FORESTRY IDEAS, 2020, vol. 26, No 2 (60): 435–451

THE GROUND BEETLES (COLEOPTERA: CARABIDAE) FROM A SIGNIFICANT, BUT POORLY STUDIED REGION IN NW BULGARIA. PART 2: ECOLOGY

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Received: 12 October 2020 Accepted: 22 November 2020

Abstract

This is the second part of the study representing the first overall assessment of the ground beetle fauna in the region of the Zlatiya plateau. The study aimed at analyzing the ecological structure of the carabid fauna represented by 6598 adult carabid specimens, belonging to 138 species, 49 genera and 20 tribes. The dominant structure was characteristic with the presence of 2 eudominants numbering 26 % of all specimens (*Harpalus rufipes* and *Harpalus tardus*), 4 dominants (26 %), 1 subdominant (3 %), 17 recedents (27 %) and 114 subrecedents (18 %). The analysis of the life forms showed only a slight predominance of the zoophages (71 species; 52 %) over the mixophytophages (67 species; 48 %). Similar ratio (50: 50 %) is mostly approaching to the typical for the steppe zones, for the orchards from the forest-steppe zones, and for the vast deforested territories across Europe. Humidity preferences analysis showed the larger share of the mesoxerophilous carabids. The prevalence of the macropterous carabids reflected their higher mobility and adaptiveness.

Key words: carabid communities, dominance structure, life forms, wing morphology, Zlatiya.

Introduction

Ground beetles (Coleoptera: Carabidae) represent one of the largest beetle families with cosmopolitan distribution and with decisive importance for the functioning of ecosystems. The high taxonomic richness, the large numbers and the diverse life specializations are the reasons they cover the entire environmental spectrum of fundamental natural gradients. These substantive arguments lie at the base of the possibility ground beetles and their communities to be widely used as bioindicators of terrestrial environment in the system of biological monitoring (Desender and Baert 1995, Luff 1996, Cranston and Trueman 1997, Rainio and Niemelä 2003, Pearsall 2007, Rainio 2009). Their agronomic significance together with the high diversity and well-defined ecological niches, explain their common use in ecological analyses, habitat quality evaluation and studies of ecosystem succession (Desender et al. 1994, Luff 1996, Rainio and Niemela 2003, Pearce and Venier 2006, Pearsall 2007, Ludwiczak et al. 2020) or anthropogenic impact (Paoletti and Bressan 1996, Avgin and Luff 2010, Langraf et al. 2016).

Carabids and their communities are excellent model for ecological and conservation research (Langraf et al. 2016). Many studies have been conducting with regards of different ecological and morphological characteristics of carabids. Ecological parameters of their communities can be used in assessing the state of the environment and predicting the trends in the future development of the ecological systems. This way, synecological studies are often used to characterize the influence of the biota on the environment, and the impact of human activity on the functioning, productivity and changes in the ecosystems.

This study aimed at analyzing the ecological structure of the carabid coenoses in relation to main ecological parameters, e.g. dominance structure, species richness, similarity between carabid communities, life form categorization, wing development, and humidity preferences, with a subsequent assessment of the environmental trends and anthropogenic impact in the studied area.

Materials and Methods

The design of the field work and the details about the material, including the full species list with all ecological data compiled, were presented in the first part of the research (Teofilova and Kodzhabashev 2020b). We used 97 pitfall traps, set in 8 different by vision and structure territories. In each sampling site, 12 traps were set, only in site VI the traps were 13 (Table 1). The entire period of sampling was 236 days. Sampling sites II, III, IV, and V were studied during the whole period. Sampling sites VI, VII and VIII were studied for 188

Table 1. Sampling effort and activity density of carabids in the studied habitats, and share of the species found in only one habitat (further called 'specific' or 'unique').

	Sampling site	Number of traps		Trap-days		Specimens		No ex./ 100 trap-days	Species	
		Set	Collected [sampling period]	Total number	% realised	Number	Share, %		Number	Unique sp./site
I	Harvested, not plowed wheat field	12	9 [1]; 2 [2]	606	37.0	182	3.0	30.0	24	4
II	Micro dam, shore	12	8 [1]; 9 [2]; 7 [3]	1874	69.0	637	10.0	34.0	70	22
III	Micro dam, pseudo-steppe-like habitat	12	10 [1]; 9 [2]; 9 [3]	2172	77.0	944	14.0	43.5	51	5
IV	Ogosta River shore	12	12 [1]; 9 [2]; 6 [3]	1965	69.0	1641	25.0	83.5	58	5
V	Mesophilic oak forest	12	7 [1]; 7 [2]; 11 [3]	2056	73.0	1413	21.0	68.7	38	3
VI	Loess steppe-like habitat near Shishmanov Val Dam	13	13 [2]; 12 [3]	2343	96.0	1186	18.0	50.6	53	13
VII	Loess steppe-like habitat near the Danube River	12	3 [2]; 9 [3]	1170	52.0	313	5.0	26.7	37	1
VIII	Grazed pasture with bushes	12	10 [2]; 11 [3]	1981	88.0	282	4.0	14.2	33	0
	Total	97		14167	71	6598	100	46.6	138	53

days (two collecting periods), and sampling site I was studied only for 135 days (two collecting periods). The material was collected thrice, the first sampling period (spring) [1] being of 48 days, the second (summer) [2] of 87 days, and the third (autumn) [3] – 101 days. Four of the sites were sampled twice, which was considered in calculating the activity density of carabids. 'Activity density' is the number of specimens per 100 trap-days during the trapping period.

This part of the research encompassed some ecological characteristics of the carabid communities.

In order to determine the dominance structure, the relative abundance (or degree of dominance) was used: $D = (n_i/N)\cdot 100$, where n_i is the number of individual representatives of each species, and N – their total number. The classical four-level classification of Tischler (1949) for invertebrates, modified by Sharova (1981) with the initiation of a 5th category 'eudominant', was adopted: eudominants (> 10 % of all individuals); dominants (5 to 10 %); subdominants (3 to 5 %); recedents (1 to 3 %); subrecedents (< 1 %). For the assessment of the species with a significance < 1 %, we used the following 5-ball scale, according to calculations based on Pesenko (1982): single species (represented by 1 ex., D < 0.02 %); random (2–7 ex., D = 0.02–0.1 %); sporadic (8–20 ex., D = 0.1–0.3 %); very rare (21–33 ex., D = 0.3–0.5 %); rare species (34–66 ex., D = 0.5–1 %).

Species richness in both studied habitats was calculated using the Margalef's species richness index (Margalef 1958) [$D_{Mg} = (S–1)/\ln N$] and Menhinick's species richness index (Menhinick 1964) [$D_{Mn} = S/\sqrt{N}$], where S is the number of species, and N is the number of specimens.

Categorization of the species in respect of their life forms followed the classification of Sharova (1981). Species were also classified into three groups according to their hind wing development: winged or macropterous (always possessing wings), wing dimorphic/polymorphic (only part of the population being fully winged), and brachypterous (wingless), according to the commonly accepted classification of Den Boer et al. (1980).

According to their ecological requirements in terms of humidity, the established carabid species were divided into six categories (Teofilova 2018a): hygrophilous, mesohygrophilous, mesophilous, mesoxerophilous, xerophilous, and eurybionts.

The data were processed with MS Excel and PRIMER 6 (Clarke and Gorley 2005).

Results

During the study, a total of 6598 adult carabid specimens were captured. Beetles belonged to 138 species, classified into 49 genera and 20 tribes (see Teofilova and Kodzhabashev 2020b). In total, over the entire study period, 14167 trap-days were realised with the exposure of the 97 pitfall traps. This accounted for 71 % of the potentially possible trap-days (Table 1). These sampling results could be considered successful and used for ecological analyses. The only exception was the sampling site I (an arable agricultural area), where collection periods were limited by the agricultural programmes. For this site we considered that the life cycles of its inhabitants were ephemeral, characteristic of similar natural communities in the steppes of Eurasia, as well as for agrocoenoses with a one-year crop cycle and subsequent ploughing for the following year. The sampling success in all other sampling sites was more than 50 % (even > 90 % in site VI), making the biological information suitable for analysis.

Dominance structure and rare species

The dominance structure of the entire carabid complex was characterised by the presence of 2 eudominants (with a total number of 26 % of all caught specimens), 4 dominants (26 %), 1 subdominant (3 %), 17 recedents (27 %) and 114 subrecedents (18 %). The eudominant species were *Harpalus tardus* (Panzer) and *H. rufipes* (De Geer), dominants were *Pterostichus melas* (Creutzer), *Abax carinatus* (Duftschmid), *Calathus fuscipes* (Goeze), and *Brachinus crepitans* (Linnaeus), and the subdominant species was *Ophonus laticollis* Mannerheim (Table 2). The dominance structure showed a presence of seven dominant species (*D* > 3 %) (5 % of all species). Subrecedents (*D* < 1 %) were 83 % of the species and 18 % of the specimens. Together with the recedent species (*D* = 1–3 %) (17 species, 12 %), the total share of the recedent community component made up 95 % of the species. Thus, the ratio of the quantitative significance of the dominant community component to the recedent component was 55 % : 45 %, and the qualitative ratio was 5 % : 95 %.

Twenty-five of the 114 subrecedent species were presented with one individual (18 % of the species and only 0.4 % of specimens) (Table 3). These single species were most numerous in the coastal territory, due to the many extra- and intrazonal phytophilic species. In other habitats, this category was represented by 1–3 species. Most of these species are usually less abundant due to their stenotopic nature.

Table 2. Dominance structure.

Category	Species	No
eudominant	*Harpalus rufipes*, *Harpalus tardus*	2
dominant	*Abax carinatus*, *Brachinus crepitans*, *Calathus fuscipes*, *Pterostichus melas*	4
subdominant	*Ophonus laticollis*	1
recedent	*Amara anthobia*, *A. convexior*, *Anchomenus dorsalis*, *Calathus ambiguus*, *Carabus coriaceus*, *C. ullrichi*, *Harpalus atratus*, *H. caspius*, *H. flavicornis*, *H. rubripes*, *H. subcylindricus*, *Ophonus azureus*, *O. cordatus*, *O. sabulicola*, *Platyderus rufus*, *Stenolophus mixtus*, *Trechus quadristriatus*	17
subrecedent	all the rest	114

Table 3. Subrecedent species (*D* < 1 %) in the different sampling sites.

Category	I		II		III		IV		V		VI		VII		VIII		Total	
	No	%	No	%	No	%	No	%	No	%	No	%	No	%	No	%	No	%
Single	2	1.5	12	8.7	3	2.2	2	1.5	3	2.2	2	1.5	1	0.7	-	-	25	18.1
Random	8	5.8	18	13.0	10	7.2	14	10.1	3	2.2	13	9.4	6	4.3	5	3.6	46	33.3
Sporadic	4	2.9	12	8.7	10	7.2	10	7.2	5	3.6	10	7.2	5	3.6	4	2.9	25	18.1
Very rare	2	1.5	2	1.5	3	2.2	4	2.9	2	1.5	4	2.9	5	3.6	4	2.9	10	7.2
Rare	1	0.7	4	2.9	5	3.6	6	4.3	3	2.2	6	4.3	5	3.6	5	3.6	8	5.8
Total	17	12.4	48	34.8	31	22.4	36	26.0	16	11.7	35	25.3	22	15.8	18	13.0	114	82.5

Random species ($D < 0.1$ %) were 46 (33 % of the carabid fauna and 3 % (183 ex.) of the total catch). They showed a strong presence in the coastal habitats. Sporadic ($D = 0.1–0.3$ %) were 25 species (18 %), accounting for 5 % (328 ex.) of all specimens. Very rare ($D = 0.3–0.5$ %) were 10 species (7 %) with 4 % (266 ex.) of all specimens. Eight species were rare, accounting for 6 % of the area's carabid fauna and 27 % (1788 ex) of the total catches.

The communities in sampling sites I, VII, VIII and VI were clearly distinguishing by the number of rare species in them, respectively by their spatial, structural and functional capacity, reflecting the degree of successional development: e.g. arable land – 17 rare species, pasture – 18 species, abandoned pasture after fire – 22 species, and loess steppe formed secondary at the place of an abandoned pasture – 35 species.

Diversity indices and similarity

The α-diversity of carabid communities calculated with Menhinick's and Margalef's indices showed that humid habitat near the lake shore (site II) had the highest species richness. The lowest values were in the climax oak forest (V) and intensive wheat field (I) (Table 4).

Table 4. Species richness of carabid communities in Zlatiya Plateau.

Indicators	Sampling sites							
	I	II	III	IV	V	VI	VII	VIII
Number of specimens, $N = 6598$	182	637	944	1641	1413	1186	313	282
N, %	3	10	14	25	21	18	5	4
Number of species, $S = 138$	24	70	51	58	38	53	37	33
S, %	17	51	37	42	27	38	27	24
$D_{Mg} = (S–1)/\ln N = 15.6$	4.4	10.7	7.3	7.7	5.1	7.4	6.3	5.7
$D_{Mn} = S/\sqrt{N} = 1.7$	1.8	2.8	1.7	1.4	1.0	1.5	2.1	2.0

According to the taxonomic structure and species abundance, the similarity dendrogram showed that the quantitative significance of the species (based on their abundance) strongly depended on the way of modern land management and the succession processes that took place in the recent past (Fig. 1). Sampling sites with similar microclimatic, edaphic and physiographic conditions (II and III, IV and V) were grouped at a relatively high degree of similarity. These natural habitats were separated, allowing the hypothesis that the quantitative significance of the carabids is indicative of the degree of anthropogenic influence. In this case, the heavily influenced habitats I and VII (eroded slopes and abandoned pastures overgrown with weeds and synbovine ruderals) were grouped as a single couple with a very low degree of similarity. They were clearly separated from those that have become 'loess pseudo-steppes' after the cessation of the intensive grazing (VI, VIII), and from the natural riparian (II, III) and forest (IV, V) habitats with relatively poorly modified biotic parameters of the environment.

The grouping of the habitats by qualitative similarity (species composition of carabids) was analogous to the quantitative, but even more definite (Fig. 2). Clearly distinguishable were the three habitat types according to their anthropogenic impact: arable land (I), loess pseudo-steppes and pastures (VI, VII, VIII), and natural habi-

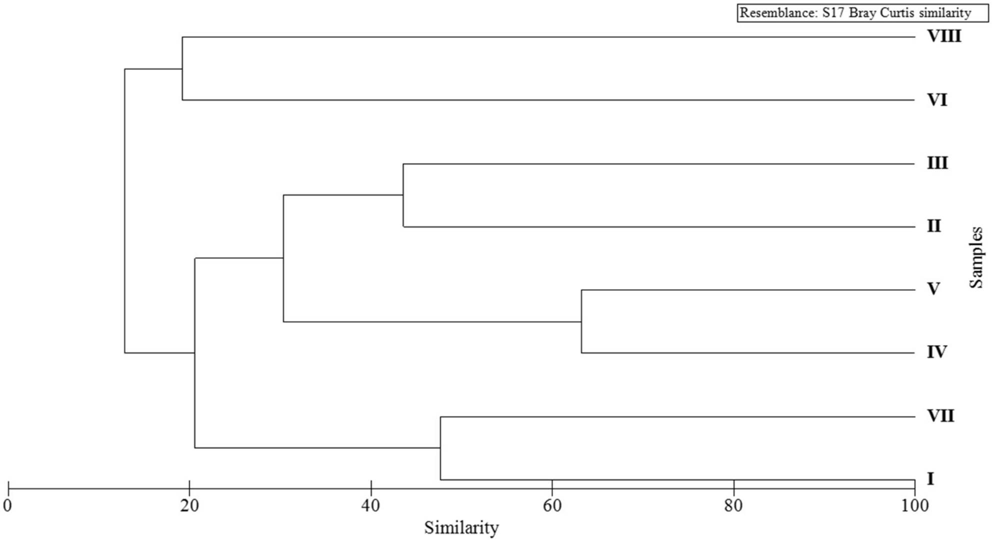

Fig. 1. Dendrogram of the similarity based on quantitative significance.

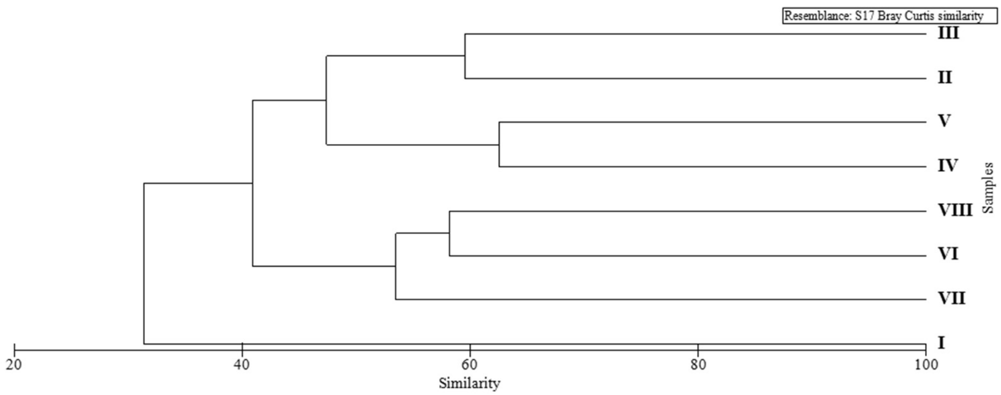

Fig. 2. Dendrogram of the similarity based on qualitative significance.

tats (II and III, IV and V).

Life forms

The 138 ground beetle species belonged to two classes and 18 life form groups proposed by Sharova (1981) – 12 zoophagous and 6 mixophytophagous. The life forms of each species were given in the first part of the study (Teofilova and Kodzhabashev 2020b). The analysis of the life forms occurring in the whole complex of ground beetles showed only a slight predominance of the zoophages (71 species; 52 %) over mixophytophages (67 species; 48 %). In quantitative aspect the ratio was quite different: zoophagous were 3011 ex. (46 %), while mixophytophagous were 3587 ex. (54 %). It was noticeable the significant percentage of the mixophytophagous harpaloid geohortobionts, mainly due to the increased presence of species from the genus *Harpalus* (Table 5).

Table 5. Life forms of the ground beetles from the Zlatiya Plateau.

Life forms		No sp.	%	No ex.	%
	Class: Zoophagous				
	Life form subclass: 1.1 – Phytobios				
1.1.2	Stem-dwelling hortobionts	1	0.7	1	0.01
1.1.3	Leaf-dwelling dendrohortobionts	2	1.4	3	0.04
	Life form subclass: 1.2 – Epigeobios				
1.2.2	Large walking epigeobionts	5	3.6	316	4.8
1.2.3	Running epigeobionts	2	1.4	13	0.2
1.2.4	Flying epigeobionts	2	1.4	32	0.5
	Life form subclass: 1.3 – Stratobios				
	Series: 1.3(1) – crevice-dwelling stratobionts				
1.3(1).1	Surface & litter-dwelling	16	11.6	327	5.0
1.3(1).2	Litter-dwelling	18	13.0	1038	15.7
1.3(1).3	Litter & crevice-dwelling	11	8.0	498	7.5
1.3(1).4	Endogeobionts	1	0.7	1	0.01
1.3(1).6	Bothrobionts	1	0.7	24	0.4
	Series: 1.3(2) – digging stratobionts				
1.3(2).1	Litter & soil-dwelling	11	8.0	755	11.4
	Life form subclass: 1.4 – Geobionts				
1.4.2(1)	Small digging geobionts	1	0.7	3	0.04
	Zoophagous total	**71**	**52.0**	**3011**	**45.6**
	Class Mixophytophagous				
	Life form subclass: 2.1 – Stratobios				
2.1.1	Crevice-dwelling stratobionts	7	5.1	202	3.1
	Life form subclass: 2.2 – Stratohortobios				
2.2.1	Stratohortobionts	18	13.0	1471	22.3
	Life form subclass: 2.3 – Geohortobios				
2.3.1	Harpaloid geohortobionts	33	23.9	1812	27.5
2.3.1(1)	Crevice-dwelling harpaloid geohortobionts	1	0.7	1	0.01
2.3.2	Zabroid geohortobionts	5	3.6	67	1.0
2.3.3	Dytomeoid geohortobionts	3	2.1	34	0.5
	Mixophytophagous total	**67**	**48.0**	**3587**	**54.4**

Note: the first figure in the index shows the class of life form, the second shows the subclass, and the third indicates the life form group; the figure in brackets after the subclass shows the series, if any.

When examining in detail the structure of the life forms, the significance of three subclasses was emphasised. Of the class Zoophagous, the most significant was the subclass Startobios comprising 58 species (42 % of all species) and 1888 ex. (29 % of all specimens), and of the class Mixophytophagous – the subclass Geohortobios with 42 species (30 %) and 1914 ex. (29 %), as well as the subclass Stratohortobios with 18 species (13 %) and 1471 ex. (22 %).

The most numerous life form groups were the harpaloid geohortobionts (33 species; 24 %) and the stratohortobionts (18 species; 13 %) from class Mixophytophaga, and the litter-dwelling stratobionts (also 18 species; 13 %) and the surface & litter-dwelling stratobionts (16 species; 12 %) from class Zoophaga (Table 5).

Wing morphology

The degree of hind wing development allowed distinguishing of three groups of carabids: brachypterous (hind wings shorter than elytra or missing), macropterous (winged), and dimorphic (some individuals have fully developed wings, others only vestigial ones). For one species in our study (1 %) there were no data about its wing morphology. Macropterous beetles represented 69 % (95 species) of all collected carabid species. Pteridimorphic species were 22 % of all (31 species), and brachypterous were only 8 % (11 species) (Fig. 3).

Humidity preferences

Analysis of the humidity preferences (Fig. 4) of the ground beetles showed the prevalence of the mesoxerophilous carabids (50 species, 36 % of all established species). Mesophilous were 27 species (20 %). Less represented were mesohygrophilous (17 species), xerophilous (15 species), and hygrophilous (14 species) carabids.

Discussion

The established average activity density for the entire study period, with 6598 specimens collected over a period of 14167 trap-days, was 46.57 specimens per 100 days, meaning a relatively high activity density averaged for Bulgaria (Teofilova 2013, Kodzhabashev 2016). The large range of variation of the average activity density of the areas studied was remarkable. The minimum value of 14.24 ex./100 trap-days was recorded in the intensively grazed pasture, where the regular removal of plant biomass was probably an extremely important factor in the energy capacity of the habitat, leading to a limitation of the density of carabids in general. Such low values of activity density have the arable lands, recently abandoned pastures or

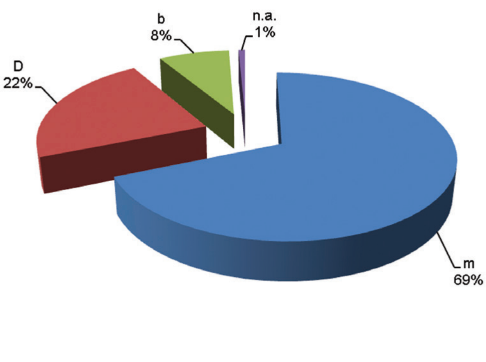

Fig. 3. Wing morphology of carabid species in Zlatiya plateau.

Note: m – macropterous, D – wing di(poly) morphic, b – brachypterous, n.a. – no data.

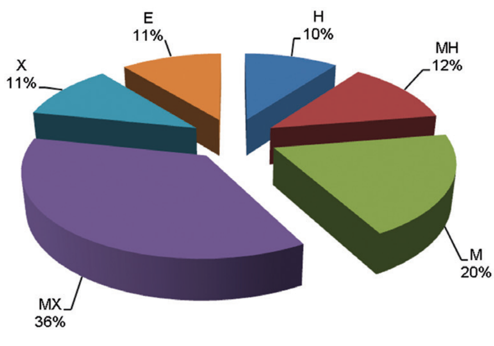

Fig. 4. Humidity preferences (number of species) of the carabids.

Note: H – hygrophilous, MH – mesohygrophilous, M – mesophilous, MX – mesoxerophilous, X – xerophilous, E – eurybiont.

synanthropic habitats, where, depending on the strength and duration of human impacts, a trend in biocoenoses degradation is observed (Aidamirova 2011, Sukhodolskaya et al. 2020).

Especially high were the values of activity density (respectively, of ecosystem productivity) in the forest and riparian habitats (83.51 and 68.73, respectively), which can be explained with their climax state. The activity density values usually correspond proportionally with the numbers of the specimens caught, when the total percentage of trap-days realised was more than 50 % and the samplings were carried out throughout the study period.

According to the results obtained about the activity density, the number of specimens and species collected, and the species unique to each territory, we may divide the habitats into two categories: 1) natural habitats with a natural course of ecological development, in or near a climax state, and 2) synanthropic habitats with varying degrees of influence depending on the purpose and manner of the land use. Forest and riparian habitats, in addition to their high activity density, had a rich and stable species composition and a relatively large number of specific species. In the synanthropic habitats, we found the significant differences in their ecological characteristics to be typical. Relatively low activity density, poor fauna, and lack or limited number of specific species were found in the wheat field (I), followed by the intensively grazed pasture (VIII), and the regularly burnt grassland on the Danube coast (VII). The exception was the abandoned pasture on the shore of the Shishmanov Val Dam (VI), where processes of advanced secondary succession were observed, consisting in relatively high activity density, rich species composition and presence of a large number of specific species. This was probably due to the relatively long period of lack of anthropogenic intervention and subsequent successional processes under the specific conditions of the changed environment. The absence of conditions for the development of woody vegetation due to erosion and degradation processes, given the strong slope and subsequent pasture exploitation after the deforestation, were the reason for the establishment of perennial xerophilic grass formations, creating an environment and conditions for the development of a specific carabid coenose representing a complex of heterogeneous in origin, distribution, taxonomic and ecological affiliation species.

The analysis of the dominance structure showed the presence of eudominant species, which seems typical for anthropogenically influenced and unsustainable ecosystems, and was also established by Kodzhabashev and Mollov (2000), Kostova (2004), and Teofilova (2015). There is a proportionate imbalance and a distorted ecological structure lacking evenness between the species. The relative share of species with significance less than 1 % of total catches was 114 species (83 %), and that of dominant species (*D* > 3 %) was only 7 species (5 %). Similar ratio was established in the region of Cape Emine, where dominant species (*D* > 3 %) were 7 %, and the sudrecedends (*D* < 1 %) were 82 % of the species (Teofilova 2015).

Rare species (*D* < 1 %) were represented by 1177 specimens (20 %), and the dominant species (*D* > 3 %) had 3615 specimens (55 %). The ratio in the region of Cape Emine was similar, i.e. 15 % and 60 %, respectively (Teofilova 2015). Such results seem characteristic of plain territories with developed agriculture, where arable land covers all suitable terrains, and natural and semi-natural habitats are severely limited to small patches preserved mainly along the steep gullies and the banks of rivers and standing water bodies. For the carabid fauna, these habitats act as local refugia of extremely high conservation importance for the survival of most species.

The quantitative significance was 26 % for the two eudominants (*Harpalus tardus* and *H. rufipes*), 26 % for the four dominants (*Pt. melas*, *A. carinatus*, *C. fuscipes*, and *Br. crepitans*), and 3 % for the subdominant species *O. laticollis*. The two eudominants in the region of Cape Emine (*Carabus coriaceus* Linnaeus and *Chlaenius nitidulus* (Schrank) had similar abundance – 35 % of all specimens (Teofilova 2015). *Harpalus rufipes* is a widespread Palaearctic, ecologically plastic eurybiont. It is dominant in most researches with pitfall traps (Popov and Krusteva 1988, Shishiniova et al. 2001, Aidamirova 2011, Kodzhabashev 2016, Trushitsyna et al. 2016, Putchkov et al. 2020, Sukhodolskaya et al. 2020). In agrocoenoses it can reach very high densities, especially if it lacks competition due to intensive chemical agriculture. This species is registered in all sampling sites, having relatively low density and numbers only in pastures and dry pseudo-steppes. The second eudominant, *H. tardus*, is eurytopic with preferences for shady habitats. In studies of the carabid coenoses of Dobrudzha this species was dominant in forest habitats (Penev 1993, Kodzhabashev 2016). Its absence in the arable territories is inexplicable, given its great ecological plasticity and its occurrence in other anthropogenised areas of the Danube Plain (Kodzhabahsev 2016). Two of the other dominants (*C. fuscipes* and *Br. crepitans*) are eurytopic in open habitats, and have usually high numbers and density in both natural and synanthropic coenoses, including agrocoenoses (Shishiniova et al. 2001, Aleksandrowicz et al. 2009, Aidamirova 2011, Teofilova 2013, Kodzhabashev 2016, Trushitsyna et al. 2016, Putchkov et al. 2020). The other three species, *A. carinatus*, *P. melas* and *O. laticollis*, have high densities in forest habitats. We may consider them as indicators of that type of habitat for the area of the Zlatiya plateau, along with *Nebria brevicollis* (Fabricius), *Leistus rufomarginatus* (Duftschmid), *Notiophilus rufipes* Curtis, *Carabus ullrichi* Germar, *Myas chalybaeus* (Palliardi), *Platyderus rufus* (Duftschmid), *Amara saphyrea* Dejean. As quantitative indicators for the secondary steppe and agricultural habitats in the Western Danube Plain, we could classify *Calathus ambiguus* (Paykull), *C. erratus* (Sahlberg), *Amara aenea* (De Geer), *Ophonus azureus* (Fabricius), *O. cribricollis* (Dejean), *Harpalus rubripes* (Duftschmid), and *H. zabroides* Dejean.

Recurring ecological model in biocoenotic researches is the presence of a few abundant species and the predominance of the variety of rare species (Preston 1962), which is confirmed by the results of this study, showing the greatest number of species from the category of the subrecedents. The presence of many species with very low numbers may also be due to a methodical deficiency, i.e. many phytophilous species rarely climb down and move on the ground substrate, which is the reason for their low density in pitfall traps. The large share of the subrecedents (D < 1 %), i.e. 114 species (83 %), requires their detailed examination. The share of these species was found to be between 40 and 45 % in highly urbanized territories in Ukraine (Putchkov et al. 2020). The group of subrecedent species was divided according to the scale developed on the basis of the faunal abundance used by

Pesenko (1982). The species represented with only one specimen, called single (see Table 3), have always been of research interest. Species-rich genera and whole tribes do not fall into the traps or fall accidentally, with single specimens, due to low activity, excessively small size, and endogeic or horto-dendrobiont way of life. Such are the whole tribes Clivinini, Dyschiriini, Trechini, some Bembidiini, and some genera of the Lebiini and Harpalini.

Highly impressive was the small number of subrecedents in the forest habitat, possibly due to the climax state of the old mesophilic deciduous forest, with expressed evenness of the species and stable dominant structure of typical forest species. The most affected habitats, such as the agricultural lands, also have very few rare species (17 in total), the possible cause being in the severely disturbed dominant structure due to intensive land use and the lack of microhabitat diversity. High number of recedent species had the coastal habitats, where extra- and intrazonal (mostly phytophilic) species were recorded in low numbers, as well as the open secondary habitats with a low degree of recent anthropogenic intervention – the two abandoned pastures. Their modern appearance is of loess pseudo-steppes, overgrown with xerophilic and xerothermic herbaceous vegetation. In these habitats, rare species represent a sum of typical steppe and thermophilic xerobionts, and plastic species in a process of initial expansion. In general, the dominant structure of these communities is imbalanced, with a preponderance of the dominant community component and a great number of rare species, which is characteristic of communities in an initial phase of succession. Stenotopic species in these habitats are relatively few (5–6 species), but their presence can be considered an evidence of refugium for this type of fauna in the given area.

Cluster analysis of the communities' similarity showed higher rates of taxonomic similarity between associations, in comparison with the communities from the region of Cape Emine, where the habitats were much more diverse (Teofilova et al. 2015). More homogenous were the agrocoenoses near the city of Sofia (Shishiniova et al. 2001, Kostova 2004). The dendrograms showed that geographical location is essential for the spatial distribution of the habitats. However, the grouping also showed the succession path and the ecological transformation of degraded pastures, after the cessation of grazing and the change in edaphic and hydrothermal conditions. The change of the pasture management regime was a prerequisite for the establishment of complexes of plastic species of ground beetles, characteristic of the arid territories in the steppes and forest-steppes of Eurasia and open habitats of the Mediterranean. The deforestation of the Danubian plain in NW Bulgaria has radically changed the natural vegetation appearance and the natural faunistic complexes along with it. The vast arable and synanthropic territories have fundamentally changed the landscape and microclimate in the area. The persistent tendency towards steppification, as a consequence of mass aridization and soil erosion lead to the establishment of specific faunistic complexes.

In relation to the life forms, the same ratio between the two classes (Zoophages: Mixophytophages) as in our study was found by Kodzhabashev and Mollov (2000) when exploring open habitats in synanthropic habitats around Sofia, as well as by Kodzhabashev (2016), in open semi-natural areas around the Srebarna Reserve. Ratio 54: 46 % was found in xerophytic pseudo-maquis communities from the low mountain belt of southern Pirin Mts. (Teofilova 2020). Similar ratio (50: 50 %) between the classes of life forms is mostly approaching to the typical for the steppe zones and for the orchards from the forest-steppe zones, as well as the vast deforested territories across Europe (Sharova 1981). According to Sharova (1981), the normal ratio between the two classes is 60: 40 % for the forest-steppe areas, and 70: 30 % for the nemoral forest zone. Close to the normal ratios between the classes were established in the Srebarna Reserve – 60: 40 % (Kodzhabashev 2016), the region of Cape Emine – 57: 43 % (Teofilova 2013, 2015), and the Lower Tundzha Valley – 62.5: 37.5 % (Teofilova 2017). The average ratio in Bulgarian grasslands was calculated as 55: 45 % (Teofilova 2018b). Close to the normal for the nemoral zone was the ratio in the Western Rhodopes Mts. – 67: 33 % (Teofilova 2018a). Quantitative data about the life forms further demonstrate the anthropogenic impact in the study area, where the ratio increases to 54 % in favour of the mixophytophages. We found a predominance of the stratobiont zoophages, which has also been established amongst Dagestan carabids (Mammaevna et al. 2011), and harpaloid geohortobionts from class Mixophytophaga, which were also the most species rich category in pseudomaquises in SW Bulgaria (Teofilova 2020), as well as in the Eastern Rhodope Mts. (Teofilova and Kodzhabashev 2020a).

The structure we established most likely results from the changes in landscape and land use that have led to habitat xerophytisation due to deforestation and ploughing for agricultural purposes, the subsequent monocultural intensive farming, and soil erosion with 'stripping' of the base sediment (loess), which is heavily drained and easily evaporates soil moisture. Vast areas sown with cereals are close in microclimate factors to the natural steppes, but are monocultural. All these changes lead to strong structural changes of the spectra of life forms and, accordingly, to a change in the ratio of the two classes due to the replacement of the indigenous carabid fauna with a new thermo-xerophilic one.

Carabidae are mainly meso-, meso-hygro- and hygrophilous, and xerobionts have a relatively limited distribution in arid landscapes (Kryzhanovskij 1983). In contrast to the small share of the eurybionts (4 %) found in the Eastern Rhodope Mts. (Teofilova and Kodzhabashev 2020a), they accounted for 11 % here. Eurybionts were 8–10 % in sub-Mediterranean Balkan pseudomaquis habitats in SW Bulgaria (Teofilova 2020), and 9 % in the region of Cape Emine (Teofilova et al. 2015). The same share of mesoxerophiles (36 %) as in Zlatiya, was found in the Eastern Rhodope Mts. too (Teofilova and Kodzhabashev 2020a). According to Kryzhanovskij (1965, 1983), carabid eurybionts are mostly species with extensive Palaearctic or Eurasian ranges, and they are also ecologically plastic which provides them conditions for life in synanthropic and semi-natural environments, such as arable lands, pastures and forest plantations. The large number of eurybionts in the Zlatiya Plateau probably stems from the presence of extensive agricultural lands, where the synanthropic environment favours species with high ecological plasticity. In the studied region, forest habitats have undergone a strong reduction and after their transformation into agricultural lands, the mesophilous species composition has been proportionally changed and replaced by mesoxerophilous, i.e. there was a process of aridization of the habitats and, accordingly, of carabid coenoses, due to the replacement of mesophilous forest species with eurybionts. That explains the lower presence of the mesophiles (20 %). Similar changes have been found in other plain areas where the forest massifs have been destroyed and the land has been turned into agricultural, such as the Upper Thracian Lowland (Teofilova 2020a) and Dobrudzha (Kozhabashev 2016), as well as in xerothermic pseudomaquis habitats from the southern Pirin Mts. and Struma Valley, where deforestation took place (Teofilova 2020). As a comparison, in the Western Rhodope Mts., the share of the mesophilous carabids was 37 % of the species and 64 % of the specimens, due to the mountain and forest species (Teofilova 2018a).

The proportions and ratios between the different carabids' wing morphs, and their flight capabilities, respectively, can be used as indicators of the specific environmental conditions and tendencies in the development of carabid faunas and carabid coenoses in a given geographical area, since the migratory component comprises mainly macropterous species, whereas the stable component comprises mainly brachypterous species and predominantly brachypterous morphs of dimorphic species (Chernov and Makarova 2008). Such targeted and specialized studies on the ratio, proportions and structure of the wing forms of ground beetles in Bulgaria have not been conducted, with the exception for the analysis of the wing polymorphism of carabids in oilseed rape fields (*Brassica napus* L.) (Teofilova 2020b).

Specifically, for the Zlatiya Plateau, all mass eurytopic species were winged forms, explaining their wide range of distribution (Kryzhanovskij 1965). Wingless forms were only 8 %, of which six (*Carabus ullrichi*, *C. convexus*, *Myas chalybaeus*, *Pterostichus melas*, *Abax carinatus*, *Platyderus rufus*) are forest species, and another four (*Zabrus spinipes* (Fabricius), *Acinopus ammophilus* Dejean, *Licinus cassideus* (Fabricius), *Microlestes fulvibasis* (Reitter) can be classified as thermophilic stenobionts. It is probable that the requirements for specific environmental conditions are causing the lack of winged forms in these species, and the availability of the extensive spatial resource does not require the ability to disperse and move by flight. The reduction of the forests as a living resource in the Zlatiya can be taken as a synanthropic change that occurred relatively late, as evidenced by the presence of wingless forest forms, although they were not many. The value of di(poly)morphic species is difficult to be assessed in comparative terms, given the lack of information. Among these species we found both intrazonal epigeic hygrophiles (*Nebria brevicollis, Dyschirius globosus* (Herbst)*, Bembidion lampros* (Herbst), *Stomis pumicatus* (Panzer), *Pterostichus anthracinus* Illiger, *Pt. nigrita* (Paykull), *Pt. strenuus* (Panzer), *Pt. ovoideus* (Sturm), and forest species (*Leistus rufomarginatus*, *L. ferrugineus* (Linnaeus), *Ophonus laticollis*, *Harpalus atratus* Latreille). Within this group we also found some of the open habitats' species characteristic of the vast synanthropic habitats – agricultural land and pastures. They probably develop winged or wingless form, according to the need to fly, depending on the phase of distribution and expansion. This group included the polymorphic forms of the genera *Calathus*, *Ophonus*, *Harpalus*, *Microlestes*, and *Brachinus*.

Since macropterous wings are mainly used for dispersal flights, winged species seem normally especially abundant in scattered or disturbed habitats, e.g. cultural land. On the other hand, brachypterous species often are stenotopic (e.g. forest) inhabitants with a low dispersal ability (Kryzhanovskij 1965, Kromp 1999, Chernov and Makarova 2008). Our results are in accordance with Gray's hypothesis, that the proportion of flight capable pioneer species should increase with increasing disturbance, and the proportion of flightless species should decrease (Gray 1989). Very similar results about the wing morphology of carabids were obtained about oilseed rape fields in four European countries (Bulgaria, Germany, Romania and Switzerland) (Teofilova 2020b).

Conclusions

Activity density, combined with the number of specimens caught and the number of species identified, can be considered as a function of the spatial resource, productivity of the habitat and its energy capacity, allowing the values to be included in the interpretation of the habitats' biodiversity in the analysis of their nature, origin and condition.

The established dominant structure is characteristic of highly anthropogenically affected areas, where the share of ecologically plastic species is severely increased, and that of sporadic and random species is low. The imbalance in species distribution is strongly pronounced. The dominant component of the community ($D > 3$ %) includes seven species, representing 55 % of the specimens caught, and the remaining 131 species ($D < 3$ %) consisted of only 45 % of the total numbers.

Rare carabid species, qualitatively and quantitatively, have a relatively low presence both in the heavily influenced, and in climax communities, and gradation in their number can be used as a criterion for the degree of successional development, as there is a visible increase in their number as the succession progresses.

The two types of analysis of the similarity of the carabid coenoses – in quality and quantity, complement each other and reinforce the argumentation about the primacy of the natural landscape and microclimate for the area, as well as the changes occurred in the carabid communities after the mass deforestation, agricultural cultivation (ploughing), soil erosion and subsequent steppification as a result of strong microclimatic and microhabitat aridization.

There is a direct link between life forms and their taxonomic and zoogeographical affiliations (discussed in the Part 1 of the paper, see Teofilova and Kodzhabashev 2020b). Neareastern, Euro-Asiatic (steppe) and Mediterranean elements include mainly xero- and mesoxerophilous species of genera and tribes adapted for living in open habitats, regardless of the origin of grass communities and monocultures. The increased presence of eurybionts and the considerable share of the mesoxerophilous component are probably resulting from the drastic anthropogenic changes that have led to a significant reduction of forest habitats and their replacement by a 'cultural steppe'.

By the changes in the ratios between the wing morphs of carabid coenoses and the specific forms of the wing polymorphic species, the speed of environmental changes could be analysed, and the trend in regional microclimatic changes could be predicted. The prevalence of the macropterous carabids reflects their higher mobility and adaptiveness, and evidences the initial stage of formation of coenoses, as well as the unstable state of carabid populations.

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