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Spatial Heterogeneity of a Ground Beetle (Coleoptera, Carabidae) Population along a Forest-Steppe Transect: Local Level of Consideration

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Abstract—Carabid diversity has been studied in the forest–steppe in southern West Siberia along a continuous 180-m transect from the center of a small birch forest outlier through steppe and mesophytic meadows to a single tree. Carabid communities characteristic of open and forest habitats are different. Communities of open habitats are more differentiated than forest ones. The former can be further subdivided into steppe and meadow variants. Some species are generalists, exhibiting no preferences to particular open habitats.

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Diverse and species-rich carabid communities have intricate spatial and temporal structures [1]. These structures are still obscure in many cases. The small- and medium-scale spatial distribution of carabids is influenced by vegetation [2–4]. Carabids are unspecialized predators, and they depend on the life forms of plants, grass density, and other parameters, which are difficult to take into account, rather than on the species composition of the plant communities housing them [5, 6].

Herpetobiont count is commonly performed at boundaries between plant associations to involve distinct and, as far as possible, contrasting habitats. This approach is sound if the whole diversity of habitats in a locality is overviewed. It allows full investigation of a local fauna and determination of the confinedness of species to certain habitats [7]. However, it is necessary to record beetles along a continuous transect with distances between test plots close to the sizes of the plots themselves when our objectives are to estimate "from the ground beetle viewpoint" the width and permeability of plant cenosis borders, distinctness of transitional habitats, and tolerance ranges and to reveal zones of maximum species richness and abundance.

We investigated the variation of carabid fauna and relative species abundance patterns along a 180-m long transect drawn in a forest–steppe in southern West Siberia. This transect included the plant cenoses of a birch forest outlier, the forest margin, isolated trees, and mesophytic and steppe meadows. Examination of particular habitats in this locality showed that carabid communities could be divided into those characteristic of forest and grassland habitats [8]. Similar data were formerly obtained for another group of soil-associated arthropods, springtails (Collembola) [9] and even for aerobionts, true flies (Muscidae) [10]. Here we consider the fine structure of this carabid cenosis, small but representative.

STUDY AREA, MATERIALS, AND METHODS

The study was carried out on a plain divide in the Barabinsk forest–steppe, southern West Siberia, near Troitskoe Village, Karasuk raion, Novosibirsk oblast: 53°42.8′N, 77°42.5′E, from May 28 till June 21 and from July 5 till 22, 2008. A continuous transect of 180 m in length was drawn from the center of a small birch forest outlier across various types of mesophytic and steppe meadows. Nineteen rows of traps were set across the transect at 10-m intervals, five traps in a row. The traps in the rows were 1 m apart. Six groups of trap rows (positions) were established.

Positions 1–3. Aspen–birch forest on bleached turfy solodic forest soil, 200–300 m in diameter, with low trees (*Betula pendula* Roth and *Populus tremula* L.) and shrubs. The overall projective cover is about 100%. The forest has well-developed litter of dead leaves and sparse forest herbage.

Positions 4–6. Sparse periphery of the forest, consisting of tall birch trees, 10–20 m wide, with projective cover about 70% on gray forest soil. The herbage includes meadow species: *Peucedanum morisonii* Besser

ex Spreng., *Anemone* sp., *Calamagrostis epigejos* (L.) Roth., *Fragaria viridis* (Duchesne) Weston, *Iris ruthenica* Ker Gawl., *Vicia cracca* L., *Phlomis tuberosa* (L.) Moenich, etc.

Positions 7–11. Reed grass–*Peucedanum* near-forest steppe meadow with isolated birches. 30–50 m in width. Codominated by steppe, meadow, and halophytic herbs: *Festuca valesiaca* Gaudin, *Artemisia*s pp., *Galatella* sp., *Plantago media* L., *Achillea millefolium* L., *Poa pratensis* L., etc. Species richness 35–40 species in 100 m^2 on meadow–chernozem alkaline soil, Subdivision within this group: 7–8, meadow near the forest border; 9–10, open meadow dominated by *P. morisonii;* 11, ditto, in a small depression.

Positions 12–13. Wormwood–feather grass–fescue alkaline steppe areas on medium-columnar and deep sodic soils occurring in spots 10–15 m in diameter in steppe meadow. Codominants: *Elytrigia repens* (L.) Nevsk., *C. Epigejos*, *Koeleria* sp., *P. pratensis*, *Potentilla argentea* L., and *Artemisia* spp. Total projective cover 60–80%, 34 species in 100 m^2.

Positions 14–17. Steppe meadow on common chernozem. Projective cover 80–90%, 40–60 species in 100 m^2. Dominants: *P. Morisonii*, *Scabiosa* sp., *Poa* spp., *Koeleria* sp., *A. millefolium*, *Trifolium pratense* L., *Onosma simplicissima* L., and *Carex macroura* Meinsh.

Positions 18–19. Isolated birches (*B. pendula*). Large multitrunk trees scattered over steppe meadow on common chernozem 100–150 m apart. Crown cover 10–12 m, with meadow and steppe herbage beneath the crown: *Stipa krylovii* Roshev., *F. valesiaca, Poa* spp., *Anemone* spp., *Pulsatilla patens* (L.) Mill., *Medicago sativa* L., and *Artemisia* spp.

The traps were plastic cups 6.5 cm in diameter with 3% acetic acid as a preservative. The cups were examined at 5-day intervals. A total of 5000 examination-days yielded about 1500 specimens of 57 ground beetle species (table). The results were processed with ECOS 1.3 [11] and PAST 1.57 [12] software.

RESULTS AND DISCUSSION

Ranking of species in abundance. The abundances of carabid species recorded over the study time were ranked in descending order (table). The decrease with rank is irregular. Carabid species were divided into five groups according to their relative abundances in the overall population. The first group includes one species, the absolute dominant in the total dynamic density, *Poecilus fortipes* Chaud. Its relative abundance is about 21%. The second group includes 8 species, which constitute about 50% in total; the third, 7 (15%), and the fourth, 18 (10%). The fifth group includes insignificant, rare, and occasionally found species. Their number is the greatest among the groups, and their cumulative abundance is the least, about 4%. This distribution fits best the model of a random boundary of an econiche with niche overlap, or the McArthur broken rod model, type II [11]. This model accounts for 94.66% of data dispersion. This abundance distribution is typical of species-rich carabid communities, whose formation is governed mainly by the consumption of independent resources on the coexistence basis rather than by competition [13].

Classification of species according to habitat confinedness. The confinedness of carabid species to certain habitats was analyzed. The rare species of the fifth group were neglected. A dendrogram of species similarity in spatial distribution over the profile was constructed by the unweighted paired group method according to Jaccard indices (Fig. 1). Two clusters are clearly seen: species of open habitats and species confined to forest associations. However, use of a continuous series of test plots allows consideration of the distribution of species over habitats within tens of meters and individual phytocenotic contours.

Consider the species confined to forest associations. This cluster contains a small branch including *C. melanocephalus* and *Amara consularus*. They occur mainly in the margin of the birch forest (positions 4–6), but their smaller numbers can also be found in meadows (7–11). *Curtonotus castaneous* branches off the remaining part of the cluster. It is abundant in the forest margin but also present in the near-forest meadow. The cluster also contains the branch of *Badister bullatus* and *P. versicolor*, which occur only in the forest margin. The remaining species of the cluster occur in all or nearly all forest associations (positions 1–5) but nowhere else. They include *Pterostichus oblongopunctatus*, *Agonum gracilipes*, and several species of the genus *Amara*: *A. brunnea*, *A. eurynota*, *A. bifrons*, and *A. communis*.

The carabid species of open habitats are widely differentiated. First, species confined to steppe meadow (positions 14–16) but hardly found in sodic soil positions of the profile (12–13) branch off the main cluster: *A. equestris*, *Ophonus puncticollis*, and *Carabus cribellatus*. Another branch includes insignificant species occurring in most meadow positions: *H. rubripes* and *A. biarticulata*. The next branch also includes two species, *Cymindis angularus* and *H. anxius*. They prefer the most humid positions: near-forest meadow (7–8) and Peucedanum-dominated meadow (9–11). Then steppe species branch off the cluster. *Taphoxenus gigas* and *H. kirgisicus* occur only in steppe positions (12–13), and *H. politus* occurs, although seldom, in neighboring meadows (6, 11, 15, 17). The next branch consists of one species, *Syntomus truncatellus*. It occurs not only in open habitats but also in forest positions. The remainder of the cluster consists of species most similarly distributed along the profile. They are subdivided into two branches: confined to meadows and to sodic soils. The meadow steppe branch includes *P. Fortipes*, *Calathus erratus*, and *H. cisteloides*. The last species sometimes occurs at the boundary of the forest but does not penetrate inside it. The species of

The overall dynamic density of carabid individuals per 100 traps per day in the forest–meadow transect near the town of Karasuk. For habitat description, see text

Species, position No.		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	Total
1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22
1	*Poecilus fortipes* Chaud.	4	0	6.7	20	8	103.3	32	24	16	20	32	51.3	20	48	59.3	218	352.7	100	8	763.9
2	*Calathus erratus* (C. R. Sahlb.)	8	4	4	0	32	108	24	16	8	4	12	4	0	8	12	44	8	60	0	356
3	*Pterostichus oblongopunctatus* (F.)	36	62	205.3	40	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	347.3
4	*Amara communis* (Panz.)	8	52	52.7	124	67.3	7.3	0	0	0	0	0	0	0	0	0	0	0	0	0	258.6
5	*Harpalus cisteloides* Motsch.	4	8	0	8	28	31.3	20	11.3	12	0	8	0	0	0	16	32	20	28	12	238.6
6	*Poecilus sericeus* (F.-W.)	0	0	4	0	0	0	8	0	8	4	4	79.3	31.3	12	12	12	16	16	0	206.6
7	*Agonum gracilipes* (Duft.)	12	34	40.7	8	84	20	0	0	0	0	0	0	0	0	0	0	0	0	0	158
8	*Amara bifrons* (Gyll.)	4	8	38	4	4	44	4	4	0	0	0	0	0	0	0	0	12	0	0	122
9	*Amara eurynota* (Panz.)	4	20	44	32	8	0	0	0	0	0	0	0	0	0	0	0	4	0	0	112
10	*Carabus marginalis* F.	4	0	16	16	44	4	0	0	0	0	0	0	0	0	4	0	4	0	0	92
11	*Harpalus smaragdinus* (Duft.)	0	0	0	0	0	4	12	4	7.3	0	4	8	4	0	4	16	16	12	0	91.3
12	*Amara brunnea* (Gyll.)	4	20	70.7	52	12	0	0	0	0	0	0	0	0	0	0	0	0	0	0	88
13	*Cymindis angularis* (Gyll.)	0	0	0	0	36	0	0	4	0	0	16	0	0	0	0	4	23.3	0	0	83.3
14	*Amara equestris* (Duft.)	0	0	0	0	0	0	4	0	0	0	0	0	0	0	0	8	0	60	0	72
15	*Syntomus truncatellus* (L.)	0	20	0	8	0	3.3	7.3	4	4	4	18. 7	0	0	0	0	0	0	3.3	0	53.9
16	*Badister bullatus* (Schrank)	0	0	38	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	42
17	*Harpalus anxius* (Duft.)	0	0	0	0	0	0	0	4	0	8	4	0	4	4	0	3.3	4	0	0	31.3
18	*Taphoxenus gigas* (F.-W.)	0	0	0	0	0	0	0	0	0	3.3	7.3	4	4	4	4	0	0	3.3	0	29.9
19	*Harpalus rubripes* (Duft.)	0	0	0	4	0	4	0	4	0	0	0	0	0	0	0	0	12	3.3	0	27.3
20	*Poecilus versicolor* (Sturm)	0	0	6.7	16	8	0	0	0	0	0	0	0	0	0	0	0	0	3.3	0	27.3
21	*Harpalus kirgisicus* Motsch.	0	0	0	0	0	0	0	0	0	4	4	3.3	4	3.3	4	0	0	4	0	26.6
22	*Calathus melanocephalus* (L.)	0	0	0	0	20	0	0	0	0	0	0	0	0	0	0	0	4	0	0	24
23	*Carabus cribellatus* Adams	0	0	0	0	0	0	0	0	0	4	0	0	4	0	0	12	0	4	0	24
24	*Harpalus politus* Dej.	0	0	0	0	0	3.3	0	0	0	0	3.3	4	4	0	4	0	4	0	0	22.6
25	*Curtonotus castaneus* (Putz.)	0	0	0	4	12	0	0	0	0	0	0	0	4	0	0	0	0	0	0	20
26	*Ophonus puncticollis* (Payk.)	0	0	0	0	0	0	0	0	0	0	0	0	0	4	0	12	0	4	0	20
27	*Amara praetermissa* (C. R. Sahlb.)	0	4	10	0	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	18
28	*Amara biarticulata* Motsch.	0	0	0	4	0	0	4	0	0	0	0	0	0	0	0	0	4	4	0	16
29	*Harpalus calceatus* (Duft.)	0	0	0	0	0	4	0	4	0	0	0	0	4	0	4	0	0	0	0	16

Table. (Contd.)

Species, position No.		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	Total
1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22
30	*Amara consularis* (Duft.)	0	0	0	0	8	0	0	0	0	0	3.3	3.3	0	0	0	0	0	0	0	14.6
31	*Dolichus halensis* (Schall.)	0	0	0	0	0	0	0	0	0	0	4	0	0	0	0	0	0	8	0	12
32	*Harpalus akinini* Tschitsch.	0	0	0	0	0	0	0	0	4	0	0	8	0	0	0	0	0	0	0	12
33	*Harpalus amplicollis* Men.	0	0	0	0	4	4	0	0	4	0	0	0	0	0	0	0	0	0	0	12
34	*Harpalus pumilus* (Sturm)	0	0	0	0	0	0	0	0	0	4	0	0	0	0	4	4	0	0	0	12
35	*Amara aenea* (De Geer)	0	0	0	0	0	0	8	0	0	0	0	0	0	0	0	0	0	0	0	8
36	*Amara infima* (Duft.)	0	0	0	0	0	0	0	0	0	4	4	0	0	0	0	0	0	0	0	8
37	*Chlaenius tristis* (Schall.)	0	0	0	4	0	4	0	0	0	0	0	0	0	0	0	0	0	0	0	8
38	*Cymindis equestris* Gebl.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	8	0	8
39	*Harpalus rufuscapus* Gebl.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	8	0	0	0	8
40	*Synuchus vivalis* Ill.	4	0	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	8
41	*Harpalus rufipes* (De Geer)	0	0	0	3.3	0	0	0	0	0	0	0	0	0	0	0	0	0	4	0	7.3
42	*Amara similata* (Gyll.)	0	0	6.7	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	6.7
43	*Badister lacertosus* Sturm	0	0	6.7	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	6.7
44	*Amara majuscula* (Chaud.)	0	0	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4
45	*Amara saxicola* Zimm.	0	0	0	0	0	0	0	4	0	0	0	0	0	0	0	0	0	0	0	4
46	*Calosoma denticolle* Gebl.	0	0	0	0	0	0	0	0	0	0	0	0	0	4	0	0	0	0	0	4
47	*Cymindis lateralis* F.-W.	0	0	0	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4
48	*Cymindis variolosa* (F.)	0	0	0	0	0	0	0	0	0	0	0	4	0	0	0	0	0	0	0	4
49	*Harpalus brevicornis* Germ.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	4
50	*Harpalus calathoides* Motsch.	0	0	0	0	0	0	0	0	0	0	0	0	4	0	0	0	0	0	0	4
51	*Harpalus latus* (L.)	0	0	0	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4
52	*Harpalus* sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	4	0	0	0	0	0	4
53	*Harpalus subcylindricus* Dej.	0	0	0	0	0	0	0	0	0	0	4	0	0	0	0	0	0	0	0	4
54	*Notiophilus germinyi* Fauv.	0	0	0	0	0	4	0	0	0	0	0	0	0	0	0	0	0	0	0	4
55	*Panagaeus bipustulatus* (F.)	0	0	0	0	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4
56	*Pterostichus strenuus* (Panz.)	0	0	0	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4
57	*Harpalus brevis* Motsch.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3.3	0	3.3
	Total	92	232	380.7	363.3	387.3	348.5	123.3	83.3	63.3	59.3	109.9	169.2	87.3	91.3	127.3	373.3	131.3	328.5	24	3575.1

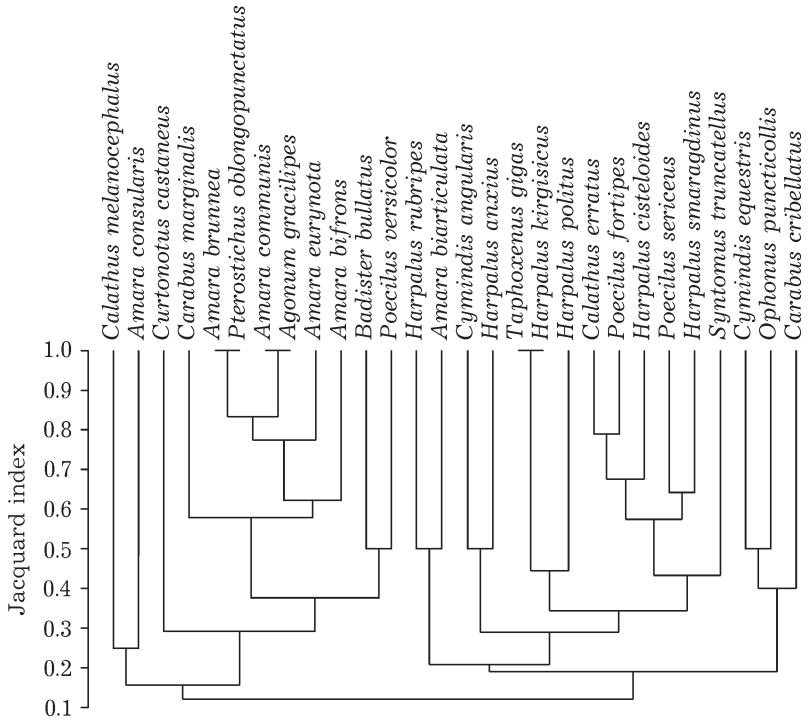

Fig. 1. Co-occurrence of species in the carabid community in southern forest–steppe in terms of Jacquard indices, the unweighted paired group method.

meadow associations, preferring sodic salts, include *P. sericeus* and *H. smaragdinus*.

Classification of population variants. The carabid communities of the transect under study can be divided into variants characteristic of open and forest habitats. The populations of open habitats, in turn, can be assigned to variants associated with mesoxerophytic steppe and mesophytic meadow habitats (Fig. 2).

The community variants from positions 1 to 5, dominated by *P. oblongopunctatus*, were assigned to the forest group. The steppe group is more heterogeneous. It can be divided, in turn, into two subgroups. The first subgroup includes the carabid communities of positions 16 and 18, dominated by *P. fortipes*. Its recognition is determined by a large number of *C. erratus* beetles, because *P. fortipes* is predominant in all open habitats. The second subgroup includes the communities of positions 10–15. Its characteristic feature is the abundance of *S. truncatellus* and *P. sericeus*. The third group is confined to meadows. It is also subdivided into two subgroups. One subgroup includes the communities of positions 7 and 9, formed mainly by *H. Smaragdinus*, *H. cisteloides*, and *Calathus erratus*. The other includes the communities of positions 6, 8, and 17. In addition to the listed species, the genus *Amara* is present, in particular, *A. bifrons*. The carabid population beneath the crown of an isolated birch (19) stands apart because of its species poverty and scarcity.

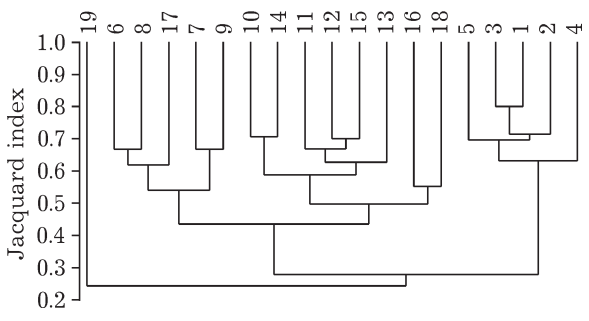

Fig. 2. Similarity of carabid populations on the forest–meadow transect in terms of Jacquard indices, the unweighted paired group method. Numerals indicate habitats (trap line positions) as enumerated in the text.

In the classification of species according to their confinedness to habitats (Fig. 1), the species of open cenoses do not form close "meadow" or "steppe" variants, although the meadow populations are distinct from steppe ones when carabid communities of different positions are grouped (Fig. 2). This observation can be explained by a lesser selectivity of abundant species with regard to habitats. Scarce species are more specialized, and their sets determine specific features of particular habitats.

Spatial distribution of predominant carabid species. Four groups can be recognized on the base of analysis of the confinedness of species to certain habitats with regard to the distribution of their abundance along the profile (Fig. 3). Group 1 includes species of forest associations. Species of open habitats form groups prefer-

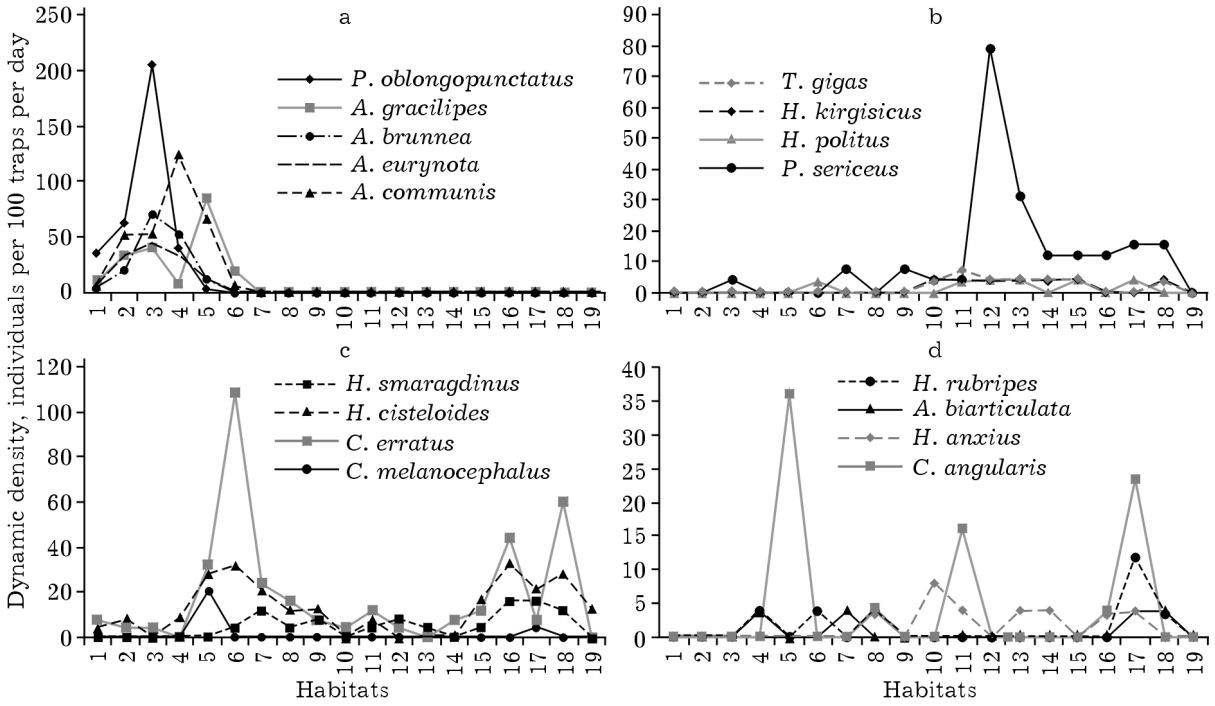

Fig. 3. Distribution of carabid species along the forest–meadow transect: (a), forest habitats, (b) meadow habitats, (c) steppe habitats, (d) generalist species of open habitats.

ring (2) meadow positions, (3) steppe positions, and (4) giving no preference to any particular open habitat. The directly determined distribution of predominant species over habitats generally agrees with that obtained by the cluster analysis of the population of the whole profile.

Some scientists believe that abundant species perceive the environment as more heterogeneous than scarce ones. Thus, there are more generalist species among the former and specialists among the latter [14]. This feature of abundant species may be the cause of their wider environmental flexibility. For example, *P. fortipes* is a generalist, but it differentiates forest and open habitats. Among inhabitants of open habitats, several other abundant species are generalists: *C. Erratus*, *H. cisteloides*, *P. sericeus*, and *C. angularis*. There are no generalists among forest species.

Zoogeographical characterization of species. We followed the formerly proposed classification of carabid ranges [15, 16], based on M. G. Sergeev's [17] classification. The latitudinal and longitudinal aspects of the range are considered separately. The boreal, subboreal humid, subarid, and polyzonal groups are recognized in the latitudinal aspect. The northern boundary of the boreal group is drawn in the tundra or forest–tundra belts. In the south, boreal species penetrate to the steppe zone in the central sector of the Palearctic or to the belt of broad-leaved forests in the western and eastern sectors. The subboreal humid group includes species not found north of middle taiga in the central sector of the Palearctic. The southern boundary of the range of these species goes in the steppe belt. The subarid group includes species occurring no farther north than the forest–steppe. The distribution of polyzonal species in the north is similar to that of boreal ones. In the south, they penetrate into the semidesert belt or even farther.

Latitudinal groups of species ranges are recognized from the occurrence of species with regard to the Panatlantic, continental, and Panpacific sectors of the Palearctic [18]. The carabid species found in the Barabinsk southern forest–steppe are divided into four longitudinal groups: trans-Palearctic (in all the three sectors of the Palearctic), West-Palearctic (in the Panatlantic and continental sectors), and East-Palearctic (the continental and Panpacific sectors).

The proportions of areographic carabid groups throughout the profile and in the most contrasting habitats are shown in Fig. 4.

Considering the richness of species belonging to various latitudinal belts in the fauna under study, we see that subarid species rank first, constituting 36% of all species. They are followed by subboreal humid (31%) and polyzonal species (22%). Boreal species constitute only 11%. With respect to the longitudinal sectors, the study area is dominated by West-Palearctic species (61%), and the number of trans-Palearctic species is also significant: 25%. Central and East-Palearctic species are the fewest: 11% and 3%, respectively. In general, the carabid fauna of the study area can be classified as steppe and West-Palearctic.

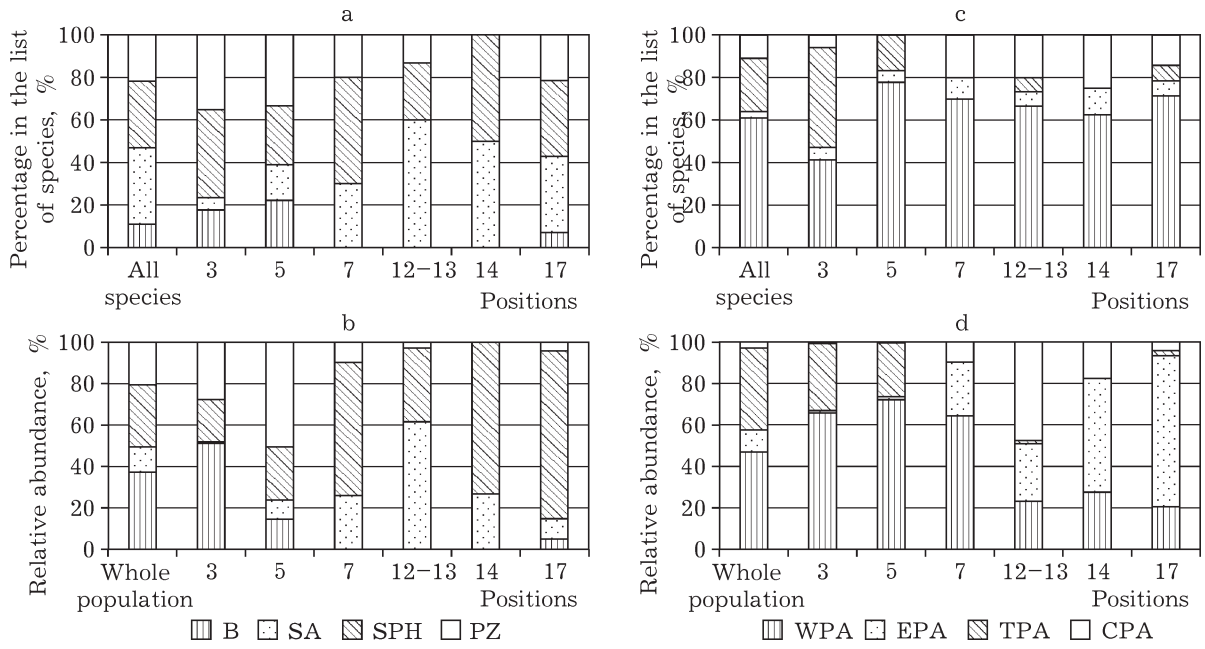

Fig. 4. Prevalence of carabid groups of different areographic groups on the whole transect and in its most contrasting habitats. For habitat designations, see text. (a, b) Ranges in the longitudinal aspect. Designations: B, boreal; SA, subarid; SBH, subboreal humid; PZ, polyzonal species; (c, d) ranges in the latitudinal aspect. Designations: WPA, West Palearctic; EPA, East Palearctic; TPA, trans-Palearctic: CPA, central Palearctic.

The species abundance pattern of the carabid population is determined primarily by predominant species: *A. brunnea*, *P. oblongopunctatus*, *P. fortipes*, *A. communis*, *H. cisteloides*, and *C. marginalis*. Boreal species are predominant, their cumulative species abundance being 37%. They are followed by subboreal humid (30%). Polyzonal and subarid species constitute 21 and 12%, respectively. With regard to the longitudinal aspect, the carabid population, as well as the fauna, is dominated by West Palearctic species (47%). Trans-Palearctic species are also abundant (40%), whereas East and central Palearctic ones are scarce: 10 and 3%, respectively. Thus, the carabid population of southern forest–steppe can be characterized as forest–steppe, or even forest, and, like the fauna, West-Palearctic.

The difference is related to the fact that most species responsible for the steppe habit of the fauna are scarce. The majority of the population in the forest and meadows is constituted by boreal and subboreal humid species. The only abundant species *P. fortipes* makes the percentage of East Palearctic carabids significant.

Thus, the local transition zone between the forest and open cenoses in the West Siberian forest steppe compares to both of them in area and differs in carabid species composition. According to confinedness to habitats, carabid species can be classified into forest, steppe, and those preferring the boundary between the forest and steppe.

When passing to smaller biotope units, we see that different habitats (forest, meadow, or steppe) have different carabid faunas and populations according to the vegetation type, and the population of meadow habitats is intermediate between the forest and steppe ones. The species composition and relative abundance patterns are also determined by the type of vegetation cover. This abrupt change occurs within no more than tens of meters. Even carabids, relatively mobile animals, display strict confinedness to habitats and, apparently, small areas of individual migration, confined to certain vegetation contours.

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