Евразиатский энтомол. журнал 2(4): 235–242

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Distribution patterns of ants in different natural zones and landscapes in Kazakhstan and West Siberia along a meridian trend

Характер зонального и ландшафтного распределения муравьев на меридиональном разрезе через Западную Сибирь и Казахстан

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Abstract. Distribution patterns of 70 ant species in the Kazakhstan–West Siberian along a meridian trend from deserts to the southern taiga is described. The arid zone, as well as the forest-steppe zone, support most diverse ant fauna. Natural habitats of more than half of the observed species are entirely restricted to one zone. Those species which possess wide natural habitats covering several native zones display similar patterns of zonal change of habitats [in a sense of Bey-Bienko, 1930]. Assemblages in which *Formica pratensis* was dominant were considered as the main example. Such communities maintain a constancy of species composition from the forest zone to the southern boundaries of the steppe zone. This should be taken into account when considering the conservation of ants, not only of key species but also of ant communities as a whole.

Резюме. Выявлено зональное и ландшафтное распределение 70 видов муравьев на меридиональном разрезе через Западную Сибирь и Казахстан и проанализирован характер зональной смены местообитаний разных видов по Бей-Биенко [Bey-Bienko, 1930] и структура многовидовых сообществ. Максимальное видовое богатство отмечено для пустынной и лесостепной зон. Выяснено, что виды муравьев с широкими ареалами обладают сходными тенденциям зональной смены местообитаний. В качестве наиболее показательного проанализирована структура сообществ с доминированием лугового муравья *Formica pratensis.* Продемонстрировано, что эти сообщества сохраняют основу видового состава и структурную целостность на большей части ареала доминанта, от лесной зоны до полупустынь. Выявленные закономерности должны быть приняты во внимание при разработке подходов к сохранению муравьёв, так как межвидовое окружение, с его специфическими связями, составляет естественную биотическую среду для доминирующих видов.

Introduction

Finding assembly rules, i.e. orderliness in the pattern of species coexistence as well as the mechanisms that affect coexistence, is one of the major challenges in community ecology. This knowledge is extremely important for species conservation since key species are often closely associated with other members of the species community and, in some situations, may be less viable in the absence of these other members.

Ants, with their great abundance and easily observed social behaviour, are superb organisms for studying the organization of species communities. Dominance hierarchy among different ant species is one of the most complex mechanisms that increases species richness. Kaczmarek [1953] was the first to use the terms «dominant», «subdominant» and «influent» in their ethological sense to explain ant community structure. Although there have been numerous studies on community structure [e.g. Brain, 1965; Wilson, 1971; Greenslade, 1971; Reznikova, 1971, 1983, 1998a,b, 1999; Galle, 1975; Fox, Fox, 1982; Elmes, Lepage, 1994; Deslippe, Savolainen, 1995], surprisingly little work has been devoted to investigating species composition. Meanwhile stable long standing ant communities have been revealed: Dlussky [1981] has investigated such communities in deserts and named them «co-adaptive complexes», Andersen [1993, 1997] and Herbers [1994] described patterns of organization of ant communities in different arid zones in Australia and compared them with those in North America, and Savolainen et al. [1989] have investigated many boreal ant communities.

There is a very intriguing situation in West Siberia and Kazakhstan where the ethological dominant of steppe ant communities — *Formica pratensis* — is spread from the northern taiga to deserts. In our previous studies [Stebaev, Reznikova, 1972; Reznikova, 1975, 1982, 1994, 1998a,b; Reznikova, Kulikov 1978;

Reznikova, Bogatyreva 1984; Reznikova, Samoshilova, 1981] we demonstrated that *F. pratensis*, dominating in species communities, has a fundamental influence on the spatial distribution, daily activity, as well as composition and quantity of prey in those ant species which dwell in it's feeding territories. The situation mentioned above provides an opportunity to consider changes in the structure of ant communities grouping around the same dominant species along huge area.

The results of long term investigation of ant fauna and community structure in West Siberia and Kazakhstan are presented here. Earlier the ant fauna in Siberia was studied mainly in forest biomes. Investigations of Ruzsky [1905, 1907], Karavajev [1912], Kuznetzov-Ugamsky [1926], Dmitrienko, Petrenko [1976] were devoted to the forest environment of Tomsk, Omsk and Tobolsk, the Yenisei valley and the Baikal Basin. Marikovsky [1979] studied ant fauna of desert regions in Kazakhstan. The ant fauna in the greater part of the area under investigation here was unknown.

Materials and methods

The ant fauna was investigated along a meridian trend across the southern part of the West Siberian Plain and adjacent regions to the south. To estimate the constancy of ant species communities, the work concentrated on the communities dominated by *Formica pratensis.*

The valleys of Irtysch and of some of its tributaries (Ishim, Ui, Tui, Tara and Char) and of some rivers flowing into Balkhash Lake and Zaysan Lake, namely Ayaguz, Kurchum, Kolguti, Black Irtysch and Ile, as well as the Alakol and Balkhash basins were investigated (see Fig. 1 and Table 1). There were 18 valley profiles and 5 main geomorphological levels within each profile: lower and upper flood-plains, lower and upper terraces and the divide.

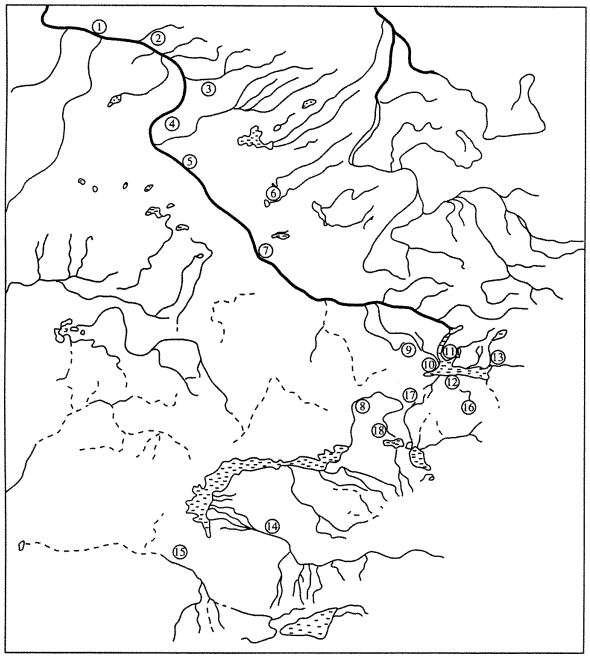

Fig. 1. Location of valley transects 1-18 [from: Reznikova, 1999] (explanations as in Tabl. 1).

Рис. 1. Локализация долинных профилей 1-18 [из: Reznikova, 1999] (обозначения см. табл. 1).

Small-size ant species' nests were counted in 5x5 m plots. There were 15 plots per each geomorphologic level. Anthills of the subgenus *Formica* s.str. as well as underground nests of the genus *Camponotus* were counted on 2 km record belts, three for each geomorphologic level. Inventories were completed by thorough direct searching.

To estimate the constancy of species communities, only assemblages dominated by *F. pratensis* were investigated. For 10 of the 18 valley profiles such assemblages were detected on 6 plots (each of area 1600 m^2) — 60 plots in total. To compare the structure of the different assemblages, a relative value was used: the number of nests of each species per one feeding territory of *F. pratensis*. This value was recalculated for the same standard area corresponding to the average feeding territory of *F. pratensis*, namely, 800 m^2. The average values from 6 measurements are provided in Table 2.

Results

Analysis of the ant fauna

The forest zone (see profiles 1–3 in Table 1). The inspected territory embraces the southern taiga subzone and the birch-aspen forests in the subtaiga subzone. Mixed pine forests and high bogs occupy the divides. Herbaceous meadows are usual in the flood-plains. The greatest species richness has been recorded in the birch-aspen forests. Among them there are typical forest species such as *Formica rufa*, *F. polyctena*, *F. aquilonia*, *Myrmica lobicornis* and *Camponotus vagus*, as well as those species which are more usual in the southern regions: *F. pratensis*, *F. cunicularia*, *M. scabrinodis* and *Tetramorium caespitum.*

Species richness diminishes in the southern taiga because of the disappearance of those species more typical of the forest-steppe, such as *F. cunicularia* and *T. caespitum*, which were not encountered north of forest-steppe boundaries.

The forest-steppe zone (profiles 4–6 in Table 1). Mosaics of vegetation and soils are characteristic of this zone in the West Siberian Plain due to a combination of high summer temperature and much soil water lying on salt loam. There are mixed grass meadows in the flood-plains and carnation-grass meadows and swamps in the watersheds. The species richness in this zone is higher than in neighbouring ones. The most typical species are *F. pratensis*, *F. sanguinea*, *F. cunicularia*, *F. rufibarbis*, *M. scabrinodis*, *M. salina*, *Tetramorium caespitum* and *Lasius alienus*. In this zone boreal species dwell in proximity to steppe and Turan-steppe species. Apart, species with rather different preferences for moisture and heat dwell in this

Table 1. Ant diversity in different zones and landscapes.
Таблица 1. Распределение муравьёв в различных природных зонах и подзонах.

Species / Numbers of profiles	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
Myrmica rubra L.	V	V	P	P	P	P		P		P						P, T,S	V	
M. ruginodis Nyl.	T	T	W														V	
M. bergi Ruzs.												F		F				
M. rugulosa Nyl.	V	V	P	P	V	F							T					
M. stangeana Ruzs.												V	V					
M. slovaca Sad.					P													
M. scabrinodis Nyl.		V	P	P	P	P	P	P									S	
M. salina Ruzs.					P	W		F	F	F	F	F		F				
M. sabuleti K. Arn.															P			
M. lobicornis Nyl.			P	P	P	P	P		P		P					S		
M. deplanata Ruzs.			P	P	W	W	P	P	P	P	F	V	V			V,S		
M. schencki Em.			P	P	P	P	P	T				F						
M. sulcinodis nigripes																S		
Messor clivorum Ruzs.							P	P	P	W	P	P	P					V
Messor denticulatus K.-Ug.														P	P			
Messor marikovskii K. Arn.														P			P	
M. aralocaspius infumatus K.-Ug.														P	P			V,P
Tetramorium caespitum L.			T	P	P	W	W	W	W	W	W	W	V	F	F	W	W	W
T. schneideri Em.														V	W			
T. indocile Sanschi														W	T			
T. inerme Mayr														V	T			P
Leptothorax tuberum Fabr.															F			
L. nassonovi Ruzs.						P	P			P								
L. acervorum Fabr.				P	P	P												
L. muscorum Nyl.		V	V	V	V													
L. balchaschensis K. Arn.								V							V			V
L. serviculus Ruzs.						P		P										
Solenopsis fugax Latr.					P	P	W	V	V	F	F	F	F	F	F			
Crematogaster subdentata Mayr														F	V			
Cardioconlyla elegans Em.														F				
C. stambuloffi Ruzs.														F				
Pheidole pallidula Nyl.															P			
Strongylognathus christophi Em.							P				P							
Formica rufa L.	W	V	P															
F. polyctena Foerst.	W	W	W	P	P	P		S								P,S		
F. aquilonia Yarr.	T	P																
F. lugubris Zett.	T																	
F. pratensis Retz.	V	V	P	P	P	W	W	W	W	V	V	V	V	V		T,S	S	S,V
F. sanguinea Latr.		W	W	T	P	P	P											

Table 1. (continuation).
Таблица 1. (продолжение).

Species / Numbers of profiles	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
Formica cinerea Mayr					P													
F. fusca L.	W	W	W	P	P			S										
F. picea Nyl.	P			V												S,V		
F. rufibarbis Fabr.					P	P	W		W		T		T	W				
F. cunicularia glauca Ruzs.			W	P	P	P	W	W	W	W						W	S,V	S,V
F. pressilabris Nyl.			W	P	P	P												
F. exsecta Nyl.	V	V	F	P	P	P	P	V								T		
F. brunneonitida Dluss.								V								T,S		
Camponotus herculeanus L.	T	T	P	P	P													
C. saxatilis Ruzs.	W	W	W	P														
C. vagus Scop.													F			T,V		
C. japonicus Mayr										V		T	T					
C. interjectus Mayr										P						S	P	
C. turcestanus Ern. Andre.								P	P	P		T	T	W	V			
C. turcestanicus Mayr														V				
C. lameerei Mayr														F				
C. fedchenkoi Mayr														T				
Lasius fuliginosus Latr.				P	P	P				F			F					
L. niger L.	W	W	W	W	W	W	F	F,P	F	F		V				V	S, V	S,V
L. flavus Fabr.	W	W	W	W	W	W	F	F			V	V	V					
L. alienus Foerst.				P	P	P	W	P	W	P	W		W			W	S	S,P
Cataglyphis aenescens Nyl.					P	W	W	W	W	W		W		W	V	S,T		V
C. setipes turcomanica Em.															P			
C. pallida Mayr															P			
Proformica epinotalis K.-Ug.								F						P	V		S,P	S
P. mongolica Dluss.													T					
Polyergus rufescens Latr.							P	P	V	V								
Plagiolepis sp.								T	P	P			T	V	W		S,P	
Dolychoderus quadripunctatus L.													F					
Tapinoma sp.														V	V		S	S
general number of species	15	15	21	23	24	24	20	22	17	17	12	15	18	23	19	16	13	13

Indications. 1–18 — valley profiles in the vicinity of the following villages and towns (see Fig. 1): *South taiga*: **1** — the village Ust-Ischim, **2** — the village Tevris, **3** — the village Artin; *Northern forest-steppe*: **4** — the village Krutaya Gorka; *Southern forest-steppe*: **5** — the village Cherlak, **6** — the town Karasuk; *Steppe*: **7** — the town Pavlodar, **8** — the town Ayagus; *Semidesert*: **9** — the town Charsk, **10** — the village Kurchum, **11** — nord-west Zaysan land, **12** — lower sream of Kolguti valley, **13** — Black Irtysh valley, the village Buran; *Desert*: **14** — Ili valley, village Bakanas, **15** — Chu valley, the village Furmanovka; *Mountain slopes and mountain valleys*: **16** — upper stream of Kolguti river, **17** — slopes of Kungey and Tarbagatay ranges, **18** — Zhalmara valley. **P** — plain, divide; **T** — middle terraces, **V** — valleys, **F** — flood plains, **W** — widely spread, **S** — mountain slopes.

Обозначения. 1–18 — долинные профили в окрестностях следующих населённых пунктов (см. рис. 1): *южная тайга*: **1** — с. Усть-Ишим, **2** — с. Тевриз, **3** — с. Артын; *северная лесостепь*: **4** — с. Крутая Горка; *южная лесостепь*: **5** — с. Черлак, **6** — г. Карасук; *степь*: **7** — г. Павлодар, **8** — г. Аягуз; *полупустыня*: **9** — г. Чарск, **10** — с. Курчум, **11** — северо-западный берег оз. Зайсан, **12** — нижнее течение р. Колгуты, **13** — долина Чёрного Иртыша, с. Буран; *пустыня*: **14** — долина р. Или, с. Баканас, **15** — долина р. Чу, с. Фурмановка; *горные склоны и долины горных рек*: **16** — верхнее течение р. Колгуты, **17** — склоны хр. Кунгей и Тарбагатай, **18** — долина р. Жалмара. **P** — плакоры, **T** — средние террассы, **V** — долины, **F** — поймы, **W** — широкое распространение, **S** — низкогорные междуречья.

zone. They are able to contend with the climate of the forest tundra (*Leptothorax acervorum*, *Myrmica lobicornis)* and combine with the extremely xerophilous *Cataglyphis aenescens* and *Myrmica deplanata.*

The steppe zone (profiles 7, 8 in Table 1). In the northern outskirts of this zone there is a transitional strip with the birch-aspen forest islets within xerophilous vegetation composed mainly of feather-grass and sheep's fescue. Dry steppe extends in the south from Pavlodar. In the Ayagus valley there are low steppe hills covered with feather grass, sheep's fescue and wormwood. Typical inhabitants of the divides are *Cataglyphis aenescens*, *Myrmica deplanata*, *M. schenki*, *Messor clivorum*, *Leptothorax serviculus*, *L. nassonovi*, *Tetramorium caespitum*, *Lasius alienus*, *Formica cunicularia* and *F. rufibarbis.* Some species which dwell here in the valleys are also encountered in the forest-steppe and even in forest divides from adjacent zones*:* *Lasius niger*, *L. flavus*, *Formica fusca*, *F. exsecta*, *F. polycten* and *Myrmica rubra.* On the sand dunes of the high Ayagus flood-plain, *Proformica epinotalis* and *Formica brunneonitidae* occur, the latter being found by Dlussky [1967] in Mongolia and Tuva.

The semi-deserts (profiles 9–13 in Table 1). In the Zaysan hollow there is xerophytic vegetation composed of wormwood and sheep's fescue and common saltwort plant communities on plains and in the flood-plains. Ant species' communities in the flood-plains differ somewhat from those of the divides. In the flood-plains the species composition is similar to that of the divides in the more northern forest-steppe zone. The following species are common: *Myrmica rubra*, *M. salina*, *Solenopsis fugax*, *Formica pratensis*, *F. cunicularia* and *Lasius fuliginosus.* In the poplar forest on the flood-plain of the Black Irtysch *Camponotus vagus* and *Dolichoderus quadripunctatus* were found, species which are known from deciduous forests of the Caucasus and the Crimea. The typical community of the plains and low mountains is composed of *Camponotus turcestanus*, *Messor clivorum*, *Proformica mongolica*, *Myrmica deplanata*, *Plagiolepis* sp. and *Tapinoma* sp.

The specific feature of the ant fauna in undercurrent of Black Irtysh and Kurchum is the high diversity and density of *Camponotus* species: *C. vagus* is numerous in the flood-plains and low terraces, *C. japonicus* is numerous in the salt meadows of middle terraces, *C. turcestanus* on the plains, and *C. interjectus* on the slopes of low mountains.

The North-West Zaysan land is the most arid area here. The small river Kolguti flowing down from Kurchum, dries up and bores into the crumbly alluvium. In its flood-plain there are meadows composed of Spanish liquorice and grisebach. *Myrmica bergi*, *M. stangeana*, *M. salina*, *M. schencki*, *Formica cunicularia*, *Lasius niger* and *L. flavus* are found here, as well as *Tetramorium caespitum* and *Cataglyphis aenescens* in the higher parts. On the slopes and plains, only 3 species were encountered: *C. aenescens*, *Messor clivorum* and *Plagiolepis* sp.

The deserts (profiles 14–15 in Table 1). There are northern sand desert landscapes in the middle and upstream of Ile, in the Sari Ishik Sands: saxauls grow on the plains, willow underbushes and salt-tree with canes grow in the flood-plains, and salt meadows occur on the terraces.

The ant species richness is higher here than in the neighbouring northern zones; in all, 24 species were found (Table 1). On the plains, besides the common species of semi-deserts and steppes (such as *Camponotus turcestanus*, *Cataglyphis aenescens*, *Proformica epinotalis*, *Plagiolepis* sp.), there are several species which are only found in this zone, such as *Tetramorium schneideri*, *Camponotus fedchenkoi*, *Messor aralocaspius infumatus* and *M. denticulatus*.

The mountain slopes and valleys (profiles 16–18 in Table 1). In the lower and middle reaches of the Kolguti river on the inland slopes *Messor clivorum*, *Myrmica deplanata*, *Cataglyphis aenescens*, *Camponotus turcestanus*, *C. japonicus*, *Tetramorium caespitum*, *Formica pratensis*, *F. cunicularia* and *L. niger* occur. Ant diversity increases in the upper Kolguti. The nearness of the Mongol part of Altai and Northern China influences the ant fauna here. There are numerous nests of *F. brunneonitida*, *F. picea* and *Camponotus vagus*. It is interesting that *F. uralensis* replaces *F. pratensis* in the vicinity of the mountain lake Markacol. In the Karabuga valley, in the internal Tarbagatay foothills, *Myrmica deplanata*, *M. lobicornis*, *M. schenki*, *F. picea*, *F. mesasiatica*, *F. rufibarbis* and *Tetramorium caespitum* were found. The last two species, together with numerous *F. pratensis* and *Camponotus vagus*, were encountered on the meadows in the vicinity of the foothills. On the arid low front Tarbagatay foothills, only *Camponotus turcestanus* and *Plagiolepis* sp. were found. The ant fauna of the river valleys from the Alakol and Balkhash basins includes Turan species (*Myrmica bergi*, *M. stangeana*, *Tetramorium inerme*, *Crematogaster subdentata*, *Camponotus turcestanicus*, *C. lameerei*), Kazakhstan species (*Tetramorium indocile*, *Leptothorax balchaschensis*) and Mediterranean species (*Cardiocondyla elegans*).

The constancy of species communities dominated by *Formica pratensis*

Comparing Table 1 and Table 2, one can see that those species which have wide natural habitats, central parts of which fall in the forest-steppe and the steppe, are included in the same species communities not only within the central parts of their natural habitats but also in the forest zone and in the northern deserts (e.g. *Formica pratensis*, *F. cunicularia*, *Lasius alienus*, *Myrmica salina*, *M. deplanata*, *M. scabrinodis*, *Tetramorium caespitum*). When analysing the inter-relationships of the ethological dominant *F. pratensis* with other species lacking protected food territories, one can see that near the edge of its natural habitat, *F. pratensis* becomes a member of species' communities differing from those in the central part of its area. Thus, in the northern part of the area this species enters an impover-

Table 2. Number of ant' nests per one feeding territory of the dominant *Formica pratensis* in different zones (average values recalculated per the same square).

Таблица 2. Число гнёзд муравьёв разных видов, приходящихся на один кормовой участок *Formica pratensis* в разных зонах (приведённое к одинаковой площади).

Number of ant's nests / numbers of profiles	1	2	4	5	6	7	9	10	13	14
Formica fusca	1.2±0.4	2.3±0.8								
F. cunicularia			4.2±1.3	5.3±1.8	5.7±2.1	7.3±2.4	8.3±3,2		5.7±1.9	
F. rufibarbis								6.2±2.9		5.1±2.2
Lasius niger	1.7±0.8	2.3±0.7								
L. alienus			4.7±1.9	11.8±4.9	12.2±5.4	10.2±2.7	12.1±3.4	7.5±3.3	8.1±3.1	
Myrmica ruginodis	5.1±1.8	6.2±2.8								
M. scabrinodis			8.2±3.1	6.7±2.8	8.9±3.7	7.3±4.2				
M. schenki		8.3±3.5	3.9±1.8	6.2±1.9	5.3±1.4	6.2±0.9				
M. salina				10.4±3.8	12.7±5.2	8.2±1.9	5,2±1.3	6.2±2.4		4.1±2,2
M. deplanata			4.2±2.1	5.2±3.4	10.2±3.9	8.9±2.7	5.6±1.9	5.1±0.9	13.2±4.1	
M. bergi										3.1±0.9
Tetramorium caespitum			4.3±0.8	6.3±3.4	10.2±4.3	15.2±4.8	11.1±3.8	6.1±1.8	7.1±3.5	3.1±1.3
T. inerme										4.2±0.9
T. indocile										6.1±2.3
T. schneideri										1.7±0.5
Camponotus turcestanicus										2.1±0.7
Plagiolepis sp.										2.2±0.9

Indications. Numbers of profiles correspond to Table 1 and Fig. 1.

Обозначения. Номера долинных профилей соответствуют таблице 1 и рис. 1.

ished variant of a forest species community. Actually, such steppe species as *F. cunicularia*, *F. rufibarbis*, *L.alienus*, *M. salina*, *M. deplanata* and *T. caespitum* do not extend into the forest zone. At the same time the forest species *Myrmica ruginodis*, *M. rubra*, *M. rugulosa*, *Formica fusca* and *Lasius niger* are numerous in the typical zonal landscapes, where *F. pratensis* is rather rare. Thus, *F. pratensis* is only observed with small numbers of *F. fusca*, *M. ruginodis* (and *M. schenki* in some cases) and *L. niger* (profiles 1, 2 in Table 2) . On the contrary, in the flood-plains of the desert rivers, *F. pratensis* enters an enriched variant of species community. Here are not only steppe species but also those which dwell in intrazonal landscapes together with *F. pratensis*, namely *Myrmica bergi*, *Tetramorium inerme*, *T. indocile*, *T. schneideri*, *Plagiolepis* sp., and *Camponotus turcestanicus* . Therefore, the species richness in the communities dominated by *F. pratensis* increases from north to south, from 3 to 9 species.

It is interesting that in the central part of *F. pratensis'* natural habitat, not only is species composition maintained, but also the numerical proportion of nests of different species which dwell in the feeding territories of the dominant. There are 4–8 mounds of *Formica cunicularia* or *F. rufibarbis*, 5–12 *Myrmica* nests (*M. scabrinodis*, *M. salina*, *M. schencki*), almost the same for *Lasius alienus* and 10–15 nests of *T. caespitum*. In semi-desert and desert landscapes there is a somewhat different proportion as a result of a lack of *L. alienus* and decreasing numbers of *T. caespitum* but, in general, a constant image of species community is maintained.

Discussion

Analysing ant distributions across the vast region covering several zones, one can see that the arid zone as well as the forest-steppe zone support more diverse ant fauna than other zones: 29 species were found in the deserts (valley profiles 14, 15) and 31 species in the forest steppe (profiles 4–6). For comparison, there are 24 species in the forest zone (profiles 1–3) and 25 in the semi-desert (profiles 9–13).

The ranges of more than half of the observed species are restricted to a single zone; for example, *Myrmica ruginodis*, *Formica rufa*, *F. aquilonia* and *F. lugubris* coincide with the forest zone, while *Leptothorax nassonovi* and *L. serviculus* only coincide with the steppe. The greater part of the group of species with locally restricted distributions consists of stenothermic Turan

species coinciding with the deserts, such as *Tetramorium schneideri*, *T. inerme*, *T. indocile*, *Myrmica stangeana* and all species of the genus *Messor*.

It is interesting to consider patterns of distribution in those species which possess exceptionally vast natural habitats covering several zones; for example, *Formica pratensis*, *F. cunicularia*, *Tetramorium caespitum*, *Lasius niger* and *Myrmica deplanata* are widespread from the forest to the arid zones. It is probable that the main mechanism for the expansion of range in these species is the zonal change of habitats, as discovered by Bey-Bienko [1930] for Acrididae when he considered their distributions in West Siberian and Zaisan Plains. In those ant species which have wide distributions, central parts of which lie in the forest-steppe and steppe zones, the zonal change of habitats is displayed both in southern and northern directions.

Thus, *F. pratensis* in the steppe and in the southern forest steppe dwells in all possible biomes and has a maximum of nest numbers in the typical zone landscapes (5–7 nests per 10 000 m^2). In the northern parts of the forest-steppe, this species chooses the hottest and driest habitats. In contrast, in the arid zones, *F. pratensis* occurs in the intrazonal landscapes such as moist parts of the valleys and the flood plains. The maximum number of nests decreases in both directions up to 1–2 nests per 10 000 m^2. Similar patterns of distribution are characteristic of *F. cunicularia*, *F. rufibarbis*, *Lasius alienus*, *Tetramorium caespitum*, *Myrmica salina*, *M. deplanata* and, partly, of *Myrmica scabrinodis* ; for example, as one can see from Table 1, from the forests to the steppe zone *M. deplanata* occurs in the zonal landscapes (the plains), while in the arid zones (profiles 11–13, 16), it moves to the floodplains and valleys.

Those species which have optimal parts of their natural habitats in the forest zone, penetrate into more southerly regions by occupying divides and hollows of the lower terraces; for example, *Lasius niger* and *L. flavus* in the forest zone dwell in all possible biomes and have a maximum of nest numbers in the typical zonal landscapes (about 300 nests per 10 000 m^2). In the steppe zone, these species only occur in hollows and the number of nests is 4–5 times less than in the forest zone. Species closely connected with forests, such as *Formica polyctena*, *F. fusca* and *F. pressilabris*, penetrate into southern regions only by inhabiting islands of forest.

It seems to be of special interest that those species which use similar ways to change habitats compose the main body of constant species communities. As noted earlier, several species have patterns of zonal and landscape distribution similar to those of *F. pratensis*. Precisely these species compose the main body of communities in which *F. pratensis* shows dominance, which is maintained from the forests to the arid zones. Such a constancy of community structure would suggest that the co-adaptive ant complex is composed of species with a wide tolerance and huge natural habitats that have overlapping ecological niches. This should be taken into account when considering ant conservation, not only of key species but also of ant communities as a whole.

Acknowledgments

I am grateful to Prof. Donald Michie and Dr Annie Lamb for their helpful comments on this paper. This work was supported by a grant from the Russian Fund for Basic Research (02–04–48386) and from the fund of Dr Frank Salter (Humanethologie und Humanwissenschaftliches Zentrum der Ludwig — Maximilians Universitaet, Muenchen).

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