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Article

Ecological grouping of ground beetles (Carabidae, Coleoptera) by biotopic preferences in the forest-meadow landscape of Udmurtia

A.G. Borisovskiy 

Udmurt State University, Universitetskaya St. 1, Izhevsk, 426034 Russia

borisovscky.alexander@yandex.ru

Abstract. Ground beetles collected in 2022 in the forest-meadow landscape of Udmurtia were studied in terms of biotopic preferences via using the indicator value index (INDVAL). This method provides the identification of indicator species for different hierarchal levels of habitats and the assessment of statistical significance of the obtained results. In the republic, the method was applied in the ground beetle investigations for the first time. It was found that for most studied species, the biotopic preferences generally coincided with those reported in the literature. However, some species were distinguished by a local specificity of biotopic preferences. In particular, 9 analyzed species out of 56 turned out to be the indicators of forest edges.

Keywords: indicator species, INDVAL, habitats

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ORCID:

A.G. Borisovskiy, <https://orcid.org/0009-0008-5032-3461>

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Научная статья

Экологические группы жужелиц (Carabidae, Coleoptera) по биотопическому преферендуму в лесолуговом ландшафте Удмуртии

А.Г. Борисовский 

Удмуртский государственный университет, 426034, Россия, г. Ижевск, ул. Университетская, д. 1

borisovscky.alexander@yandex.ru

Аннотация. По результатам сборов жужелиц, проведенных в 2022 г. в лесолуговом ландшафте Удмуртии, проведено исследование биотопических преференций жуков с помощью индекса индикаторной ценности (INDVAL). Метод позволяет выявлять виды-индикаторы для разных уровней иерархии местообитаний и оценивать статистическую значимость результатов. Ранее этот метод при исследовании жужелиц на территории республики не применялся. Обнаружено, что для большего числа исследованных видов биотопическая приуроченность в целом совпадает с известными по литературе особенностями. При этом для ряда видов выявлена местная специфика биотопических преференций. В том числе 9 видов из 56 использованных в анализе проявили себя как индикаторы лесных опушек.

Ключевые слова: виды индикаторы, INDVAL, местообитания

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ORCID:

А.Г. Борисовский, <https://orcid.org/0009-0008-5032-3461>

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Introduction

Carabid beetles (Carabidae) have been extensively studied in European Russia, including the Udmurt Republic (Dedyukhin, 2012). Biotopic preferences of ground beetles dwelling in the republic have been discussed in two studies (Dedyukhin, 2008, 2023).

Microclimatic factors play a decisive role in distribution of ground beetle species across habitats (Thiele, 1977). Depending on zonality or landscape features, optimal microclimatic conditions for the species may develop in the externally different habitats. Therefore, the range of habitats colonized by many (especially widespread) ground beetle species may vary within their range. For example, *Pterostichus melanarius* is an open-space species in the northern taiga, but in the southern steppe zone it populates the forested areas of river floodplains (Sharova and Filippov, 2004). A number of widely spread ground beetle species characteristic of open habitats in Western Europe, occupy dry forests in the forest-steppe zone of Russia (Thiele, 1977). In Central Europe and Fennoscandia, certain ground beetle species also exhibit a tendency to inhabit different biotopes (Lindroth, 1992b). In some cases, such a spatial variation in habitat colonization falls under the 'principle of zonal shifting of habitats (Bei-Bienko, 1966; Chernov, 1975). Landscapes within a single natural zone can also vary greatly in environmental conditions (Isachenko, 1991) which should affect the biotopic preference of ground beetles.

The principles of species ranking by ecological groups based on biotopic preferences are described in works of K.V. Arnoldi et al. (1972), A.G. Voronin (1999), V.G. Mordkovich and I.I. Lyubchansky (2010), I.Kh. Sharova and B.Yu. Filippov (2004). Most often, such an ecological grouping is implemented using the generalized data for large areas: Fennoscandia (Lindroth, 1992a), the forest zone of the Middle Urals (Voronin, 1999), the Belarusian Lake District (Solodovnikov, 2008), and the Netherlands (Turin et al., 1991). For meta-analysis, a number of studies combine the data from several regions (Magura and Lövei, 2020). In some publications, the data on beetles affiliation to ecological groups are processed in relation to the study area (Aleksanov and Alekseev, 2019; Bieringer et al., 2013; Niemelä et al., 2007; Sharova and Filippov, 2004; Solodovnikov, 2008), indicating that just authors decide how to treat the information from the reference books.

Identification of biotopic preferences of the species can be viewed as an independent task. Furthermore, when conducting ecological studies, a necessity often arises to consider a biotopic preference as an initial parameter for analysis. In this case, the goal is usually to attribute a species to one of three categories: forest, open-habitat, or generalist species. Such a species assigning to a particular ecological group based on biotopic preferences directly affects the calculation results. Studies of the influence of industrial pollution (Belskaya and Zinoviev, 2007), urbanization (Magura et al., 2004) and conditions gradients in the forest-edge-meadow system (Magura and Lövei, 2019, 2020) on the ground beetle assemblages are vivid examples.

When the generalized information for a given area is used without its adjusting to local conditions, the flaw of "argumentation based on closed-loop logic" (Shitikov et al., 2012) may arise. For example, if at the regional level a certain species is classified as "forest", but locally it exhibits the features of the "field" or "forest-edge" ones, its affiliation to the "forest" category in local studies will lead to contradictory results. Thus, the clarification of local specifics of biotopic preferences can be of fundamental importance.

Biotope-based distribution may be complicated by seasonal and inter-annual changes in biotopic preferences of species. Hence, depending on the study objective, assigning a species to a particular ecological group is feasible at several spatial and temporal scales. The larger the scale is, the more generalized data can be obtained.

The aim of this study is to identify biotopic preferences of ground beetle species at the local level through calculating the indicator value index.

Materials and methods

Study area

The data collection was conducted in 2022 in the Zavyalovsky District (Udmurt Republic) located in the subtaiga natural zone (Atlas Udmurtskoi Respubliki, 2020). The study area is located in the vicinity of Nepremennaya Ludzha village and represents a 1.7×1.7 km plot of the developed landscape (N 56.70398° E 53.06748°), including a forest area, adjacent meadows, and a field with perennial grasses. The site is situated on the northeastern slope of a ridge. The gradient of its elevation is 47 m and of the terrain – about 4°. Soils are light loamy throughout. Recreational pressure on meadows and forests is negligible. A total of 15 trap lines (Fig. 1) were laid in habitats of five types: forests (4 lines), forest edges (4 lines), meadows (3 lines), fields (2 lines), and river banks (2 lines). In this study, forest edges were considered as separate habitats because of a probable occurrence of the ecotone effect there (Odum, 1975). The distance between trap lines was at least 100 m. In forests and meadows, they were set 100 m (or more) from the forest-meadow boundary to avoid the edge effects (Murcia, 1995). Note that a distance exceeding 25 m between trap lines is recommended to obtain statistically independent samples (Digweed et al., 1995). The distance between the trap lines on river banks and the nearest lines in the forest or at the edges made up 10–20 m.

Trap lines in the forest were placed in the areas of maturing (approximately 70-year-old trees) wood. Line 1.1 was set in the flat area covered with the spruce-linden forest, line 1.2 – on the slope in the spruce-sorrel forest, line 1.3 – at the bottom of the slope in the spruce-sorrel forest, line 1.4 – in the spruce-sorrel forest of the small river valley.

The forest edge was on the flat plateau (trap line 2.1), on the slope (lines 2.2 and 2.3), and on the river terrace (line 2.4). Forest edges border meadows. Here, weed-ruderal-forb plant communities develop.

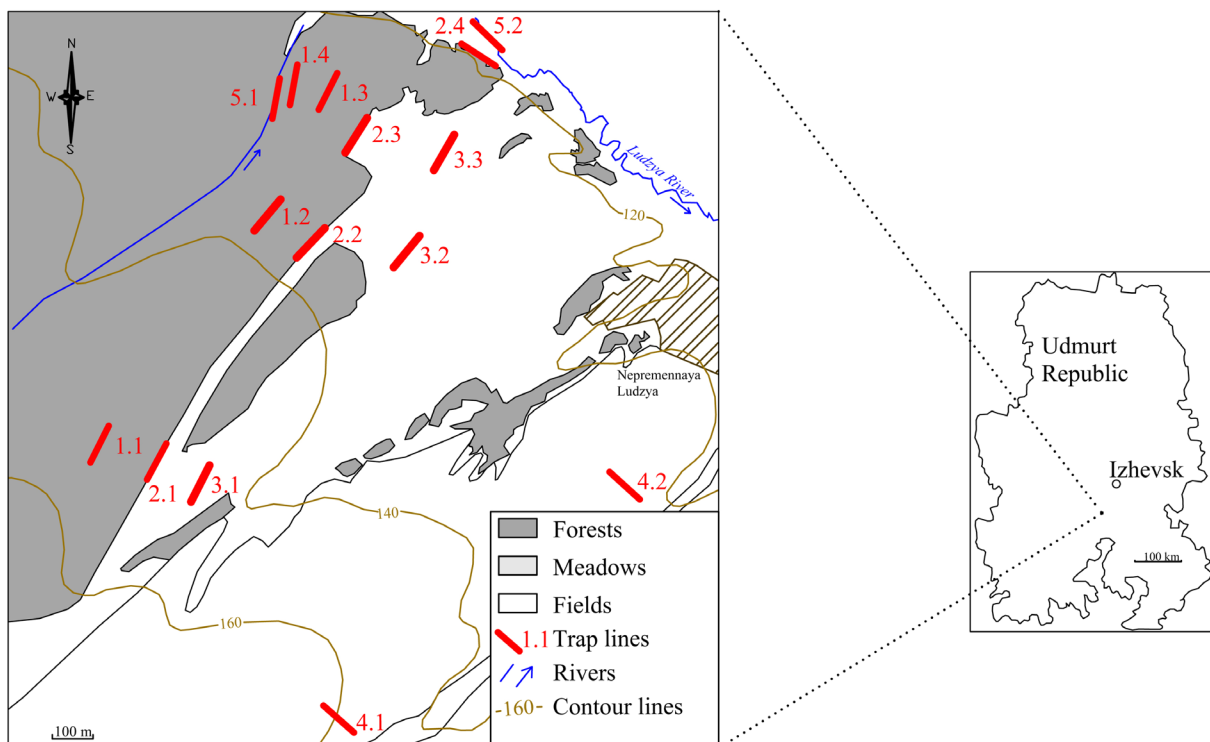


Fig. 1. Layout of trap lines.

Meadows (lines 3.1–3.3) represent originally overgrown fallow lands. Their economic use was ceased approximately 20 years ago. Here, making and grazing are not done anymore. Strawberry-*Pimpinella* and strawberry-forb communities have formed. Currently, these meadows are occupied by *Pinus sylvestris* L. trees, mostly of 2–4 m tall.

The perennial grass field (lines 4.1 and 4.2) sown with alfalfa more than 10 years ago has not been plowed since. Grass stand of this mown annually field consists of the alfalfa-grass community.

Trap lines 5.1 (open space) and 5.2 (streamside spruce forest) were located on the banks of small rivers, i.e. moistened soil strips along the water's edge.

Data collection and analysis

Each line contained 10 pitfall traps (Barber, 1931) representing disposable transparent plastic cups with a capacity of 320 ml and an opening diameter of 75 mm. The distance between traps reached 10 m. A 4% formalin solution was used as a fixer. We added a small amount of unscented liquid detergent to relieve the surface tension; trap lids were not used. Trapped animals were removed once every 7 days.

Traps were in operation from May 1, 2022 to October 9, 2022. On the river banks, they were set on May 7, 2022 since there was still some snow on May 1, 2022. Some of these traps were unused because of occurring uncontrollable factors (wildlife activity, floods, haymaking). Therefore, the number of trap-days per season on different lines varied from 1368 to 1610 (see Appendix). To test the influence of differences in sampling efforts on the analysis results, a verification calculation of the indicator value index (INDVAL) was performed applying the standardized (specimens per 100 trap-days) data. The outcomes turned out to be similar to the calculations based on the non-standardized data used in this study. Our investigation dealt with a total of 23,087 trap-days. Data from one trap line per season were combined into one sample and assumed to be an experimental unit (Kozlov, 2015).

For identification of all ground beetle species, the author used special Keys (Isaev, 2002; Kryzhanovsky, 1965; Lindroth, 1974; Lompe, 2002). The scientific names of the taxa are given in accordance with the systematic lists of ground beetles of Udmurtia (Dedyukhin, 2012; Dedyukhin et al., 2005) and Russia (Makarov et al., 2020). The correctness of identification of some species (*Amara*, *Harpalus*) was confirmed by B.M. Kataev (Zoological Institute of the Russian Academy of Sciences, St. Petersburg), while the rest were verified by S.V. Dedyukhin (Udmurt State University, Izhevsk). Since the species *Pterostichus nigrita* (Paykull, 1790) and *P. raeticus* Heer, 1837 were difficult to distinguish (Angus et al., 2000), all related data were combined under the name *P. nigrita* aggr. A complete list of the identified ground beetle species is given in Appendix.

Indicator species were defined using the INDVAL (Indicator Value Index) method proposed by M. Dufrière and P. Legendre (1997). It allows to identify the indicator species and species assemblages that characterize habitat groups. INDVAL can be calculated for any given habitat typology or for any level of their hierarchical classification. In INDVAL calculations, the average number of species individuals present in each of the identified habitat groups is used; this eliminates the influence of sites number in various groups and differences in abundance between sites within the same group.

INDVAL can be used to distinguish two types of indicator species. Asymmetric indicators (index less than 55%) predict the presence of the species only for certain habitats within a group, whereas symmetric ones (index greater than 55%) in all habitats.

The first step in applying the INDVAL method is to classify the study units (samples) by means of any suitable method. In this study, the sample consists of the number of ground beetles of different species captured from a single habitat (a single trap line) for the whole season. To classify these data, we use the non-hierarchical k-medoids algorithm (Kaufman and Rousseeuw, 1990) that enables to specify the number of clusters. It also allows to use the Bray-Curtis distance measure, which is recommended for building a distance matrix when analyzing the ecological communities (Shitikov, 2019). The criterion for selecting the "best" clustering level for a particular species is that corresponding to the highest INDVAL value in the habitat hierarchy (Dufrière and Legendre, 1997). The ANOSIM algorithm is employed in combination with a pairwise post-hoc test to assess intergroup differences in the sample classification derived from the k-medoids application (Clarke, 1993). Statistical significance of INDVAL values and ANOSIM results is assessed via using a randomization procedure.

During our study, a total of 19693 ground beetle specimens from 117 species were captured in 15 trap lines (see Appendix). To reduce the impact of random individuals in the analysis, all quantities equal to one individual were excluded, but only if this individual amounted less than 1% of the total number of individuals in the experimental unit. All species represented by fewer than 20 specimens in total samples were also excluded from the analysis (Dufrêne and Legendre, 1997). As a result, the analysed number of species and specimens was reduced to 56 and 19256, respectively.

PAST 4.11 (Hammer et al., 2001) was used for statistical processing of the data.

Results

The results of samples' clusterization from 15 habitats using the k-medoids algorithm are presented in Fig. 2. At the two-cluster stage ($k = 2$), habitats were divided into two groups: the first included open habitats (meadows and fields) and the second all the rest. Coastal habitats were separated from forests and forest edges at the three-cluster stage ($k = 3$). At the five-cluster stage ($k = 5$), we obtained a classification matching the a priori one. Small river banks, forested and non-forested habitats were separated only at the six-cluster stage ($k = 6$).

The ANOSIM test for the five-cluster stage (Fig. 3) yields significant differences ($p = 0.0001$) between habitat groups. A pairwise post-hoc test reveals statistically significant differences between forests and forest edges ($p < 0.05$), forests and meadows ($p < 0.05$), meadow and forest edges habitats ($p < 0.05$). Differences for other combinations are not statistically significant.

Resulted calculations of indicator value indices are shown in Table 1. In addition to statistically significant, the table includes non-significant (above 55%) results. Table 1 presents 51 out of 56 species included in the analysis.

Tabulation starts from the group "all habitats" (Dufrêne and Legendre, 1997). Since the INDVAL calculation method assumes the presence of at least two site groups, we use an artificially created typology to obtain the indicator value index for the group "all habitats". This typology, along with the aforementioned group, also involves the "forests + forest edges + banks" and "meadows + fields" groups. Besides, the table presents the calculations of indicator indices of the habitat group hierarchy in accordance with the clusterization results (Fig. 2).

The superposition of the resulted clustered habitat groups (Fig. 2) and the corresponding indicator value indices for ground beetle species (Table 1) is presented as the dendrogram in Fig. 3. In typology, maximum INDVAL values are highlighted. The authors of the method propose to assess the clustering level characterized by the highest indicator value as the most appropriate for a given species (Dufrêne and Legendre, 1997). Based on this criterion, the species marked in the figure in bold can be considered as the indicator species for habitats at different levels of their hierarchy. Most of these species are symmetrical indicators with statistically significant indicator value indices.

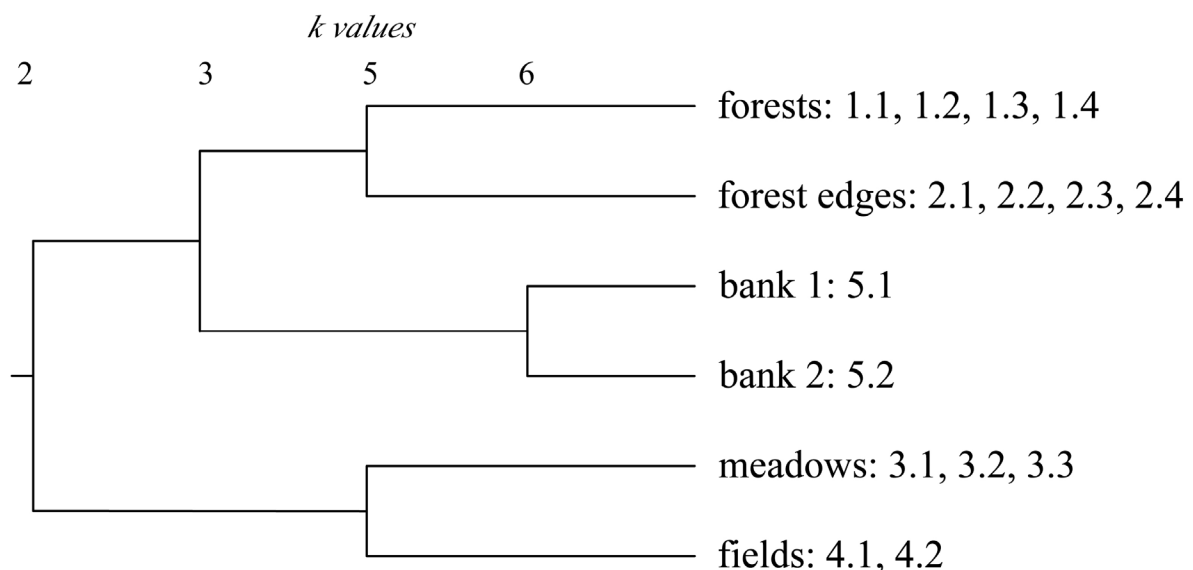


Fig. 2. Dendrogram of habitats clustering by the k-medoids method based on the Bray-Curtis similarity matrix.

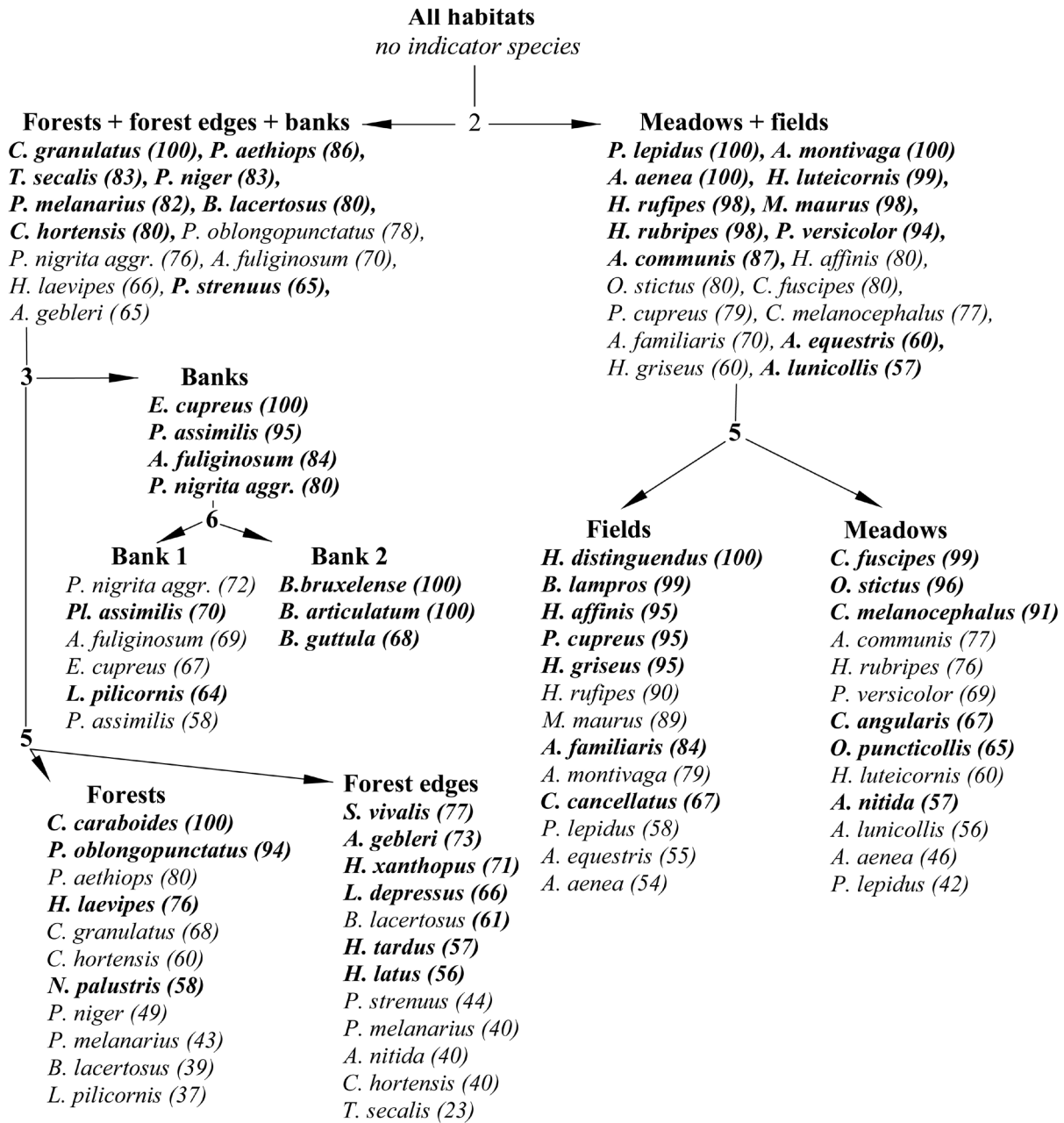


Fig. 3. Dendrogram of the distribution of indicator ground beetle species by habitat groups represented according to habitats clustering (see Fig. 2). Maximum INDVAL values for each species are given in bold.

Table 1. Resulted calculations of the indicator value index for habitats' hierarchy. In columns for each species, the numerator represents the number of captured ground beetle specimens, and the denominator - the number of habitats in the corresponding group where the species was captured. The INDVAL column shows the indicator value for the corresponding clusterization level. Statistical significance levels: * – $p < 0.05$; ** – $p < 0.01$; *** – $p < 0.001$.

Species	INDVAL	forests	forest edges	bank 1	bank 2	meadows	fields
Forests							
<i>C. caraboides</i>	100***	34/4					
<i>P. oblongopunctatus</i>	94***	907/4	36/3	6/1		8/1	
<i>P. aethiops</i>	80***	413/4	71/4	10/1		7/2	3/1
<i>H. laevipes</i>	76***	84/4	20/3				3/1
<i>C. granulatus</i>	68***	298/4	65/4	21/1	18/1		
<i>C. hortensis</i>	60**	94/4	63/4				
<i>N. palustris</i>	58**	39/3	7/2			3/1	
<i>P. niger</i>	49***	505/4	236/4	33/1	53/1	80/3	4/2
<i>P. melanarius</i>	43*	603/4	567/4	8/1	2/1	63/3	63/2
<i>B. lacertosus</i>	39*	29/4	45/4				
<i>L. pilicornis</i>	37*	25/3	2/1	12/1			
Forest edges							
<i>S. vivalis</i>	77**		31/4			7/2	
<i>A. gebleri</i>	73*	22/4	140/4			13/2	6/1
<i>H. xanthopus</i>	71**	15/2	105/4			21/1	
<i>L. depressus</i>	66**		28/3				2/1
<i>B. lacertosus</i>	61**	29/4	45/4				
<i>H. tardus</i>	57*		33/3			5/2	2/1
<i>H. latus</i>	56**	33/3	205/4		2/1	81/3	7/1
<i>P. strenuus</i>	44*	49/3	86/3	21/1		5/2	
<i>P. melanarius</i>	40*	603/4	567/4	8/1	2/1	63/3	63/2
<i>A. nitida</i>	40*		50/4			53/3	2/1
<i>C. hortensis</i>	40*	94/4	63/4				
<i>T. secalis</i>	23*	65/4	197/4		3/1	7/2	4/1
Forests + forest edges + banks							
<i>C. granulatus</i>	100***	298/4	65/4	21/1	18/1		
<i>P. aethiops</i>	86*	413/4	71/4	10/1		7/2	3/1
<i>T. secalis</i>	83*	65/4	197/4		3/1	7/2	4/1
<i>P. niger</i>	83***	505/4	236/4	33/1	53/1	80/3	4/2
<i>P. melanarius</i>	82*	603/4	567/4	8/1	2/1	63/3	63/2
<i>B. lacertosus</i>	80**	29/4	45/4				
<i>C. hortensis</i>	80**	94/4	63/4				

Species	INDVAL	forests	forest edges	bank 1	bank 2	meadows	fields
<i>P. oblongopunctatus</i>	78*	907/4	36/3	6/1		8/1	
<i>P. nigrita</i> aggr.	76	138/3	10/3	150/1	16/1	3/1	6/2
<i>A. fuliginosum</i>	70	7/3	3/3	14/1	3/1	1/1	1/1
<i>H. laevipes</i>	66*	84/4	20/3				3/1
<i>P. strenuus</i>	65*	49/3	86/3	21/1		5/2	
<i>A. gebleri</i>	65	22/4	140/4			13/2	6/1
Bank 1							
<i>P. nigrita</i> aggr.	72	138/3	10/3	150/1	16/1	3/1	6/2
<i>Pl. assimilis</i>	70	40/1		23/1			
<i>A. fuliginosum</i>	69	7/3	3/3	14/1	3/1	1/1	1/1
<i>E. cupreus</i>	67			14/1	7/1		
<i>L. pilicornis</i>	64	25/3	2/1	12/1			
<i>P. assimilis</i>	58	10/1	2/1	33/1	21/1		
Banks							
<i>E. cupreus</i>	100**			14/1	7/1		
<i>P. assimilis</i>	95**	10/1	2/1	33/1	21/1		
<i>A. fuliginosum</i>	84*	7/3	3/3	14/1	3/1	1/1	1/1
<i>P. nigrita</i> aggr.	80*	138/3	10/3	150/1	16/1	3/1	6/2
Bank 2							
<i>B.bruxelense</i>	100				127/1		
<i>B. articulatum</i>	100				29/1		
<i>B. guttula</i>	68*		9/2		16/1	5/2	7/1
All habitats							
<i>No indicator species</i>							
Meadows							
<i>C. fuscipes</i>	99**					545/3	2/1
<i>O. stictus</i>	96**					99/3	3/1
<i>C. melanocephalus</i>	91**		16/4			201/3	6/1
<i>A. communis</i>	77**	3/1	124/3			404/3	16/2
<i>H. rubripes</i>	76**		8/3			159/3	29/2
<i>P. versicolor</i>	69**	2/1	659/4		5/1	4549/3	1039/2
<i>C. angularis</i>	67*					29/2	
<i>O. puncticollis</i>	65*		2/1			64/2	
<i>H. luteicornis</i>	60*		13/4			448/3	190/2
<i>A. nitida</i>	57**		50/4			53/3	2/1
<i>A. lunicollis</i>	56*		3/1			29/2	2/1

Species	INDVAL	forests	forest edges	bank 1	bank 2	meadows	fields
<i>A. aenea</i>	46*					486/3	374/2
<i>P. lepidus</i>	42*					133/3	122/2
Meadows + fields							
<i>P. lepidus</i>	100***					133/3	122/2
<i>A. montivaga</i>	100***	2/1	4/2			269/3	677/2
<i>A. aenea</i>	100***					486/3	374/2
<i>H. luteicornis</i>	99***		13/4			448/3	190/2
<i>H. rufipes</i>	98***		9/2		11/1	18/3	248/2
<i>M. maurus</i>	98***		27/3			113/3	748/2
<i>H. rubripes</i>	98*		8/3			159/3	29/2
<i>P. versicolor</i>	94***	2/1	659/4		5/1	4549/3	1039/2
<i>A. communis</i>	87*	3/1	124/3			404/3	16/2
<i>H. affinis</i>	80**					16/2	203/2
<i>O. stictus</i>	80**					99/3	3/1
<i>C. fuscipes</i>	80**					545/3	2/1
<i>P. cupreus</i>	79**		4/2			9/2	168,2
<i>C. melanocephalus</i>	77*		16/4			201/3	6/1
<i>A. familiaris</i>	70	2/1	21/3			6/2	79/2
<i>A. equestris</i>	60*					27/1	22/2
<i>H. griseus</i>	60*					2/1	26/2
<i>A. lunicollis</i>	57*		3/1			29/2	2/1
Fields							
<i>H. distinguendus</i>	100**						29/2
<i>B. lampros</i>	99**		2/1				81/2
<i>H. affinis</i>	95**					16/2	203/2
<i>P. cupreus</i>	95*		4/2			9/2	168/2
<i>H. griseus</i>	95**					2/1	26/2
<i>H. rufipes</i>	90*		9/2		11/1	18/3	248/2
<i>M. maurus</i>	89**		27/3			113/3	748/2
<i>A. familiaris</i>	84**	2/1	21/3			6/2	79/2
<i>A. montivaga</i>	79*	2/1	4/2			269/3	677/2
<i>C. cancellatus</i>	67*	2/1	16/3		7/1		33/2
<i>P. lepidus</i>	58*					133/3	122/2
<i>A. equestris</i>	55*					27/1	22/2
<i>A. aenea</i>	54*					486/3	374/2

Among the species that represent open habitats (fields and meadows) and have high INDVAL values, two distinct groups can be specified. One includes the ground beetle species strictly confined to meadows and fields, being only occasionally encountered on forest edges, in forests, and on banks (*Poecilus lepidus*, *Amara aenea*, *Harpalus affinis*, *Ophonus stictus*, *Calathus fuscipes*, *Amara equestris*, and *Harpalus griseus*). The second group involves the species generally common for open habitats (meadows and fields), but also found in smaller numbers on forest edges and singly in forests and on river banks (*Poecilus versicolor*, *P. cupreus*, *Calathus melanocephalus*, *Amara montivaga*, *A. lunicollis*, *A. communis*, *Harpalus luteicornis*, *H. rufipes*, *H. rubripes*, and *Microlestes maurus*). A characteristic feature of open habitat species is that they are virtually (with rare exceptions as isolated individuals) never found along river banks (Table 1, Appendix). Only two species, *H. rufipes* and *P. versicolor*, have been recorded in the coastal catches.

With a decrease in the hierarchy level and open biotopes separation into “fields and meadows” (Table 1, Fig. 3), an increase in the indicator value index and/or its statistical significance is noted for some species. Thus, meadow species include *C. fuscipes*, *O. stictus*, *C. melanocephalus*, *Cymindis angularis*, *Ophonus puncticollis*, and *Amara nitida*. They are almost not detected in forests (with rare exceptions as single individuals) and found just singly on forest edges. An exception is *A. nitida*, which is equally referred both to the edge and meadow species. Encountered only in fields and not recorded in other biotopes, *Harpalus distinguendus* can be unambiguously classified as a field species. Similar species *Bembidion lampros* and *H. griseus* are caught singly in other habitats. Such species as *H. affinis*, *P. cupreus*, *Carabus cancellatus*, and *Amara familiaris* are good indicators of field biotopes in spite of their dwelling in other habitats as well.

The habitat group comprising forests, forest edges, and banks in the cluster hierarchy contrasts with open habitats and is characterized primarily by higher humidity. For example, the ground beetle species – *Carabus granulatus*, has been recorded in all biotopes of this group, but not collected in meadows or fields. Similarly, *Carabus hortensis*, *Trechus secalis*, *Pterostichus niger*, *P. melanarius*, *P. aethiops*, and *Badister lacertosus* demonstrate peak INDVAL values throughout.

The following trends are noted when “forests” and “forest edges” are separated from the previous habitat group ($k = 5$, see Fig. 2). For instance, the only ground beetle species found exclusively in the forests is *Cychrus caraboides*. *Notiophilus palustris*, *Pterostichus oblongopunctatus*, and *Harpalus laevipes* exhibit predominantly forest-dwelling characteristics, having the highest INDVAL values in this classification.

Species solely of the “forests-edges” habitats have not been detected. However, a number of ground beetle species exhibit the edges-specific behaviour; their INDVAL values in the “edges” habitat group are the highest in typology and statistically significant (Fig. 3). Among them *Synuchus vivalis* and *Harpalus tardus* are primarily observed on forest edges and are collected in fairly small quantities in adjacent meadows and fields. *Harpalus xanthopus* ssp. *winkleri* and *Harpalus latus* are abundant in forests and open biotopes.

In this paper, near-water biotopes are considered primarily to determine the diversity of habitats for typical meadow species, fields, and forests. However, the specificity of coastal species is clearly evident. According to our data, the species indicative of streams’ banks can be split into two groups. The first includes the species inhabiting only moist soil strips along the banks and not found in other habitats. These species are few in number in our collections. For example, *Elaphrus cupreus* was found in both near-water habitats, while *Bembidion bruxelense* and *Bembidion articulatum* only on the open river bank. The second group consists of species detected in other types of examined habitats. Some are characteristic only of the relatively wet biotopes (*Patrobus assimilis*, *Loricera pilicornis*), others are ubiquitous (*Pterostichus nigrita* aggr., *Agonum fuliginosum*) or inhabit only open habitats (*Bembidion guttula*).

The study suggests that when grouping the samples into 2–6 clusters, the highest INDVAL values are achieved by 46 species out of 56 analyzed (Table 1, Fig. 3).

The method for indicator species identification envisages splitting the sample groups down to the level where each group contains one sample. Note that in our case, 15 clusters can be obtained. When splitting the habitats into 7 clusters (not shown in figures), the highest INDVAL value falls on the species indicators of forest edges: *Bembidion gilvipes* (INDVAL – 100; $p < 0.01$); *Amara convexior* (INDVAL – 77; $p < 0.01$); *Harpalus tardus* (INDVAL – 76; $p < 0.05$); *Licinus depressus* (INDVAL – 80; $p < 0.05$); *Syntomus*

truncatellus (INDVAL – 69; $p < 0.05$). When grouping the habitats by 8 clusters, *Notiophilus palustris* (INDVAL – 50; $p < 0.05$; a forest indicator) is prominent, into 10 clusters – *Amara aulica* (INDVAL – 77; $p < 0.01$; forest edge indicator), 11 clusters – both *Amara lunicollis* (INDVAL – 85; $p < 0.01$) and *Cymindis angularis* (INDVAL – 96; $p < 0.05$) as meadow indicators, 12 clusters – *Amara equestris* (INDVAL – 71; $p < 0.05$; meadow indicator). At data clustering by 9, 13, and 14 clusters, the maximum index levels are not reached.

Thus, when classifying the habitats by 7 clusters, 5 more species demonstrate the maximum INDVAL value, and the remaining 5 achieve this level under splitting the samples into 8, 10, 11, and 12 clusters. Moreover, INDVAL indicators mostly exceed the threshold (55), i.e. the species at these hierarchical levels become symmetrical indicators. It should be noted that *B. gilvipes*, *A. convexior*, *H. tardus*, *L. depressus*, and *S. truncatellus* mainly serve as the indicators of edges after dividing the habitats into 7 clusters with subsequent splitting the edges into 2 groups ("2.1 and 2.2" and "2.3 and 2.4"). *B. gilvipes* indicates the edges in the lower part of the ridge (lines 2.3 and 2.4), whereas the remaining species are most characteristic of forest edges located upper (lines 2.1 and 2.2) along the relief (Fig. 1, Appendix).

Discussion

The study results of the indicator characteristics of ground beetles were compared with the data already known for Udmurtia (Dedyukhin, 2008, 2023), the regions adjacent to the republic (Tselishcheva and Alalykina, 2005; Voronin, 1999) and other territories (Aleksanov and Alekseev, 2019; Belova, 2014; Lindroth, 1992a; Magura and Lövei, 2020; Ruchin et al., 2015; Sharova and Filippov, 2004; Solodovnikov, 2008). In most cases, the identified features of species distribution within biotopes and their groups slightly differ from those already known. In general, ground beetle species do not demonstrate any specific features in terms of biotopic preferences in the studied territory. Consequently, their habitat distribution is quite predictable from the previously published data. This is particularly characteristic of species with a relatively high stenotopic state. For instance, *H. distinguendus*, *C. angularis*, and *O. stictus* are found throughout the forest zone, primarily in open habitats, while *C. caraboides* is a strictly forest species.

For more eurytopic species, habitat preferences may obviously vary due to diverse combinations of ambient conditions (temperature, humidity, etc.) in different landscapes and habitats. A striking example is *Carabus cancellatus*. This species is described as a forest-meadow representative of the forest zone of the middle Urals (Voronin, 1999); for the Kirov Region it is listed as the meadow and field species (Tselishcheva and Alalykina, 2005), for Fennoscandia – as an inhabitant of open habitats (Lindroth, 1992a), for the northern taiga – as an eurybiont (Sharova and Filippov, 2004). In the northeast of the European part of Russia, the species is not found in the taiga, but noted solely in the tundra (Kolesnikova et al., 2017). In the mixed forest subzone of the western part of the Russian Plain, this species is an eurytope (Aleksanov and Alekseev, 2019; Solodovnikov, 2008). S.Yu. Grünthal (2008) reports that *C. cancellatus* inhabits primarily fields in the taiga and coniferous-broadleaf forest subzones, and forests in the broadleaf forest subzone. S.V. Dedyukhin (2008, 2023) states that the species occupies sparse forests in Udmurtia. According to our unpublished data, *C. cancellatus* was abundant in a complex pine forest, 80 km south of the present study site, but not recorded in the adjacent barren meadows. According to 30 published papers for different regions (Magura and Lövei, 2020), the species is listed as a generalist, i.e. an eurybiont. According to our results, almost not found in forests *Carabus cancellatus* is predominantly common for open biotopes, primarily fields (Table 1, Appendix). Thus, biotopic preferences of this species exhibit local specificity, being generally consistent with the known trends.

Changes in habitat preferences of some other studied species are also noted. For example, *C. fuscipes* and *H. griseus*, according to our data, prefer open habitats, not forests. In other regions, they are encountered in forests (Aleksanov and Alekseev, 2019; Kolesnikova et al., 2017).

Among our findings is the identification of the edge species. In most previous studies, edges were generally not distinguished as separate habitats; accordingly, the edge species were not specifically identified. Even in cases where ground beetle taxocenes were studied in the forest-meadow gradient, the edge species identification was not always the goal, and in the analysis the categories "open habitat species," "forest species," and "eurytopic or generalists" were used (Brigić et al., 2014; Koivula et al., 2004; Lyubchansky and Bepalov, 2011; Voronin and Chumakov, 2015). Our data obtained due to

INDVAL approach prove that the edge-indicating species objectively exist. Hence, if we remove the "edge" habitat group from our original data table, the identified edge-specific species no longer function as indicators – their indicator value index becomes statistically insignificant.

Several studies report the identification of edge-indicating ground beetle species (Magura and Tóthmérész, 1997; Magura et al., 2000, 2001; Yu et al., 2007). The edge preference of the latter is clearly traced from spatial differentiation of abundance in soil trap catches. Moreover, the ecotone does not just represent a summation of the number of species from the adjacent habitats (forests and open biotopes), but rather forms a specific complex (Lacasella et al., 2015) that has been confirmed by our data. In addition, some of the edge-indicating species from the above-cited studies were also found in our catches. However, in our research they did not manifest themselves as characteristic of edge habitats. It can be concluded that a biotopic confinement of the species depends on numerous factors, and its precise identification at the local level is feasible only through doing special research.

In some cases, habitat preferences may be an unstable parameter, probably depending on ecological preferences of species, on the one hand, and gradients of conditions associated with zonality, longitude zonation and local landscape features, on the other. In local studies, using the data on the species-habitat relationships from other regions or landscapes may lead to inaccurate results. Therefore, it is advisable to keep a record of local habitat preferences of species when conducting ecological studies. The obtained data can be used to compile a regional summary of ground beetles.

Conclusion

The study of habitat preferences of ground beetles in the forest-meadow landscape of Udmurtia was based on calculating the indicator value index (INDVAL). The research involved 23087 trap-days, 15 surveyed habitats of five types and 117 identified ground beetle species. The biotopic distribution of family representatives in the study area generally coincided with biotopic preferences of species known from the literature. This means that under similar conditions, the ground beetle habitats are generally quite predictable. In some cases, local variations (mostly characteristic of eurytopic species) in biotope colonization were noted. Strictly edge-dwelling ground beetles were not detected, however 9 out of 56 behaved predominantly as typical edge representatives. Thus, the revealed local specificity in biotopic preferences of ground beetles can be taken into account in further research.

References

- Aleksanov, V.V., Alekseev, S.K., 2019. Kadastr zhukov zhuzhelits (Coleoptera, Carabidae) gorodskogo okruga «Gorod Kaluga» [Cadastre of ground beetles (Coleoptera, Carabidae) of the urban district "City of Kaluga"]. LLC Print, Izhevsk, Russia, 276 p. (In Russian).
- Angus, R.B., Brown, R.E., Bryant, L.J., 2000. Chromosomes and identification of the sibling species *Pterostichus nigrita* (Paykull) and *P. rhaeticus* Heer. *Systematic Entomology* **25**, 325–337. <https://doi.org/10.1046/j.1365-3113.2000.00108.x>
- Arnol'di, K.V., Sharova, I.Kh., Klyukanova, G.N., Butrina, N.N., 1972. Zhuzhelitsy (Carabidae, Coleoptera) Streletskoy stepi pod Kurskom i ikh sezonnaya dinamika aktivnosti [Ground beetles (Carabidae, Coleoptera) of the Streletskaya steppe near Kursk and their seasonal activity dynamics]. In: Naumov, S.P. (ed.), *Fauna i ekologiya zhitovnykh [Fauna and ecology of animals]*. Moscow State Pedagogical Institute Moscow, USSR, 215–230. (In Russian).
- Atlas Udmurtskoy Respubliki [Atlas of the Udmurt Republic], 2020. Rysin, I.I. (ed.). Feoriya, Moscow: Udmurtia, Izhevsk, Russia, 288 p. (In Russian).
- Barber, H.S., 1931. Traps for cave-inhabiting insects. *Journal of the Elisha Mitchell Scientific Society* **46** (2), 259–266.
- Bieringer, G., Zulka, K.P., Milasowszky, N., Sauberer, N., 2013. Edge effect of a pine plantation reduces dry grassland invertebrate species richness. *Biodiversity and Conservation* **22**, 2269–2283. <https://doi.org/10.1007/s10531-013-0435-2>

- Belova, Yu.N., 2014. Fauna i naselenie zhuzhelits (Coleoptera, Carabidae) lesnykh ekosistem na territorii Vologodskoy oblasti [Fauna and population of ground beetles (Coleoptera, Carabidae) of forest ecosystems in the Vologda region]. Vologda State University, Vologda, Russia, 124 p. (In Russian).
- Bel'skaya, E.A., Zinoviev, E.V., 2007. Struktura kompleksov zhuzhelits (Coleoptera, Carabidae) v prirodnykh i tekhnogenno-narushennykh lesnykh ekosistemakh na yugo-zapade Sverdlovskoy oblasti [Structure of the Complexes of Carabid Beetles (Coleoptera, Carabidae) in Natural and Industry-Disturbed Forest Ecosystems in the South-West of the Sverdlovsk Region]. *Sibirskiy ekologicheskiy zhurnal [Contemporary Problems of Ecology]* 4, 533–543. (In Russian).
- Bey-Bienko, G.Ya., 1966. Smena mestoobitaniya nazemnymi organizmami kak biologicheskiy printsip [Habitat change by terrestrial organisms as a biological principle]. *Zhurnal obshchey biologii [Journal of General Biology]* 57 (1), 5–21. (In Russian).
- Brigić, A., Starčević, M., Hrašovec, B., Elek, Z., 2014. Old forest edges may promote the distribution of forest species in carabid assemblages (Coleoptera: Carabidae) in Croatian forests. *European Journal of Entomology* 111, 715–725. <https://doi.org/10.14411/eje.2014.090>
- Chernov, Yu.I., 1975. Prirodnaya zonal'nost' i zhivotnyy mir sushi [Natural zonality and fauna of land]. Mysl', Moscow, USSR, 220 c. (In Russian).
- Clarke, K.R., 1993. Non-parametric multivariate analysis of changes in community structure. *Australian Journal of Ecology* 18, 117–143. <https://doi.org/10.1111/j.1442-9993.1993.tb00438.x>
- Dedyukhin, S.V., 2008. Zhuzhelitsy (Coleoptera, Carabidae) natsional'nogo parka "Nechkinskiy" [Ground Beetles (Coleoptera, Carabidae) of the National Nechkin Park]. *Vestnik Udmurtskogo universiteta. Seriya Biologiya. Nauki o Zemle [Bulletin of Udmurt university. Series Biology. Earth Sciences]* 2, 109–124. (In Russian).
- Dedyukhin, S.V., 2012. Sistematischeskiy spisok zhestkokrylykh (Coleoptera) Udmurtskoy Respubliki [Systematic list of beetles (Coleoptera) of the Udmurt Republic.]. Web page. URL: https://www.zin.ru/animalia/Coleoptera/rus/udm_list.htm (accessed: 11.04.2024). (In Russian).
- Dedyukhin, S.V., 2023. Struktura kompleksov zhuzhelits (Carabidae, Coleoptera) vodorazdel'nykh lipnyakov na territorii Udmurtii i ee izmenenie pod antropogennym vliyaniem [The structure of ground beetle complexes (Carabidae, Coleoptera) of watershed linden forests in the territory of Udmurtia and its change under anthropogenic influence]. *Vestnik Udmurtskogo universiteta. Seriya Biologiya. Nauki o Zemle [Bulletin of Udmurt university. Series Biology. Earth Sciences]* 33 (3), 281–287. (In Russian). <https://doi.org/10.35634/2412-9518-2023-33-3-281-288>
- Dedyukhin, S.V., Nikitskiy, N.B., Semenov, V.B., 2005. Sistematischeskiy spisok zhestkokrylykh (Insecta, Coleoptera) Udmurtii [Checklist of beetles (Insecta, Coleoptera) of Udmurti]. *Evraziatskiy entomologicheskiy zhurnal [Euroasian Entomological Journal]* 4 (4), 293–315. (In Russian).
- Digweed, S.C., Currie, C.R., Carcamo, H.A., Spence, J.R., 1995. Digging out the digging-in effect of pitfall traps: influences of depletion and disturbance on catches of ground beetles (Coleoptera: Carabidae). *Pedobiologia* 39, 561–576.
- Dufrêne, M., Legendre, P., 1997. Species assemblages and indicator species: the need for a flexible asymmetrical approach. *Ecological Monographs* 67 (3), 345–366. <https://doi.org/10.2307/2963459>
- Gryuntal', S.Yu., 2008. Organizatsiya soobshchestv zhuzhelits (Coleoptera, Carabidae) lesnykh biogeotsenozov Vostochno-Evropeyskoy (Russkoy) ravniny [Organization of communities of ground

- beetles (Coleoptera, Carabidae) of forest biogeocenoses of the East European (Russian) Plain]. Galleya-Print, Moscow, Russia, 481 p. (In Russian).
- Hammer, Ø., Harper, D.A.T., Ryan, P.D., 2001. PAST: Paleontological Statistics Software Package for Education and Data Analysis. *Palaeontologia Electronica* 4 (1), 9.
- Isachenko, A.G., 1991. Landshaftovedenie i fiziko-geograficheskoe rayonirovanie [Landscape science and physical-geographical zoning]. Vysshaya shkola, Moscow, USSR, 365 p. (In Russian).
- Isaev, A.Yu., 2002. Opredelitel' zhestkokrylykh Srednego Povolzh'ya (chast' 1 – Adepfaga i Myxophaga) [Key of Coleoptera of the Middle Volga Region (Part 1 – Adepfaga and Myxophaga)]. *Priroda Ul'yanovskoy oblasti [Nature of the Ulyanovsk region]* 10, 1–80. (In Russian).
- Kaufman, L., Rousseeuw, P.J., 1990. Partitioning around medoids (program PAM). Part 2. In: Gentle, J.E. (ed.), *Finding groups in data: An introduction to cluster analysis*. John Wiley, New York, USA, 68–125. <https://doi.org/10.2307/2532178>
- Koivula, M., Hyyryläinen, V., Soininen, E., 2004. Carabid beetles (Coleoptera: Carabidae) at forest-farmland edges in southern Finland. *Journal of Insect Conservation* 8, 297–309. <https://doi.org/10.1007/s10841-004-0296-9>
- Kolesnikova, A.A., Dolgin, M.M., Konakova, T.N., 2017. Fauna evropeyskogo severo-vostoka Rossii. T. 8, ch. 4. Zhuzhelitsy (Coleoptera, Carabidae) [Fauna of the European North-East of Russia. Vol. 8, part 4. Ground beetles (Coleoptera, Carabidae)]. Institute of Biology of the Komi Scientific Center of the Ural Branch of the Russian Academy of Sciences, Syktyvkar, Russia, 340 p. (In Russian).
- Kozlov, M.V., 2015. Planirovanie ekologicheskikh issledovaniy: teoriya i prakticheskie rekomendatsii [Planning of ecological research: theory and practical recommendations]. KMK, Moscow, Russia, 170 p. (In Russian).
- Kryzhanovskiy, O.L., 1965. Sem. Carabidae – zhuzhelitsy [Family Carabidae – ground beetles]. In: Bey-Bienko, G.Ya. (ed.), *Opredelitel' nasekomykh evropeyskoy chasti SSSR. T. 2 [Key of insects of the European part of the USSR. Vol. 2]*. Nauka, Moscow, Leningrad, USSR, 29–77. (In Russian).
- Lacasella, F., Gratton, C., De Felici, S., Isaia, M., Zapparoli, M., Marta, S., Sbordoni, V., 2015. Asymmetrical responses of forest and “beyond edge” arthropod communities across a forest-grassland ecotone. *Biodiversity and Conservation* 24, 447–465. <https://doi.org/10.1007/s10531-014-0825-0>
- Lindroth, C.H., 1974. Handbooks for the Identification of British Insects, Vol. IV, Part 2. Coleoptera. Carabidae. Royal entomological society of London, London, Great Britain, 148 p.
- Lindroth, C.H., 1992a. Ground Beetles (Carabidae) of Fennoscandia: a zoogeographic Study: Part I. Specific knowledge regarding the species. Smithsonian Institution Libraries and The National Science Foundation, Washington, D.C., USA, 630 p.
- Lindroth, C.H., 1992b. Ground Beetles (Carabidae) of Fennoscandia: a zoogeographic Study: Part III. General analysis with a discussion on biogeographic principles. Smithsonian Institution Libraries and The National Science Foundation, Washington, D.C., USA, 814 p.
- Lompe, A., 2002. Die Käfer Europas, Ein Bestimmungswerk im Internet, Herausgegeben von Arved Lompe, Nienburg/Weser, Begründet im September 2002. Интернет-ресурс. URL: <https://coletonet.de/coleo/texte/carabidae.htm> (дата обращения: 10.04.2024).

- Lyubchanskii, I.I., Bupalov, A.N., 2011. Spatial heterogeneity of a ground beetle (Coleoptera, Carabidae) population along a forest-steppe transect: Local level of consideration. *Contemporary Problems of Ecology* **4** (4). 388–395. <https://doi.org/10.1134/S1995425511040060>
- Magura, T., Tóthmérész, B., Molnár, T., 2004. Changes in carabid beetle assemblages along an urbanisation gradient in the city of Debrecen, Hungary. *Landscape Ecology* **19**, 747–759.
- Magura, T., Lövei, G.L., 2019. Environmental filtering is the main assembly rule of ground beetles in the forest and its edge but not in the adjacent grassland. *Insect Science* **26**, 154–163.
- Magura, T., Lövei, G.L., 2020. The type of forest edge governs the spatial distribution of different-sized ground beetles. *Acta Zoologica Academiae Scientiarum Hungaricae* **66** (Suppl.), 69–96. <https://doi.org/10.17109/AZH.66.Suppl.69.2020>
- Magura, T., Tóthmérész, B., 1997. Testing edge effect on carabid assemblages in an oak-hornbeam forest. *Acta Zoologica Academiae Scientiarum Hungaricae* **43**, 303–312.
- Magura, T., Tóthmérész, B., Molnár, T., 2000. Spatial distribution of carabids along grass-forest transects. *Acta Zoologica Academiae Scientiarum Hungaricae* **46**, 1–17.
- Magura, T., Tóthmérész, B., Molnár, T., 2001. Forest edge and diversity: carabids along forest-grassland transects. *Biodiversity & Conservation* **10**, 287–300. <https://doi.org/10.1023/A:1008967230493>
- Makarov, K.V., Kryzhanovskiy, O.L., Belousov, I.A., Zamotaylov, A.S., Kabak I.P. et al., 2020. Sistemacheskii spisok zhuzhelits (Carabidae) Rossii [Systematic list of ground beetles (Carabidae) of Russia]. Web page. URL: http://www.zin.ru/Animalia/Coleoptera/rus/car_rus.htm. (accessed: 11.04.2024). (In Russian).
- Mordkovich, V.G., Lyubchanskii, I.I., 2010. Ekologicheskie gruppy zhukov-zhuzhelits (Coleoptera, Carabidae): sushchnost', printsipy vydeleniya, sostav i vstrebovannost' [Ecological groups of ground beetle species (Coleoptera, Carabidae): characteristics, principles of isolation, composition, and demand for environmental research]. *Evrasijskiy entomologicheskii zhurnal [Euroasian Entomological Journal]* **9** (2), 195–202. (In Russian).
- Murcia, C., 1995. Edge effects in fragmented forests: implications for conservation. *Trends in Ecology and Evolution* **10**, 58–62. [https://doi.org/10.1016/S0169-5347\(00\)88977-6](https://doi.org/10.1016/S0169-5347(00)88977-6)
- Niemelä, J., Koivula, M., Kotze, J.D., 2007. The effects of forestry on carabid beetles (Coleoptera: Carabidae) in boreal forests. *Journal of Insect Conservation*. **11**, 5–18. <https://doi.org/10.1007/s10841-006-9014-0>
- Odum, Yu., 1975. Osnovy ekologii [Fundamentals of Ecology]. Mir, Moscow, USSR, 740 p. (In Russian).
- Ruchin, A.B., Egorov, L.V., Alekseev, S.K., 2015. Zhuzhelitsy (Coleoptera, Carabidae) Mordovskogo zapovednika [Ground beetles (Coleoptera, Carabidae) of the Mordovian Nature Reserve]. *Trudy Mordovskogo gosudarstvennogo prirodnogo zapovednika imeni P.G. Smidovicha [Proceedings of the Mordovian State Nature Reserve named after P.G. Smidovich]* **14**, 157–191. (In Russian).
- Solodovnikov, I.A., 2008. Zhuzhelitsy (Coleoptera, Carabidae) Belorusskogo Poozer'ya. S katalogom vidov zhuzhelits Belarusi i sopredel'nykh gosudarstv [Ground beetles (Coleoptera, Carabidae) of the Belarusian Poozerie. With a catalogue of ground beetle species of Belarus and adjacent countries]. Vitebsk State University named after P.M. Masherov, Vitebsk, Belarus, 325 p. (In Russian).

- Sharova, I.Kh., Filippov, B.Yu., 2004. Ekologiya zhuzhelits lesov v del'te Severnoy Dviny [Ecology of ground beetles in forests of the Northern Dvina delta]. Pomor University, Arkhangelsk, Russia, 114 p. (In Russian).
- Shitikov, V.K., 2019. Mnogomernyy statisticheskiy analiz ekologicheskikh soobshchestv (obzor) [Multivariate statistical analysis of ecological communities (review)]. *Teoreticheskaya i prikladnaya ekologiya [Theoretical and Applied Ecology]* 1, 5–11. (In Russian).
- Shitikov, V.K., Zinchenko, T.D., Rozenberg, G.S., 2012. Makroekologiya rechnykh soobshchestv: kontseptsii, metody, modeli [Macroecology of river communities: concepts, methods, models]. Kassandra, Tolyatti, Russia, 256 p. (In Russian).
- Thiele, H.U., 1977. Carabid beetles in their environments, a study on habitat selection by adaptations in physiology and behavior. Volume 10. Zoophysiology and ecology. Springer-Verlag, Berlin; Heidelberg, Germany; New York, USA, 369 p.
- Tselishcheva, L.G., Alalykina, N.M., 2005. Fauna zhuzhelits (Coleoptera, Carabidae) Kirovskoy oblasti i vozmozhnost' ispol'zovaniya dannykh v otsenke ekologicheskogo sostoyaniya ee territorii [Fauna of ground beetles (Coleoptera, Carabidae) of the Kirov region and the possibility of using data in assessing the ecological state of its territory]. In: Estaf'ev, A.A. (ed.), *Zakonomernosti zonal'noy organizatsii kompleksov zhivotnogo naseleniya evropeyskogo Severo-Vostoka (Trudy Komi NTs UrO RAN. T. 1, vyp. 77)* [Patterns of zonal organization of animal population complexes in the European North-East (Proceedings of the Komi Scientific Center of the Ural Branch of the Russian Academy of Sciences. Vol. 1, issue 77)]. Publishing House of the Komi Scientific Center of the Ural Branch of the Russian Academy of Sciences, Syktyvkar, Russia, 189–205. (In Russian).
- Turin, H., Alders, K., Den Boer, P.J., Van Essen, S., Heijerman, T.H., Laane W., Penterman E., 1991. Ecological characterization of carabid species (Coleoptera, Carabidae) in the Netherlands from thirty years of pitfall sampling. *Tijdschrift Voor Entomologie* 134, 279–303.
- Voronin, A.G., 1999. Fauna i komplekсы zhuzhelits (Coleoptera, Trachypachidae, Carabidae) lesnoy zony Srednego Urala (ekologo-zoogeograficheskiy analiz) [Fauna and complexes of ground beetles (Coleoptera, Trachypachidae, Carabidae) of the forest zone of the Middle Urals (ecological and zoogeographical analysis)]. Perm University Publishing House, Perm, Russia, 244 p. (In Russian).
- Voronin, A.G., Chumakov, L.N., 2015. Distribution of ground beetles (Coleoptera, Carabidae) from different ecological groups in the forest-meadow ecotone. *Russian Journal of Ecology* 46 (6), 589–591. <https://doi.org/10.1134/S1067413615060235>
- Yu, X.D., Luo, T.H., Zhou, H.Z., Yang J., 2007. Distribution of carabid beetles (Coleoptera: Carabidae) across a forest-grassland ecotone in Southwestern China. *Environmental Entomology* 36 (2), 348–355. [https://doi.org/10.1603/0046-225x\(2007\)36\[348:docbcc\]2.0.co;2](https://doi.org/10.1603/0046-225x(2007)36[348:docbcc]2.0.co;2)

Список литературы

- Александров, В.В., Алексеев, С.К., 2019. Кадастр жуков жужелиц (Coleoptera, Carabidae) городского округа «Город Калуга». ООО Принт, Ижевск, Россия, 276 с.
- Арнольди, К.В., Шарова, И.Х., Ключанова, Г.Н., Бутрина, Н.Н., 1972. Жужелицы (Carabidae, Coleoptera) Стрелецкой степи под Курском и их сезонная динамика активности. В: Наумов, С.П. (ред.), *Фауна и экология животных*. МГПИ, Москва, СССР, 215–230.
- Атлас Удмуртской Республики, 2020. Рысин, И.И. (ред.). Феория, Москва; Удмуртия, Ижевск, Россия, 288 с.

- Бей-Биенко, Г.Я., 1966. Смена местообитаний наземными организмами как биологический принцип. *Журнал общей биологии* 57 (1), 5–21.
- Бельская, Е.А., Зиновьев, Е.В., 2007. Структура комплексов жуужелиц (Coleoptera, Carabidae) в природных и техногенно-нарушенных лесных экосистемах на юго-западе Свердловской области. *Сибирский экологический журнал* 4, 533–543.
- Белова, Ю.Н., 2014. Фауна и население жуужелиц (Coleoptera, Carabidae) лесных экосистем на территории Вологодской области. ВоГУ, Вологда, Россия, 124 с.
- Воронин, А.Г., 1999. Фауна и комплексы жуужелиц (Coleoptera, Trachypachidae, Carabidae) лесной зоны Среднего Урала (эколого-зоогеографический анализ). Издательство Пермского университета, Пермь, Россия, 244 с.
- Воронин, А.Г., Чумаков, Л.Н., 2015. Распределение жуужелиц (Coleoptera, Carabidae) различных экологических групп по лесолуговому экотону. *Экология* 6, 470–472. <https://doi.org/10.7868/S0367059715060232>
- Грюнталь, С.Ю., 2008. Организация сообществ жуужелиц (Coleoptera, Carabidae) лесных биогеоценозов Восточно-Европейской (Русской) равнины. Галлея-Принт, Москва, Россия, 481 с.
- Дедюхин, С.В., 2008. Жуужелицы (Coleoptera, Carabidae) национального парка "Нечкинский". *Вестник Удмуртского университета. Серия Биология. Науки о Земле* 2, 109–124.
- Дедюхин, С.В., 2012. Систематический список жесткокрылых (Coleoptera) Удмуртской Республики. Интернет-ресурс. URL: https://www.zin.ru/animalia/Coleoptera/rus/udm_list.htm (дата обращения: 11.04.2024).
- Дедюхин, С.В., 2023. Структура комплексов жуужелиц (Carabidae, Coleoptera) водораздельных липняков на территории Удмуртии и ее изменение под антропогенным влиянием. *Вестник Удмуртского университета. Серия Биология. Науки о Земле* 33 (3), 281–287. <https://doi.org/10.35634/2412-9518-2023-33-3-281-288>
- Дедюхин, С.В., Никитский, Н.Б., Семенов, В.Б., 2005. Систематический список жесткокрылых (Insecta, Coleoptera) Удмуртии. *Евразийский энтомологический журнал* 4 (4), 293–315.
- Исаев, А.Ю., 2002. Определитель жесткокрылых Среднего Поволжья (часть 1 – Aderphaga и Muxorhaga). *Природа Ульяновской области* 10, 1–80.
- Исаченко, А.Г., 1991. Ландшафтоведение и физико-географическое районирование. Высшая школа, Москва, СССР, 365 с.
- Козлов, М.В., 2015. Планирование экологических исследований: теория и практические рекомендации. КМК, Москва, Россия, 170 с.
- Колесникова, А.А., Долгин, М.М., Конакова, Т.Н., 2017. Фауна европейского северо-востока России. Т. 8, ч. 4. Жуужелицы (Coleoptera, Carabidae). Институт биологии Коми НЦ УрО РАН, Сыктывкар, Россия, 340 с.
- Крыжановский, О.Л., 1965. Сем. Carabidae – жуужелицы. В: Бей-Биенко, Г.Я. (ред.), *Определитель насекомых европейской части СССР. Т. 2.* Наука, Москва, Ленинград, СССР, 29–77.
- Любечанский, И.И., Беспалов, А.Н., 2011. Пространственная гетерогенность населения жуужелиц (Coleoptera, Carabidae) в градиенте леса и степи: локальный уровень рассмотрения. *Сибирский экологический журнал* 18 (4), 517–525. <https://doi.org/10.1134/S1995425511040060>

- Макаров, К.В., Крыжановский, О.Л., Белоусов, И.А., Замотайлов, А.С., Кабак И.П. и др., 2020. Систематический список жужелиц (Carabidae) России. Интернет-ресурс. URL: http://www.zin.ru/Animalia/Coleoptera/rus/car_rus.htm. (дата обращения: 11.04.2024).
- Мордкович, В.Г., Любечанский, И.И., 2010. Экологические группы жуков-жужелиц (Coleoptera, Carabidae): сущность, принципы выделения, состав и востребованность. *Евразийский энтомологический журнал* 9 (2), 195–202.
- Одум, Ю., 1975. Основы экологии. Мир, Москва, СССР, 740 с.
- Ручин, А.Б., Егоров, Л.В., Алексеев, С.К., 2015. Жужелицы (Coleoptera, Carabidae) Мордовского заповедника. *Труды Мордовского государственного природного заповедника имени П.Г. Сидовича* 14, 157–191.
- Солодовников, И.А., 2008. Жужелицы (Coleoptera, Carabidae) Белорусского Поозерья. С каталогом видов жужелиц Беларуси и сопредельных государств. ВГУ им. П.М. Машерова, Витебск, Беларусь, 325 с.
- Целищева, Л.Г., Алалыкина, Н.М., 2005. Фауна жужелиц (Coleoptera, Carabidae) Кировской области и возможность использования данных в оценке экологического состояния ее территории. В: Естафьев, А.А. (ред.), *Закономерности зональной организации комплексов животного населения европейского Северо-Востока (Труды Коми НЦ УрО РАН. Т. 1, вып. 77)*. Издательство Коми НЦ УрО РАН, Сыктывкар, Россия, 189–205.
- Чернов, Ю.И., 1975. Природная зональность и животный мир суши. Мысль, Москва, СССР, 220 с.
- Шарова, И.Х., Филиппов, Б.Ю., 2004. Экология жужелиц лесов в дельте Северной Двины. Поморский университет, Архангельск, Россия, 114 с.
- Шитиков, В.К., 2019. Многомерный статистический анализ экологических сообществ (обзор). *Теоретическая и прикладная экология* 1, 5–11.
- Шитиков, В.К., Зинченко, Т.Д., Розенберг, Г.С., 2012. Макроэкология речных сообществ: концепции, методы, модели. Кассандра, Тольятти, Россия, 256 с.
- Angus, R.B., Brown, R.E., Bryant, L.J., 2000. Chromosomes and identification of the sibling species *Pterostichus nigrita* (Paykull) and *P. rhaeticus* Heer. *Systematic Entomology* 25, 325–337. <https://doi.org/10.1046/j.1365-3113.2000.00108.x>
- Barber, H.S., 1931. Traps for cave-inhabiting insects. *Journal of the Elisha Mitchell Scientific Society* 46 (2), 259–266.
- Bieringer, G., Zulka, K.P., Milasowszky, N., Sauberer, N., 2013. Edge effect of a pine plantation reduces dry grassland invertebrate species richness. *Biodiversity and Conservation* 22, 2269–2283. <https://doi.org/10.1007/s10531-013-0435-2>
- Brigić, A., Starčević, M., Hrašovec, B., Elek, Z., 2014. Old forest edges may promote the distribution of forest species in carabid assemblages (Coleoptera: Carabidae) in Croatian forests. *European Journal of Entomology* 111, 715–725. <https://doi.org/10.14411/eje.2014.090>
- Clarke, K.R., 1993. Non-parametric multivariate analysis of changes in community structure. *Australian Journal of Ecology* 18, 117–143. <https://doi.org/10.1111/j.1442-9993.1993.tb00438.x>
- Digweed, S.C., Currie, C.R., Carcamo, H.A., Spence, J.R., 1995. Digging out the digging-in effect of pitfall traps: influences of depletion and disturbance on catches of ground beetles (Coleoptera: Carabidae). *Pedobiologia* 39, 561–576.

- Dufrêne, M., Legandre, P., 1997. Species assemblages and indicator species: the need for a flexible asymmetrical approach. *Ecological Monographs* **67** (3), 345–366. <https://doi.org/10.2307/2963459>
- Hammer, Ø., Harper, D.A.T., Ryan, P.D., 2001. PAST: Paleontological Statistics Software Package for Education and Data Analysis. *Palaeontologia Electronica* **4** (1), 9.
- Kaufman, L., Rousseeuw, P.J., 1990. Partitioning around medoids (program PAM). Part 2. In: Gentle, J.E. (ed.), *Finding groups in data: An introduction to cluster analysis*. John Wiley, New York, USA, 68–125. <https://doi.org/10.2307/2532178>
- Koivula, M., Hyyryläinen, V., Soininen, E., 2004. Carabid beetles (Coleoptera: Carabidae) at forest-farmland edges in southern Finland. *Journal of Insect Conservation* **8**, 297–309. <https://doi.org/10.1007/s10841-004-0296-9>
- Lacasella, F., Gratton, C., De Felici, S., Isaia, M., Zapparoli, M., Marta, S., Sbordoni, V., 2015. Asymmetrical responses of forest and “beyond edge” arthropod communities across a forest-grassland ecotone. *Biodiversity and Conservation* **24**, 447–465. <https://doi.org/10.1007/s10531-014-0825-0>
- Lindroth, C.H., 1974. Handbooks for the Identification of British Insects, Vol. IV, Part 2. Coleoptera. Carabidae. Royal entomological society of London, London, Great Britain, 148 p.
- Lindroth, C.H., 1992a. Ground Beetles (Carabidae) of Fennoscandia: a zoogeographic Study: Part I. Specific knowledge regarding the species. Smithsonian Institution Libraries and The National Science Foundation, Washington, D.C., USA, 630 p.
- Lindroth, C.H., 1992b. Ground Beetles (Carabidae) of Fennoscandia: a zoogeographic Study: Part III. General analysis with a discussion on biogeographic principles. Smithsonian Institution Libraries and The National Science Foundation, Washington, D.C., USA, 814 p.
- Lompe, A., 2002. Die Käfer Europas, Ein Bestimmungswerk im Internet, Herausgegeben von Arved Lompe, Nienburg/Weser, Begründet im September 2002. Интернет-ресурс. URL: <https://coleonet.de/coleo/texte/carabidae.htm> (дата обращения: 10.04.2024).
- Magura, T., Tóthmérész, B., Molnár, T., 2004. Changes in carabid beetle assemblages along an urbanisation gradient in the city of Debrecen, Hungary. *Landscape Ecology* **19**, 747–759.
- Magura, T., Lövei, G.L., 2019. Environmental filtering is the main assembly rule of ground beetles in the forest and its edge but not in the adjacent grassland. *Insect Science* **26**, 154–163.
- Magura, T., Lövei, G.L., 2020. The type of forest edge governs the spatial distribution of different-sized ground beetles. *Acta Zoologica Academiae Scientiarum Hungaricae* **66** (Suppl.), 69–96. <https://doi.org/10.17109/AZH.66.Suppl.69.2020>
- Magura, T., Tóthmérész, B., 1997. Testing edge effect on carabid assemblages in an oak-hornbeam forest. *Acta Zoologica Academiae Scientiarum Hungaricae* **43**, 303–312.
- Magura, T., Tóthmérész, B., Molnár, T., 2000. Spatial distribution of carabids along grass-forest transects. *Acta Zoologica Academiae Scientiarum Hungaricae* **46**, 1–17.
- Magura, T., Tóthmérész, B., Molnár, T., 2001. Forest edge and diversity: carabids along forest-grassland transects. *Biodiversity & Conservation* **10**, 287–300. <https://doi.org/10.1023/A:1008967230493>
- Murcia, C., 1995. Edge effects in fragmented forests: implications for conservation. *Trends in Ecology and Evolution* **10**, 58–62. [https://doi.org/10.1016/S0169-5347\(00\)88977-6](https://doi.org/10.1016/S0169-5347(00)88977-6)

- Niemelä, J., Koivula, M., Kotze, J.D., 2007. The effects of forestry on carabid beetles (Coleoptera: Carabidae) in boreal forests. *Journal of Insect Conservation*. **11**, 5–18. <https://doi.org/10.1007/s10841-006-9014-0>
- Thiele, H.U., 1977. Carabid beetles in their environments, a study on habitat selection by adaptations in physiology and behavior. Volume 10. Zoophysiology and ecology. Springer-Verlag, Berlin; Heidelberg, Germany; New York, USA, 369 p.
- Turin, H., Alders, K., Den Boer, P.J., Van Essen, S., Heijerman, T.H., Laane W., Penterman E., 1991. Ecological characterization of carabid species (Coleoptera, Carabidae) in the Netherlands from thirty years of pitfall sampling. *Tijdschrift Voor Entomologie* **134**, 279–303.
- Yu, X.D., Luo, T.H., Zhou, H.Z., Yang J., 2007. Distribution of carabid beetles (Coleoptera: Carabidae) across a forest-grassland ecotone in Southwestern China. *Environmental Entomology* **36** (2), 348–355. [https://doi.org/10.1603/0046-225x\(2007\)36\[348:docbcc\]2.0.co;2](https://doi.org/10.1603/0046-225x(2007)36[348:docbcc]2.0.co;2)

Species	Number of captured specimens														
	1.1	1.2	1.3	1.4	2.1	2.2	2.3	2.4	3.1	3.2	3.3	4.1	4.2	5.1	5.2
<i>Bembidion varium</i> (Olivier, 1795)															1
<i>Bembidion dentellum</i> (Thunberg, 1787)														1	
<i>Patrobis assimilis</i> Chaudoir, 1844				10				2						33	21
<i>Stomis pumicatus</i> (Panzer, 1796)	1	1				2	4								
<i>Poecilus versicolor</i> (Sturm, 1824)		2		1	152	211	225	71	2488	976	1085	824	215		5
<i>Poecilus cupreus</i> (Linnaeus, 1758)						2	2	2	1	3	6	162	6		
<i>Poecilus lepidus</i> (Leske, 1785)									122	9	2	105	17		
<i>Poecilus punctulatus</i> (Schaller, 1783)												3			
<i>Pterostichus strenuus</i> (Panzer, 1796)	25	16	8	1	23	29	1	34	3	2		1		3	1
<i>Pterostichus vernalis</i> (Panzer, 1796)						2					3				2
<i>Pterostichus minor</i> (Gyllenhal, 1827)														15	
<i>Pterostichus nigrita</i> aggr.**	2	1	2	134	2	3	5	1	3		1	2	4	150	16
<i>Pterostichus oblongopunctatus</i> (Fabricius, 1787)	330	261	151	165	27	6	3	1	1	8				6	
<i>Pterostichus aethiops</i> (Panzer, 1796)	212	39	36	126	29	2	37	3	5	1	2		3	10	
<i>Pterostichus macer</i> (Marsham, 1802)												2			
<i>Pterostichus melanarius</i> (Illiger, 1798)	208	85	177	133	177	36	274	80	6	9	48	53	10	8	2
<i>Pterostichus uralensis</i> ssp. krasnobaevi O. Berlov et Tilly, 1998				1	5										
<i>Pterostichus niger</i> (Schaller, 1783)	132	114	113	146	32	56	117	31	23	29	28	2	2	33	53

Species	Number of captured specimens															
	1.1	1.2	1.3	1.4	2.1	2.2	2.3	2.4	3.1	3.2	3.3	4.1	4.2	5.1	5.2	
<i>Calathus melanocephalus</i> (Linnaeus, 1758)					5	5	3	3	170	26	5	6				
<i>Calathus micropterus</i> (Duftschmid, 1812)		1														
<i>Calathus fuscipes</i> Goeze, 1777					1	1	1		407	85	53	1	2			
<i>Dolichus halensis</i> (Schaller, 1783)												2				
<i>Agonum gracilipes</i> (Duftschmid, 1812)	3				3	2	5		1							
<i>Agonum sexpunctatum</i> (Linnaeus, 1758)								1							7	
<i>Agonum viduum</i> (Panzer, 1796)														1	10	
<i>Agonum fuliginosum</i> (Panzer, 1809)	1	1			1	1	1	1	1	1			1	14	3	
<i>Platynus assimilis</i> (Paykull, 1790)	40													23		
<i>Oxypselaphus obscurus</i> (Herbst, 1784)																6
<i>Anchomenus dorsalis</i> (Pontoppidan, 1763)									2	1						
<i>Synuchus vivalis</i> (Illiger, 1798)	1				5	11	3	12	5	1	2	1				
<i>Amara plebeja</i> (Gyllenhal, 1810)																1
<i>Amara familiaris</i> (Duftschmid, 1812)	2				7	10	4		4		2	71	8			
<i>Amara lunicollis</i> Schioedte, 1837						3				21	8	2				
<i>Amara montivaga</i> Sturm, 1825			2		1	1	2	2	205	5	59	445	232			
<i>Amara eurynota</i> (Panzer, 1796)	1															
<i>Amara nitida</i> Sturm, 1825		1			13	21	9	7	23	6	24	2				1

Species	Number of captured specimens														
	1.1	1.2	1.3	1.4	2.1	2.2	2.3	2.4	3.1	3.2	3.3	4.1	4.2	5.1	5.2
<i>Harpalus latus</i> (Linnaeus, 1758)	24	2	7	1	34	21	73	77	9	31	41	7			2
<i>Harpalus signaticornis</i> (Duftschmid, 1812)									1				1		
<i>Harpalus tardus</i> (Panzer, 1796)					21	8	4		3	2		2			
<i>Harpalus luteicornis</i> (Duftschmid, 1812)					3	3	3	4	300	90	58	91	99		
<i>Harpalus xanthopus</i> ssp. <i>winkleri</i> Schauberger, 1923		2	13		67	21	13	4	21						
<i>Harpalus affinis</i> (Schrank, 1781)										11	5	94	109		1
<i>Harpalus distinguendus</i> (Duftschmid, 1812)												13	16		
<i>Harpalus rufipes</i> (DeGeer, 1774)						3	6	1	5	8	5	229	19		11
<i>Harpalus calceatus</i> (Duftschmid, 1812)												5			
<i>Harpalus griseus</i> (Panzer, 1796)										1	2	23	3		
<i>Ophonus azureus</i> (Fabricius, 1775)														1	
<i>Ophonus rufibarbis</i> (Fabricius, 1792)					1			17							
<i>Ophonus stictus</i> Stephens, 1828		1							81	16	2	3	1		
<i>Ophonus puncticollis</i> (Paykull, 1798)					2				61	3			1		
<i>Panagaeus cruxmajor</i> (Linnaeus, 1758)	2					1		2			2		1		3
<i>Panagaeus bipustulatus</i> Fabricius, 1775						1				2	1				
<i>Chlaenius nitidulus</i> (Schrank, 1781)															9
<i>Licinus depressus</i> (Paykull, 1790)	1	1			16	8		4		1	1		2		

Species	Number of captured specimens														
	1.1	1.2	1.3	1.4	2.1	2.2	2.3	2.4	3.1	3.2	3.3	4.1	4.2	5.1	5.2
<i>Badister lacertosus</i> Sturm, 1815	14	5	8	2	15	14	3	13			1		1		
<i>Badister bullatus</i> (Schrank, 1798)					1	12		1	5	2					
<i>Badister sodalis</i> (Duffschmid, 1812)	1	1			1								1	7	
<i>Lebia cruxminor</i> (Linnaeus, 1758)					1	1	1	1	1	1	1	1	2		
<i>Lebia chlorocephala</i> (Hoffmann, 1803)					1	1							1		
<i>Paradromius linearis</i> (Olivier, 1795)												1			
<i>Microlestes maurus</i> (Sturm, 1827)					6	6	15	1	90	18	5	423	325		1
<i>Syntomus truncatellus</i> (Linnaeus, 1761)					4	18	1		6			4	2		
<i>Cymindis angularis</i> Gyllenhal, 1810									27	2					
Specimens in total	1179	648	708	943	738	611	923	854	4864	1533	1639	2965	1323	355	410
Trap-days in total	1582	1596	1566	1533	1589	1610	1610	1568	1596	1546	1603	1519	1417	1421	1368
Species in total	34	29	22	24	46	47	44	43	44	42	38	54	46	20	38