 г.; 5–8 — 2000 г.; 9–11 — 1994 г.; 12–14 — 1995 г.; 15–16 — 1996 г.; (I — Araneidae, II — Clubionidae, III — Dictynidae, IV — Linyphiidae, V — Lycosidae, VI — Philodromidae, VII — Pisauridae, VIII — Salticidae, IX — Tetragnathidae, X — Theridiidae, XI — Thomisidae, XII — остальные).

nucleus for each community in each particular zonal agroecosystem, regardless of the season. In MA the herb-layer spider community of the cropland was characterized by higher proportions of Linyphiidae and Tetragnathidae (sometimes also Thomisidae and Araneidae, depending on crop type) compared to the field margins (Fig. 3: *9–17*). In KT these communities were predominantly of the families Philodromidae, Thomisidae and Araneidae (Fig. 3: *1–8*), the proportions of which were clearly higher in the cropland than in the field margins; in contrast, the Salticidae demonstrated the opposite tendency and were more diverse in the field margins. In the croplands of MA the herpetobiont fauna was predominantly Linyphiidae, Lycosidae and Tetragnathidae (Fig. 4: *1–8*), whereas that in KT was dominated by Lycosidae only (especially in the field centre) (Fig. 4: *9–16*).

Of the recorded spider species (only adults were counted), 35 species made up 12% of the total species number and over 80% of the number of individuals. These species were considered dominant (Table 4). Of these, 14 species were dominant in the field margins, eight in the croplands, and 13 were dominant both in the

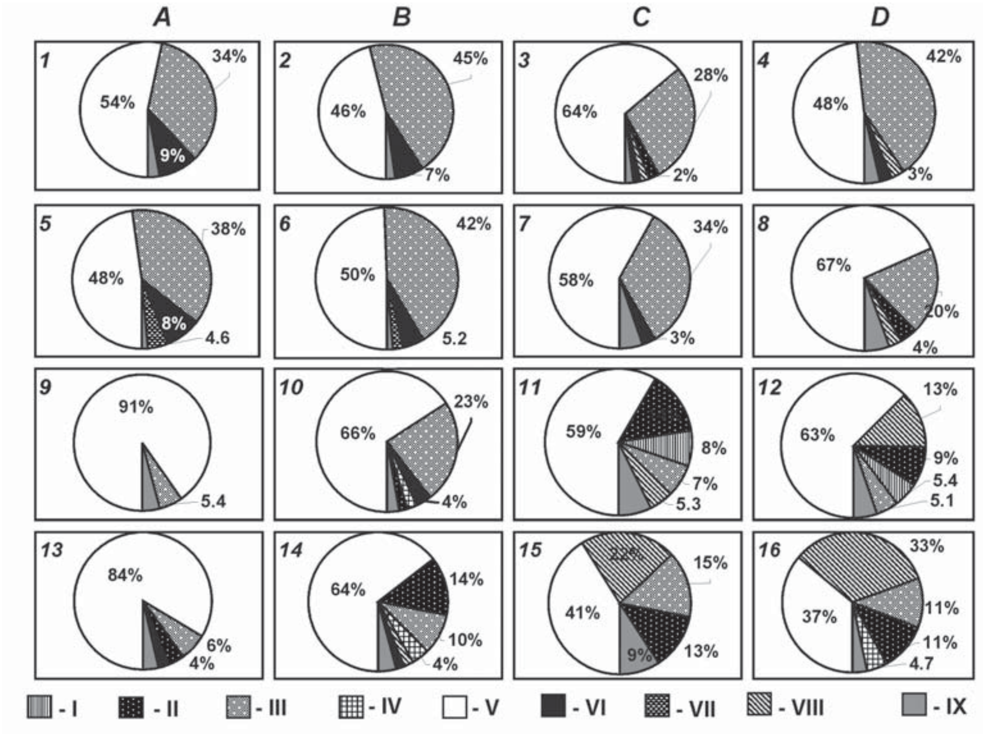

Fig. 4. The ratio between spider families in dynamic density in agroecosystems of Krasnodar territory (1–8) and Moscow area (9–16): A — field centre; B — field edge; C — margin; D — mixed forest (1998), oak grove (MA, 1999), shelterbelt (KT, 1999–2000); 1–4 — 1998; 5–12 — 1999; 13–16 — 2000; (I — Agelenidae, II — Gnaphosidae, III — Linyphiidae, IV — Liocranidae, V — Lycosidae, VI — Tetragnathidae, VII — Theridiidae, VIII — Thomisidae, IX — other families).

Рис. 4. Соотношения семейств пауков по динамической плотности в агроэкосистемах Московской области (1–8) и Краснодарского края (9–16): A — центр поля; B — край поля; C — обочина; D — смешанный лес (1998 г.), дубовая роща (МО, 1999 г.), лесополоса (КК, 1999–2000 гг.); 1–4 — 1998 г.; 5–12 — 1999г.; 13–16 — 2000 г.; (I — Agelenidae, II — Gnaphosidae, III — Linyphiidae, IV — Liocranidae, V — Lycosidae, VI — Tetragnathidae, VII — Theridiidae, VIII — Thomisidae, IX — остальные).

croplands and outside them. Except for *Trochosa robusta*, the group of dominant herpetobiont species of KT fields (i.e., *Pardosa agrestis, P. lugubris* and *Oedothorax apicatus*) were also prevalent in MA agroecosystems, with *P. agrestis* and *O. apicatus* in the croplands and *P. lugubris* in the field margins. With regards to hortobiont spiders, half of the field margin dominants and one-seventh of the species predominant in the field centre were characteristic for only one of the sampling sites. The remaining hortobionts were encountered both in KT and in MA.

Microlinyphia pusilla, *Tetragnatha extensa* and *Xysticus ulmi* were dominant in the herbage throughout the whole of the vetch-oat and winter wheat fields (MA in 1995–1996). *Misumena vatia* and *Dictyna arundinacea* predominated in the field edges of the vetch-oat and the winter wheat crops respectively. Thus, the set of dominant species was not dependent on the crop type[2] (for more details see Seyfulina & Tschernyshev [2001]).

Most of the dominant species of the field margins were either not recorded from the field centre, or encountered only occasionally[3], but all of them were recorded from the field edges. On the other hand, the species dominating the field centre were also abundant (but not nec-

[2] In 1994, during the entire season, samplings were also carried out in the maize fields (with low and sparse sprouts), but the catch of spiders was so little that it was not possible to estimate a dominance structure.

[3] Eight of the 27 dominant species were not recorded there and single or a few individuals of a further eight were encountered (Table 4).

Table 4.
Dominant spiders in agroecosystems of Moscow area and Krasnodar territory.

Таблица 4.
Пауки, доминирующие в агроэкосистемах Московской области и Краснодарского края.

No.	Taxon	Region		Agroecosystem zone				Habitat
		MA	KT	H	M	E	C	
	ARANEIDAE							
1	*Hypsosinga pygmaea* (Sundevall, 1831)	+	++	+	+	++	++	h
2	*Mangora acalypha* (Walckenaer, 1802)	–	++	++	++	+	+	h
3	*Singa nitidula* C. L. Koch, 1844	++	+	no data	++	+	+	h
	DICTYNIDAE							
4	*Dictyna arundinacea* (Linnaeus, 1758)	++	+	no data	++	(++)	+	h
	GNAPHOSIDAE							
5	*Zelotes subterraneus* (C.L. Koch, 1833)	–	++	++	++	+	–	g
	LINYPHIIDAE							
6	*Agyneta rurestris* (C.L. Koch, 1836)	+	++	(++)	(++)	(++)	(++)	h
7	*Araeoncus humilis* (Blackwall, 1841)	++	–	+	+	(++)	+	g
8	*Bathyphantes parvulus* (Westring, 1851)	++	–	++	(++)	+	–	g
9	*Centromerita bicolor* (Blackwall, 1833)	++	–	+	(++)	(++)	+	g
10	*Ceratinella brevis* (Wider, 1834)	+	++	(++)	(++)	+	–	g
11	*Diplostyla concolor* (Wider, 1834)	++	+	+	(++)	+	+	g
12	*Erigone dentipalpis* (Wider, 1834)	++	+	–	+	(++)	+	g
13	*Erigonidium graminicola* (Sundevall, 1830)	++	–	no data	(++)	+	–	h
14	*Microlinyphia pusilla* (Sundevall, 1830)	++	+	no data	+	++	++	h
15	*Oedothorax apicatus* (Blackwall, 1850)	++	++	+	(++)	++	++	g
	LYCOSIDAE							
16	*Pardosa agrestis* (Westring, 1861)	++	++	+	+	++	++	g
17	*P. fulvipes* (Collett, 1875)	++	–	+	++	+	+	g
18	*P. lugubris* (Walckenaer, 1802)	++	++	++	++	[++]	+	g
19	*P. paludicola* (Clerck, 1758)	++	+	+	(++)	+	+	g
20	*P. palustris* (Linnaeus, 1758)	++	–	+	(++)	++	++	g
21	*P. pullata* (Clerck, 1758)	++	–	+	(++)	(++)	+	g
22	*Pirata hygrophilus* Thorell, 1872	++	–	++	(++)	+	+	g
23	*Trochosa robusta* (Simon, 1876)	–	++	+	(++)	(++)	(++)	g
24	*T. terricola* Thorell, 1856	++	++	++	[++]	+	+	g
	PHILODROMIDAE							
25	*Tibellus oblongus* (Walckenaer, 1802)	+	++	+	+	+	++	h
	PISAURIDAE							
26	*Pisaura mirabilis* (Clerck, 1758)	–	++	+	(++)	+	–	h
	SALTICIDAE							
27	*Heliophanus cupreus* (Walckenaer, 1802)	–	++	++	++	++	–	h
	TETRAGNATHIDAE							
28	*Pachygnatha degeeri* Sundevall, 1830	++	+	+	+	(++)	++	g
29	*Tetragnatha extensa* (Linnaeus, 1758)	++	–	no data	++	++	++	h
	THERIDIIDAE							
30	*Enoplognatha ovata* (Clerck, 1758)	++	+	no data	++	+	–	h
	THOMISIDAE							
31	*Misumena vatia* (Clerck, 1758)	++	+	no data	(++)	(++)	+	h
32	*Misumenops tricuspidatus* (Fabricius, 1775)	–	++	(++)	(++)	(++)	+	h
33	*Ozyptila praticola* (C.L. Koch, 1837)	+	++	++	++	+	–	g
34	*Xysticus kochi* Thorell, 1872	+	++	+	+	++	(++)	h
35	*X. ulmi* (Hahn, 1831)	++	+	no data	++	++	++	h

Abbreviations: C — field centre; E, H, M — the same as in Table 1; g — herpetobionts; h — hortobionts; KT — Krasnodar territory; MA — Moscow area; «+» — species recorded; «++» — dominant species; «–» — species not recorded; «(++)» — dominant species during one season; «[++]» — dominant species in Krasnodar territory only.

Сокращения: C — центр поля; E, H, M — как в табл. 1; g — герпетобионтный; h — хортобионтный; KT — Краснодарский край; MA — Московская область; «+» — вид отмечен; «++» — вид доминирует; «–» — вид не отмечен; «(++)» — вид доминировал только в течение одного сезона; «[++]» — вид доминировал только в Краснодарском крае.

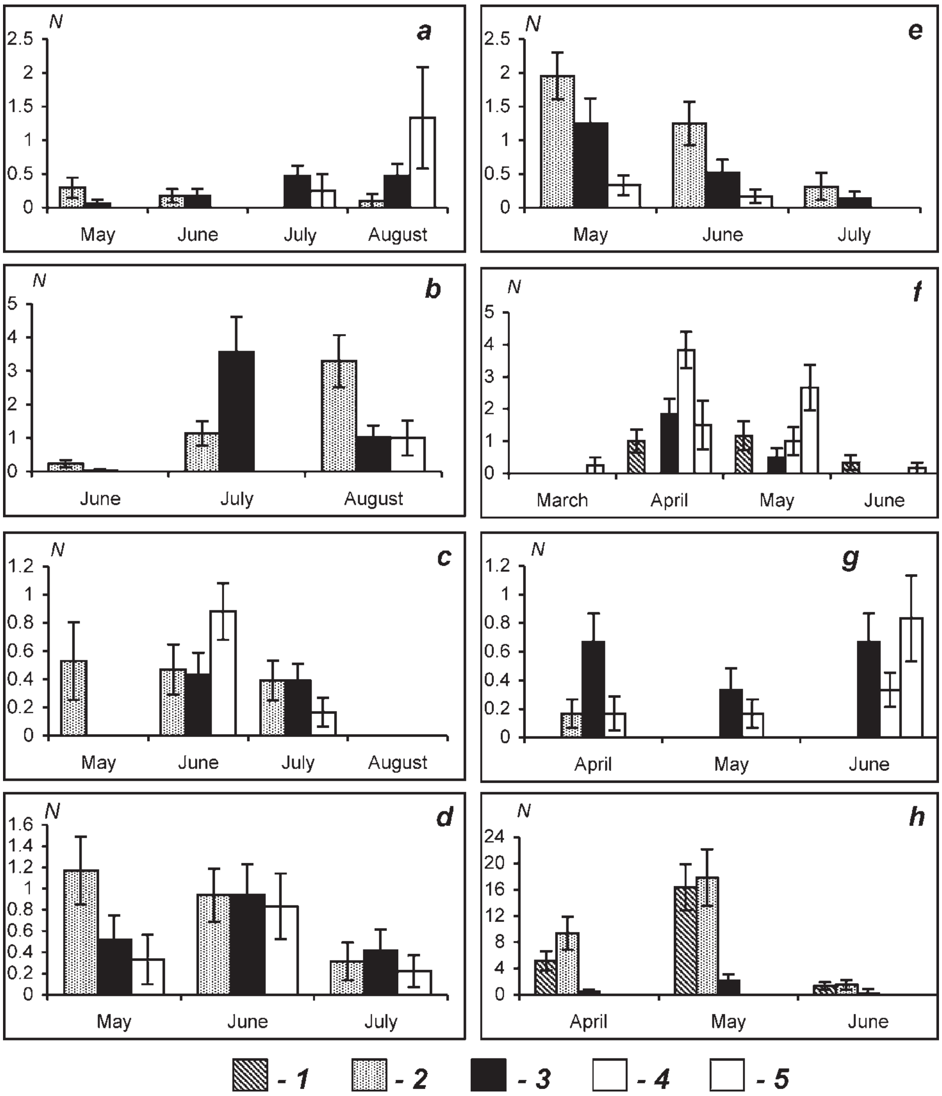

Fig. 5. Relative abundance of dominant spider species in agroecosystems of Moscow area (a–e) and Krasnodar territory (f–h): a — *Microlinyphia pusilla*, 1995; b — *Misumena vatia*, 1995; c, d — *Tetragnatha extensa*, 1995 (c), 1996 (d); e — *Xysticus ulmi*, 1996; f — *Hypsosinga pygmaea*, 1999; g — *X. kochi*, 2000; h — *Heliophanus cupreus*, 2000; [1 — forest shelterbelt; 2 — field margin; 3 — field edge; 4 — field centre, 150 m (MA) and 400 m (KT), 5 — field centre, 200 m; N — number of individuals per 100 sweeps, mean ± SE].

Рис. 5. Относительная численность пауков, доминирующих в агроэкосистемах Московской области (a–e) и Краснодарского края (f–h): a — *Microlinyphia pusilla*, 1995 г.; b — *Misumena vatia*, 1995 г.; c, d — *Tetragnatha extensa*, 1995 г. (c), 1996 (d); e — *Xysticus ulmi*, 1996 г.; f — *Hypsosinga pygmaea*, 1999 г.; g — *X. kochi*, 2000 г.; h — *Heliophanus cupreus*, 2000 г.; [1— лесополоса; 2 — обочина; 3 — край; 4 — центр, 150 м от края (МО), 400 м (КК), 5— центр, 200 м от края; N — число экземпляров на 100 взмахов, $\bar{x} \pm x$].

essarily dominant) in the field margins. All the dominants of the field centre were also dominant in the field edges, while the dominants of the latter zone were not always dominant (or even abundant) in the field centre. The 200 and 400 m sub-zones, shared the same dominant spider species. With the exception of singletons (23 species altogether), all the spider species occurring in the croplands were also recorded from outside them.

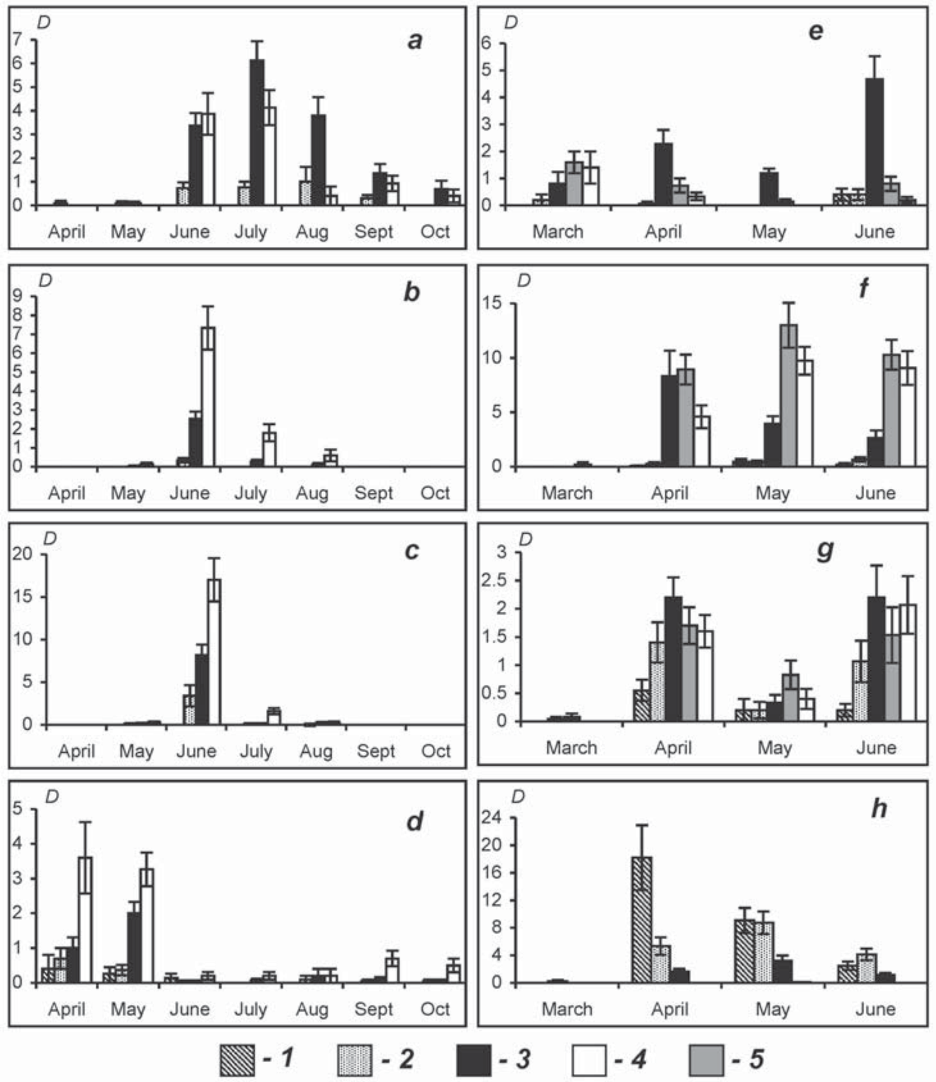

Fig. 6. Dynamic density of dominant spider species in agroecosystems of Moscow area (a–d) and Krasnodar territory (e–h): a, e — *Oedothorax apicatus*, 1999; b, f — *Pardosa agrestis*, 1998 (b), 1999 (f); c — *P. palustris*, 1998; d — *Pachygnatha degeeri*, 1998; g — *Trochosa robusta*, 2000; h — *Pardosa lugubris*, 1999; [1 — mixed forest (MA) and forest shelterbelts (KT); 2–5 same as in Fig. 1; D — number of individuals per 10 trap/days, mean ± SE].

Рис. 6. Динамическая плотность пауков, доминирующих в агроэкосистемах Московской области (a–d) и Краснодарского края (e–h): a, e — *Oedothorax apicatus*, 1999 г.; b, f– *Pardosa agrestis*, 1998 г. (b), 1999 г. (f); c — *P. palustris*, 1998 г.; d — *Pachygnatha degeeri*, 1998 г.; g — *Trochosa robusta*, 2000 г.; h — *Pardosa lugubris*, 1999 г.;[1— смешанный лес (МО) или лесополосы (КК), 2–5 — как в рис. 1; D — число экземпляров на 10 ловушко-суток, $x \pm \overline{x}$].

Spatial distribution and seasonal dynamics

According to the data, the dominant species had four patterns of spatial distribution in these agroecosystems, though for some species dissimilar patterns were observed in different crops.

(1) Spiders preferring the croplands(throughout the entire vegetation period or its significant part) (ten species). For instance, in the second half of the vegetation season, the hortobiont *Microlinyphia pusilla* was confined to the vetch-oat cropland and was not recorded in its field margins (Table 4; Fig. 5a). In the middle of the

season, *Misumena vatia* preferred the field edges of the vetch-oat crops (Table 4; Fig. 5b). The hortobionts *Hypsosinga pygmaea* and *Xysticus kochi* clearly preferred the winter wheat cropland rather than its field margins and neighbouring forest shelterbelts (Table 4; Fig. 5f,g). Their abundance in the field centre was clearly higher in the middle (*H. pygmaea*) or at the end (*X. kochi*) of the vegetation season.

Although the herpetobiont *Oedothorax apicatus* was evenly distributed over the wheat crops at the beginning of the vegetation season, it clearly demonstrated a shift towards the field edges as the crop vegetation grew (Table 4; Fig. 6a,e). This tendency was especially well pronounced in the large agricultural fields of KT. In contrast, *Pardosa agrestis*, *P. palustris* and *Pachygnatha degeeri* preferred the field centre over the field edges and margins throughout the majority of the vegetation season (Table 4; Fig. 6b–d,f). The herpetobiont linyphiids, *Araeoncus humilis* and *Erigone dentipalpis*, were also more abundant in the croplands than in the field margins (Table 4). Most of the herpetobiont species showing the same pattern belong with the agrobionts common to the temperate zone of Europe.

(2) Spiders having no clear preference (i.e., abundant throughout an agroecosystem and occurring in the field centre, margins and edges) (three species). This pattern was typical of the hortobionts *Tetragnatha extensa* and *Tibellus oblongus*, and the herpetobiont *Trochosa robusta*. *Tetragnatha extensa* was most abundant in the field margins at the beginning of the vegetation season, but later on was more or less evenly spread throughout the entire cropland (Fig. 5c,d). This species was reported by Łuczak [1995] as preferring the field margins and also as being fairly abundant in croplands. The spatial distribution of *T. robusta* did not vary significantly during the season (Fig. 6g), though there were significant fluctuations of activity, perhaps due to the complex population age structure resulting from their biennial life cycle.

(3) Spiders preferring the field margins (i.e., were less abundant towards the field centre) (seven species). This pattern was typical of winter wheat populations of the hortobionts *Microlinyphia pusilla*, *Agyneta rurestris*, *Dictyna arundinacea*, *Misumenops tricuspidatus* and *Xysticus ulmi* (Fig. 5e) and of the herpetobiont *Pardosa pullata* (Table 4).

(4) Spiders avoiding croplands (i.e., abundant only in the field margins and practically absent from the field centre) (11 species). These are the hortobionts *Mangora acalypha*, *Singa nitidula*, *Pisaura mirabilis*, *Heliophanus cupreus* and *Enoplognatha ovata* and the herpetobionts *Zelotes subterraneus*, *Ceratinella brevis*, *Diplostyla concolor*, *Pardosa fulvipes*, *P. lugubris* and *Ozyptila praticola* (Table 4). However, in KT the jumping spider *H. cupreus* and the wolf spider *P. lugubris* were also relatively abundant in the field edges (Figs 5, 6h), whereas *Heliophanus* spp. and *P. lugubris* were practically absent from crops in MA.

Relative abundance and dynamic population density

The peak activity of dominant herpetobiont spiders was observed in the first half of the vegetation season (Table 5), with two exceptions: *Oedothorax apicatus* which exhibited its peak at the end of the season, and *Trochosa robusta* which had two peaks, one at the beginning and the other at the end of the season. Most hortobiont spiders also had a maximum relative abundance during the early half of the season, whereas the crab-spiders (*Xysticus* spp.[4], *Misumena vatia*, *Misumenops tricuspidatus*) increased in numbers or at least persisted at the same level throughout the entire season (Table 6). At the beginning of the vegetation season, the relative abundance of hortobiont spiders was already high on the winter wheat crops, while it was lowest on the spring crops (maize, vetch-oat) (Fig. 5a–c).

Spider abundance characteristics (i.e., average number/dynamic density averaged over a season and maximum numbers/dynamic density) of the majority of dominant species varied from year to year (Tables 5, 6). Highly significant differences were observed when the agricultural fields of different crops were compared (Table 6). For instance, the spider abundance in the maize croplands[5] (MA in 1994) was ten

[4] MA: *Xysticus ulmi* + juvenile *Xysticus* spp., KT: *X. kochi* + juvenile *Xysticus* spp.

[5] In the climate of MA the maize crops do not form thick vegetation.

Table 5.
Dynamic density of epigeic spiders in croplands of Moscow area and Krasnodar territory.
Таблица 5.
Показатели динамической плотности пауков на полях Московской области и Краснодарского края.

Taxon	Date	D_{max}	D_{av}
Araeoncus humilis	28.04.1998	2.27±0.88	0.57±0.08
	15.06.1999	2.16±0.52	0.23±0.04
Erigone dentipalpis	28.04.1998	2.93±0.78	0.37±0.07
	15.06.1999	1.04±0.32	0.31±0.05
Oedothorax apicatus	27.07.1998	5.33±0.93	1.8±0.13
	15.07.1999 (M)	8.48±1.42	2.26±0.2
	9.06.1999 (K)	3.53±0.83	1.16±0.14
	2000*	–	0.07±0.02
Pardosa agrestis	7.06.1998	6.73±1.11	1.01±0.13
	15.06.1999 (M)	13.12±1.19	2.26±0.23
	20.04.1999 (K)	16.67±1.93	7.03±0.49
	3.05.2000	5.27±0.67	0.93±0.1
P. lugubris	11.05.1999	1.4±0.61	0.6±0.1
	3.05.2000	0.47±0.2	0.12±0.03
P. palustris	17.06.1998	22.93±2.3	2.4±0.32
	15.06.1999	7.92±1.17	1.26±0.16
P. pullata	7.06.1998	1.27±0.35	0.28±0.04
	26.05.1999	2.56±0.64	0.46±0.07
Trochosa robusta	9.06.1999	1.4±0.32	0.67±0.07
	2.06.2000	4.2±0.62	1±0.09
Pachygnatha degeeri	13.05.1998	4.33±0.52	0.73±0.08
	26.05.1999	2.16±0.55	0.52±0.08

Abbreviations: Date — time of maximum activity; D_{max} — number of individuals per 10 trap/days during the time of maximum activity, mean ± SE; D_{av} — number of individuals per 10 trap/days averaged over a season, mean ± SE; K — Krasnodar territory; M — Moscow area; «–» — activity peak not pronounced.

* = The maximum activity of *Oedothorax apicatus* was poorly marked, the mean dynamic density is shown for the entire season.

Сокращения: Дата — дата пика активности; D_{max} — число экземпляров на 10 ловушко-суток в момент пика активности, $\bar{x} \pm x$; D_{av} — число экземпляров на 10 ловушко-суток в среднем за сезон, $\bar{x} \pm x$; К — Краснодарский край; М — Московская область; «–» — пик активности не выражен.

* = Поскольку пик численности *Oedothorax apicatus* был выражен плохо, средняя динамическая плотность показана за весь сезон.

times lower than that in other crops (MA; the vetch-oat in 1995 and the winter wheat in 1996).

Discussion

These data suggest that the spider species diversity in agroecosystems approximates that of adjacent natural habitats, with a marked decrease observed only in the field centre. Evidently, not all spiders that are abundant in the field margins penetrate into the croplands beyond their edges. Herpetobiont spiders inhabiting crops (particularly their field centres) are usually represented by the agrobionts (i.e., those with a clear preference for agrocoenoses), which are widespread in the temperate zone of Europe (*Oedothorax apicatus*, *Erigone dentipalpis*, *Pardosa agrestis*, *Pachygnatha degeeri*). Amongst hortobiont spiders there are no agrobionts. Nevertheless, some of them do tend to occur in European agrocoenoses (*Xysticus ulmi*, *Tibellus oblongus*, *Tetragnatha extensa*, *Microlinyphia pusilla*, *Hypsosinga pygmaea*). The field margins are inhabited both by widespread and by local species, but the composition of dominant species is governed both by adjacent natural habitats and by the flora of the margins themselves. The dominant spider species in the field margins often prevail in the field edges, but a few of them are also dominant in the field centres.

Spider abundance and activity were largely determined by crop quality (e.g., its density) and the surrounding landscape. For instance, the dynamic population density of *Pardosa agrestis* was two times higher in thinned out

Table 6.
Relative abundance of hortobiont spiders in croplands of Moscow area and Krasnodar territory.
Таблица 6.
Показатели относительной численности хортобионтных пауков на полях Московской области и Краснодарского края.

Taxon	**Date**	N_{max}	N_{av}
Hypsosinga pygmaea	15.04.99	1.66± 0.83	0.96±0.14
	28.04.2000	2.67±0.62	0.56±0.13
Dictyna spp.	1994	–	0.01±0.01
	2.08.95	1.33±0.5	0.1±0.03
	19.05. 96	2.04±0.65	0.58±0.11
Agyneta rurestris	15.05.99	1.33±0.39	0.21±0.05
Microlinyphia pusilla	13.07.94	0.35±0.25	0.05±0.02
	2.08.95	1.51±0.51	0.28±0.05
	26.07.96	0.61±0.45	0.2±0.06
Tibellus oblongus	15.04.99	5.5±2.05	0.77±0.21
	28.04.2000	3.83±0.9	0.87±0.15
Heliophanus spp.	15.04.99	1.33±0.62	0.18±0.07
	9.05.2000	1.17±0.56	0.44±0.14
Tetragnatha spp.	1994	–	0.09±0.03
	15.06.95	3.24±1.19	0.65±0.11
	13.06.96	5.51±1.4	1.74±0.21
Misumena vatia	1994	–	0.04±0.02
	17.07.95	5.9±2.43	1.32±0.3
	5.06.96	0.41±0.28	0.2±0.06
Misumenops tricuspidatus	26.05.99	1±0.4	0.47±0.08
	19.04.2000	0.5±0.27	0.13±0.05
Xysticus spp.	1994	–	0.02±0.01
	2.08.95	3.62±0.77	0.34±0.07
	28.05.96	1.63±0.6	0.52±0.1
	12.06.99	3±0.77	0.83±0.13
	29.05.2000	2.17±0.63	0.96±0.13

Abbreviations: Date — time of maximum abundance; N_{max} — number of individuals per 100 sweeps at the time of maximum abundance, mean ± SE; N_{av} — number of individuals per 100 sweeps averaged over a season, mean ± SE; «–» — abundance peak not pronounced.

Сокращения: Date — дата пика численности; N_{max} — число экземпляров на 100 взмахов в момент пика численности, $\bar{x} \pm x$; N_{av} — число экземпляров на 100 взмахов в среднем за сезон, $\bar{x} \pm x$; «–» — пик численности не выражен.

winter wheat fields (in 1999) than in those of normal density (in 1999) (Table 5). In contrast, the meadow dweller *P. palustris* showed an opposite preference (Table 5). In 1996 the abundance of hygrophilous *Tetragnatha* species was higher in the cropland situated near a pond than in the more distant region (see Table 6), e.g., it was two times higher in the area in the immediate proximity of the pond. Particular preferences were observed for almost all dominant spider species.

The proximity of grassy field margins to the cropland is also important. In the absence of obstacles, such as roads, deep ditches etc., some spider species abundant in the field margins (those of the fourth distributional pattern) can penetrate into the field edges. For instance, in agricultural fields of Kuban Plain, which are characterized by uniform, grassy field margins closely bordering both with croplands and with forest shelterbelts, *H. cupreus* and *P. lugubris* (during the peak of their abundance) can be more abundant on the field edges than the species preferring the croplands (the first distributional pattern). It is worth noting that species like *H. cupreus* and *P. lugubris* do not increase the spider population of the rest of the cropland; this fact accords well with data in the existing literature [Alderweireldt, 1989a,b; Kromp & Steinberger, 1992; etc.].

The type of cultivated crop also affected the spatial distribution of some hortobiont spiders. For instance, *Microlinyphia pusilla* preferred croplands of the vetch-oat mixture and in the second half of the season was much more abundant in the cropland than outside it. *Misumena* *vatia* was attracted by the vetch-oat crops during vetch blooming, and it was numerous in the field edges. However, in the wheat crops both species preferred the vegetation of the field margins. No descriptions of similar cases were found in the existing literature, apparently because the attention of specialists studying the araneofauna of agroecosystems is concentrated on complexes of epigeic spiders. Among other arthropods, similar patterns of spatial distribution have been reported for specialized phytophagous insects, like the weevil-beetles *Sitona* or the aphids *Megoura* [Afonina *et al*., in press].

Spiders rapidly colonize winter crops; as a rule, most spiders that occur in the croplands (the first and second distributional patterns) invade the entire field at the beginning of the vegetation season. In the course of time, some species might leave the field centre as the agricultural vegetation ripens. It has been reported, that the dispersal activity of some linyphiid spiders increases as the cereal crop senesces [Weyman *et al*., 1995; Thomas & Jepson, 1999]. Due to later vegetation, the spider colonization of the herbage of spring crops occurred later than in the winter crops. Furthermore, the dynamics of spatial distribution in the spring crops was different, with spiders colonizing the entire field towards the middle/end of the vegetation season.

Thus, it can be concluded that the group of dominant spider species in agrocoenoses is rather constant. However, the abundance and spatial distribution of particular species, as well as their seasonal fluctuations, significantly depend on the type and structure of the crops, the period of their vegetation season and the location of the cropland within the landscape.

Colonization of agricultural fields by spiders occurs by air and by ground [Łuczak, 1979; Alderweireldt, 1989b; etc.]. However, ballooning plays a crucial role, especially as far as migration from distant habitats is concerned [Łuczak, 1979; Greenstone *et al.,* 1987; Alderweireldt, 1989b; Dennis & Fry, 1992]. The absence of a particular species in a biotope is related to the unsuitability of that habitat's conditions rather than a lack of ability of the species to penetrate into it [Samu *et al*., 1999]. This is also the case for agrocoenoses. The changing conditions during the growing and ripening of a crop can favour either colonization or avoidance of the cropland by spiders. For instance, during its blooming stage the vetch crops were attractive to *Misumena vatia*, but conversely *Oedothorax apicatus* moved away from the wheat crop during this stage. The species for which the ecological conditions are unsuitable do not penetrate the cropland further than its edges, regardless of their abundance in the field margins. In this respect, a field zone of less than 100 m wide (down the cropland) can be considered a 'barrier'. In conclusion, species penetrating beyond this barrier (in other words, the cropland's ecological conditions are suitable for them) are capable of colonizing the entire field regardless of its size.

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