Comparative analysis of the beetle fauna (Coleoptera: Carabidae) of small steppe plots in the forest-steppe zone

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Abstract. The fauna and abundance of Carabidae inhabiting small steppe plots in the forest-steppe zone of European Russia were analysed. In total, 14 such plots (biotopes) were studied, they were grouped by vegetation type into two groups: meadow steppe (5 plots) and calcareous steppe (9 plots). A total of 104 species of beetles from 6 subfamilies were collected. In meadow steppe, 91 species of beetle species were found, in calcareous steppe, 64 species were collected. Species richness was significantly higher in some meadow steppe plots (14-67 species) than in calcareous steppe plots (4-27 species). Numerical abundance of beetles was also higher in meadow steppe. Nine indicator species for calcareous steppe and no indicator species for calcareous steppe were identified. The structure of beetle dominance was analysed for individual biotopes. Beetle populations are analysed by life forms and life cycle types. NMDS scaling results are presented, demonstrating significant diversity of species composition and structure both in meadow steppe and calcareous steppe.

1 Introduction

Forest-steppe is a zonal landscape of the temperate belt. Its characteristics are the alternation of predominantly deciduous or mixed forests on grey forest soils and grassy steppes on chernozems [1,2]. To the north of the forest-steppe border there is a natural zone with the dominance of pine-small-leaved forests. Such plantations differ from taiga in their sparseness, well-developed grass cover of cereals and grasses [3-5]. It is on the border of these natural zones that significant in area “islands” of forest-steppes are located. There, meadow steppes, steppe meadows, and areas of birch and pine forests alternate. A significant part of island forest-steppes is ploughed or used as pastures and hayfields [1].

Grasslands of the temperate belt have received considerable attention in the scientific literature, as this habitat type, formed in the process of long-term interaction of abiotic

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factors, vegetation, animal populations and traditional nature use and possessing high biodiversity, is vulnerable due to the loss of traditional nature use and climatic changes. Of particular interest are calcareous grasslands. It is one of the most species-rich habitat types in Europe and many rare species are associated with it, which is why it has received much attention in ecological studies in Western and Central Europe [6-8]. The EUNIS habitat classification brings this habitat type closer to continental steppes which are zonal type of habitat [9]. However, there are significant differences between steppe and forest belt habitats in terms of animal populations [10]. Given the relatively high level of study of calcareous grasslands in Western Europe and steppe ecosystems, information on the population of calcareous rocky outcrops in the more northern regions of Eastern Europe remains scarce. Of particular interest in this respect is the forest-steppe zone, which combines different fragments but has its own ecological and zoogeographical specificity [11].

Beetles are among the most diverse and widely studied Coleoptera living on the soil surface and in litter. They are found in a wide variety of landscapes and play a significant role in natural ecosystems [12-14]. Carabidae are very often used as indicators of landscape condition [15-17]. Carabidae are a good object for ecological monitoring. Species diversity, seasonal migrations and other aspects of beetle life cycles serve as indicators of the state of communities [18,19]. In the forest-steppe zone, beetle beetles have been studied in detail in the Central Black Earth region of Russia [20,21] and in Western Siberia [22]. In the eastern regions of European Russia, they have not been studied sufficiently. In other regions, many forest-steppe habitat types have been studied, but calcareous grasslands have not been studied sufficiently. In the northern forest-steppe landscape, “islands” of steppes are scattered in a mosaic of forest ecosystems and agroecosystems. Therefore, such habitats serve as a refuge for many steppe species and the study of Carabidae fauna of these places is very important.

2 Materials and methods

The material for this study was collected in the Republic of Mordovia and Ulyanovsk Region (European Russia) in 2007-2008, 2021, 2022. A total of 14 calcareous grasslands were studied. Conditionally these plots were divided into two groups: 1) meadow steppe (5 plots) and 2) calcareous steppe (9 plots). When analysing the results, individual plots were indicated by the names of the nearest settlements (Table 1).

Table 1. List of studied localities with coordinates.

№№	Type	Region	District	Locality	Coordinates
1	meadow steppe	Mordovia	Ruzaevka	Levzhensky	54.1012, 45.0999
2	meadow steppe	Mordovia	Ichalki	Endova	54.6601, 45.2169
3	meadow steppe	Mordovia	Ardatov	Selishchi	54.6745, 46.2349
4	meadow steppe	Mordovia	Torbeevo	Drakino	54.0348, 43.2170
5	meadow steppe	Mordovia	Torbeevo	Surgod	54.0306, 43.0689
6	calcareous steppe	Mordovia	Bolshie Berezniki	Gart	54.1536, 45.6588
7	calcareous steppe	Mordovia	Dubenki	Yavleika	54.3194, 46.4036
8	calcareous steppe	Mordovia	Chamzinka	Kamenka	54.5025, 45.8575
9	calcareous steppe	Mordovia	Bolshie Berezniki	Veise	54.2476, 46.1325
10	calcareous steppe	Mordovia	Ardatov	Piksyasi	54.6577, 46.3204
11	calcareous steppe	Mordovia	Bolshie Berezniki	Simkino	54.2548, 46.1941
12	calcareous steppe	Mordovia	Ardatov	Olevka	54.9981, 46.0789

13	calcareous steppe	Ulyanovsk	Inza	Maloe Shuvatovo	54.1615, 46.2900
14	calcareous steppe	Ulyanovsk	Inza	Tiyapino	54.1528, 46.1594

Meadow-steppe vegetation is widespread on watersheds and in river valleys, mainly within the Volga Uplands. The most famous of them are Endova site and "Levzhensky hillsides" site. The peculiarities of climate and soil conditions favour joint growth of xerophilous and mesophilous perennials in such sites. Together with xerophilous species *Stipa* ssp., *Festuca valessiaca* Gaud. s. l., *Koeleria* ssp., *Phleum phleoides* (L.) H. Karst, there are other species in the herbage: *Calamagrostis epigeios* (L.) Roth, *Galium* ssp., *Bromopsis riparia* (Rehmann) Holub, *Phleum pratense* L., *Filipendula vulgaris* Moench, *Vicia tenuifolia* Roth, *Trifolium* ssp., *Fragaria viridis* Weston, *Ranunculus polyanthemos* L., *Phlomis tuberosa* L., *Salvia stepposa* Des.-Shost., *Adonis vernalis* L., *Thymus marschallianus* Willd., *Stachys recta* L., *Iris aphylla* L., *Delphinium cuneatum* Stev. ex DC., *Scorzonera purpurea* L. and many other species. Usually, the projective coverage of herbaceous vegetation in such biotopes is 100%. The turf is very dense.

Xerophytic-steppe vegetation (in calcareous steppe) often develops on calcareous rocky outcrops and carbonate-rich soils (sites "Simkino hillsides", "Lasha hillsides", slopes of southern and south-western exposure near settlements in the east of the Republic of Mordovia and west of the Ulyanovsk region, etc.). In the composition of plant communities, in addition to the mentioned xerophytes and mesoxerophytes, there is a large share of southern calciphilic species (*Elytrigia lolioides* (Kar. et Kir.) Nevski, *Melica transsilvanica* Schur, *Anemone sylvestris* L., *Linum flavum* L., *Hypericum elegans* Steph., *Artemisia armeniaca* Lam., *Artemisia latifolia* Ledeb., *Aster amellus* L., *Centaurea ruthenica* Lam. и др. In the washed-out calcareous rocky outcrops, there are *Echinops ritro* L., *Polygala sibirica* L., *Bupleurum falcatum* L., *Thymus cimicinus* F.K. Blum ex Ledeb.). In general, they are very rich in floristic composition and structure [23] and are typical for northern steppe areas. Outcrops of calcareous rocky outcrops are often found in such areas.

Pitfall traps were used to collect beetles. One line of pitfall traps consisting of 10 traps was installed in each biotope. Traps were 0.5-litre plastic cups containing 200 ml of 4% formalin solution. The distance between traps was 1.5-2.0 m. Identification of Carabidae species was performed according to Müller-Motzfeld [24] and Isaev [25]. Modern nomenclature was used [26]. In the list of species, subfamilies are arranged in systematic order, in subfamilies species are arranged alphabetically.

Life forms of beetles are characterised according to I.H. Sharova [27]. Information on life cycles was taken from the work of A.V. Matalin [28]. Mathematical processing was carried out in R version 2.13.0 environment. One-way analysis of variance (ANOVA) was used to assess the contribution of habitat type to the traits of the beetle complex. Diversity and similarity indices were calculated in vegan 1.17-11 [29][Oksanen, 2022]. Non-metric multidimensional scaling (NMDS) was performed in the MASS package. To assess the relationship of species to habitat types, analysis of indicator values of species [30] in the indicspecies package [31] was applied. The Shannon index was used to assess the diversity of complexes, and the Simpson index was used to assess evenness.

3 Results

In total, significantly more species of beetles were found in meadow steppe than in steppe plots in calcareous steppe (91 species vs. 64), despite the smaller number of sample plots (Table 2). Species richness in individual biotopes in meadow steppe was also significantly higher, on average twice as high (Table 3, 4). The total abundance of beetles was also significantly higher in meadow steppes, more than doubling on average (Table 3, 4).

Table 2. Species composition of ground beetles in steppe plots (number of specimens).

Taxon	Calcareous steppe	Meadow steppe	Total
Brachininae			
Brachinus crepitans (Linnaeus, 1758)	5		5
Carabinae			
Carabus cancellatus Illiger, 1798	1	4	5
Carabus convexus Fabricius, 1775	12	88	100
Carabus hortensis Linnaeus, 1758		8	8
Carabus granulatus Linnaeus, 1758		1	1
Carabus stscheglowi Mannerheim, 1827		69	69
Carabus schoenherri Fischer von Waldheim, 1820			
Cicindelinae			
Cicindela campestris Linnaeus, 1758	4	11	15
Broscinae			
Broscus cephalotes (Linnaeus, 1758)	1		1
Harpalinae			
Acupalpus elegans (Dejean, 1829)	3	1	4
Acupalpus meridianus (Linnaeus, 1761)		6	6
Agonum gracile Sturm, 1824		1	1
Agonum gracilipes (Duftschmid, 1812)		1	1
Agonum muelleri (Herbst, 1784)		1	1
Agonum sexpunctatum (Linnaeus, 1758)			
Amara aenea (De Geer, 1774)	26	244	270
Amara apricaria (Paykull, 1790)			
Amara aulica (Panzer, 1796)	2	15	17
Amara bifrons (Gyllenhal, 1810)	2	3	5
Amara communis (Panzer, 1797)	10	11	21
Amara convexior Stephens, 1828		1	1
Amara eurynota (Panzer, 1796)	2	3	5
Amara familiaris (Duftschmid, 1812)	1	3	4
Amara ingenua (Duftschmid, 1812)	1	3	4
Amara littorea C.G. Thomson, 1857	2		2
Amara ovata (Fabricius, 1792)		3	3
Amara montivaga Sturm, 1825	1	1	2
Amara nitida Sturm, 1825		1	1
Amara plebeja (Gyllenhal, 1810)		3	3
Amara praetermissa (C.R. Sahlberg, 1827)	1	2	3
Amara similata (Gyllenhal, 1810)	1	5	6
Amara spreta Dejean, 1831	3		3
Amara tibialis (Paykull, 1798)	3	3	6
Anchomenus dorsalis (Pontoppidan, 1763)		40	40
Anisodactylus binotatus (Fabricius, 1787)		5	5
Anisodactylus nemorivagus (Duftschmid, 1812)		4	4
Anisodactylus signatus (Panzer, 1796)	3	14	17
Badister bullatus (Schrank, 1798)	2	2	4
Badister lacertosus Sturm, 1815		2	2
Badister meridionalis Puel, 1925		2	2

Badister unipustulatus Bonelli, 1813		3	3
Bradycellus caucasicus (Chaudoir, 1846)	1	1	2
Calathus ambiguus (Paykull, 1790)		1	1
Calathus erratus (C.R. Sahlberg, 1827)	5	65	70
Calathus fuscipes (Goeze, 1777)			
Calathus melanocephalus (Linnaeus, 1758)	2	14	16
Calathus micropterus (Duftschmid, 1812)		12	12
Callistus lunatus (Fabricius, 1775)	2	13	15
Cymindis angularis Gyllenhal, 1810	2	1	3
Cymindis humeralis (Geoffroy, 1785)	1		1
Dolichus halensis (Schaller, 1783)		22	22
Harpalus affinis (Schrank, 1781)	28	95	123
Harpalus autumnalis (Duftschmid, 1812)	1		1
Harpalus calathoides Motschulsky, 1844	5		5
Harpalus distinguendus (Duftschmid, 1812)	1	21	22
Harpalus griseus (Panzer, 1796)	5	69	74
Harpalus latus (Linnaeus, 1758)	16	4	20
Harpalus modestus Dejean, 1829	3		3
Harpalus progrediens Schauberger, 1922	26	4	30
Harpalus pumilus Sturm, 1818	34	7	41
Harpalus rubripes (Duftschmid, 1812)	124	75	199
Harpalus rufipes (De Geer, 1774)	35	935	970
Harpalus signaticornis (Duftschmid, 1812)	2	6	8
Harpalus smaragdinus (Duftschmid, 1812)	2	27	29
Harpalus tardus (Panzer, 1796)	20	4	24
Harpalus xanthopus winkleri Schauberger, 1923	1	14	15
Harpalus zabroides Dejean, 1829	7	1	8
Lebia chlorocephala (J.J. Hoffmann, 1803)		1	1
Lebia cruxminor (Linnaeus, 1758)		1	1
Licinus depressus (Paykull, 1790)	3		3
Limodromus assimilis (Paykull, 1790)		170	170
Limodromus krynickii (Sperk, 1835)		1	1
Masoreus wetterhallii (Gyllenhal, 1813)	1	2	3
Microlestes maurus (Sturm, 1827)	15	73	88
Microlestes minutulus (Goeze, 1777)	31	60	91
Oodes helopioides (Fabricius, 1792)		1	1
Ophonus azureus (Fabricius, 1775)	13	5	18
Ophonus laticollis Mannerheim, 1825		3	3
Ophonus puncticollis (Paykull, 1798)	7	27	34
Ophonus rufibarbis (Fabricius, 1792)	2	7	9
Ophonus stictus Stephens, 1828	2	5	7
Panagaeus bipustulatus (Fabricius, 1775)	1		1
Poecilus cupreus (Linnaeus, 1758)	15	721	736
Poecilus lepidus (Leske, 1785)		15	15
Poecilus punctulatus (Schaller, 1783)			
Poecilus versicolor (Sturm, 1824)	5	1382	1387
Pterostichus anthracinus (Illiger, 1798)		21	21
Pterostichus diligens (Sturm, 1824)			
Pterostichus macer (Marsham, 1802)	6	14	20

Pterostichus mannerheimii (Dejean, 1831)	1		1
Pterostichus melanarius (Illiger, 1798)	7	68	75
Pterostichus niger (Schaller, 1783)	1	7	8
Pterostichus nigrita (Paykull, 1790)		8	8
Pterostichus strenuus (Panzer, 1796)		16	16
Pterostichus oblongopunctatus (Fabricius, 1787)		92	92
Pterostichus vernalis (Panzer, 1796)		11	11
Stenolophus mixtus (Herbst, 1784)		2	2
Stomis pumicatus (Panzer, 1796)	1		1
Synuchus vivalis (Illiger, 1798)	1	3	4
Syntomus truncatellus (Linnaeus, 1761)	9	2	11
Nebriinae			
Leistus ferrugineus (Linnaeus, 1758)	9	2	11
Notiophilus germinyi Fauvel, 1863		1	1
Notiophilus palustris (Duftschmid, 1812)			
Trechinae			
Asaphidion flavipes (Linnaeus, 1761)		1	1
Asaphidion pallipes (Duftschmid, 1812)			
Bembidion biguttatum (Fabricius, 1779)		1	1
Bembidion guttula (Fabricius, 1792)		4	4
Bembidion lampros (Herbst, 1784)		6	6
Bembidion properans (Stephens, 1828)		92	92
Bembidion schueppelii Dejean, 1831		1	1
Bembidion quadrimaculatum (Linnaeus, 1761)	1	15	16
Trechus secalis (Paykull, 1790)	27		27
Number of species	**64**	**91**	**104**
Total of trap-days	**7087**	**4410**	**11497**
Total of individuals	**567**	**4796**	**5363**

Table 3. General characteristics of the ground beetles fauna.

Indicator, Mean (min – max)	Calcareous steppe (n=9)	Meadow steppe (n=5)
Total abundance, ex./ 100 pitfall traps	32.2 (4.6-23.3)	73.2 (11.9-159.2)
Species number	15.3 (4-27)	32.8 (14-67)
Shannon index	2.11 (1.12-2.76)	2.07 (1.46-2.33)
inverse Simpson index	6.11 (2.57-10.41)	4.62 (2.16-5.86)

Table 4. Assessment of the influence of the "biotope type" factor on the main features of the ground beetles fauna in biotopes (ANOVA).

Indicator		df	SS	MS	F	p
Total abundance	Factor	1	13095.8	13095.8	11.97	0.0047*
	Residuals	12	13126.4	1093.87		
Species number	Factor	1	980.6		5.376	0.0389*
	Residuals	12	2188.8	182.4		
Shannon index	Factor	1	0.0124		0.049	0.829
	Residuals	12	3.0401	0.2534		
inverse Simpson index	Factor	1	17.21		2.487	0.141
	Residuals	12	83.04	6.92		

According to diversity indices that take into account the evenness of communities (Shannon and inverse Simpson indices), meadow steppe and calcareous steppe beetle complexes do not differ significantly (Table 3, 4).

The species composition of beetles in both habitat types varies significantly. Only 3 common species (*Harpalus rubripes, H. smaragdinus, Microlestes minutulus*) were found for 5 meadow steppe sites, and only 1 common species (Harpalus rubripes) was found for 9 calcareous steppe sites; 6 species were present in more than half of the calcareous steppe habitats (all species characteristic of meadow steppe, as well as *Harpalus latus, H. tardus, Amara aenea*). More than half of the species list (52 out of 93) were found in only one meadow steppe biotope, and for calcareous steppe half of the species list (33 out of 66) were found in only one biotope.

Beetle populations in both habitat types are heterogeneous, with no clear contrast between meadow steppe and calcareous steppe complexes. According to faunistic similarity, we distinguish Nos. 11, 13, 14 (Fig. 1). In terms of abundance, three meadow steppe sites No. 1, No. 3, and No. 2 are the most distinctive (Fig. 2).

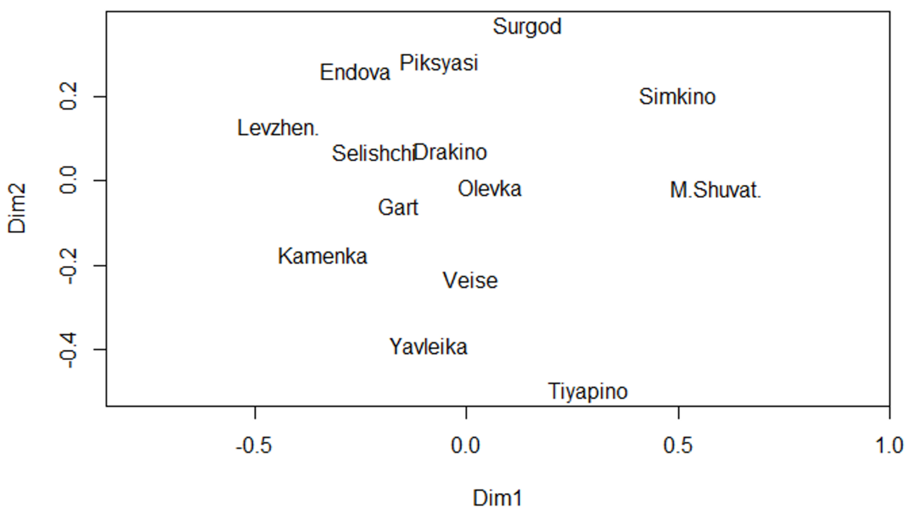

Fig. 1. Non-metric multidimensional scaling plot of ground beetles communities based on binary Jaccard index (without abundance)

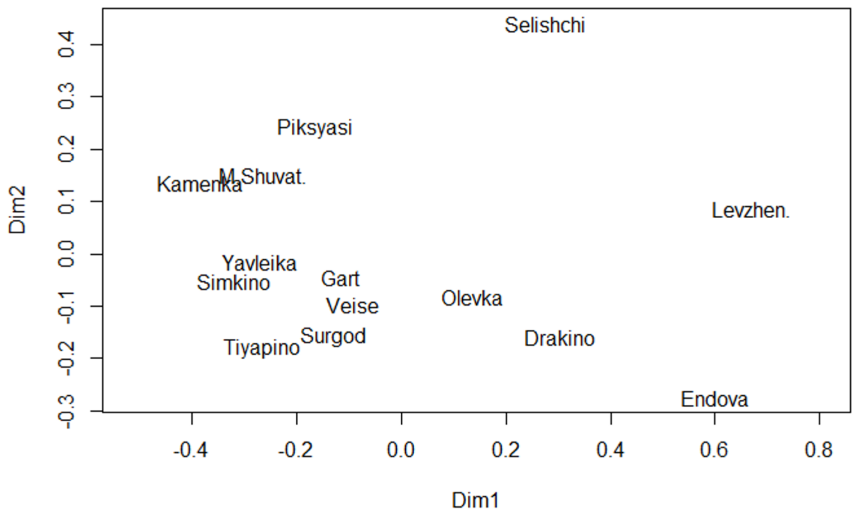

Fig. 2. Non-metric multidimensional scaling plot of ground beetles communities based on Jaccard index with abundance assessment

The calcareous steppe is dominated by *Harpalus rubripes*, which accounts for 9 to 54% of beetles. *Microlestes minutulus* and *Amara aenea* dominate in 4 biotopes. Another 21 species of beetles are dominants in 1-3 biotopes of this type. The spectrum of life forms in calcareous steppe is dominated by Harpalus-like mixophytophages geohortobionts and zoophagous litter-and-crevice-dwelling stratobionts (like *Microlestes*). Dominants in the majority of biotopes belong to the named groups of life forms. Only in 4 biotopes, along with them, representatives of other groups of life forms belong to the dominants: walking zoophagous epigeobionts (*Carabus convexus* in plot No.7), litter-and-soil-dwelling zoophagous stratobionts (*Poecilus cupreus*, No.7 и No.8, *Pterostichus melanarius* – No.8, *Pterostichus macer* – No.12), litter-dwelling zoophagous stratobionts (*Leistus ferrugineus* – No.8, *Trechus secalis* – No.10). The presence of Zabrus-like mixedophytophagous geohortobiont, well adapted to digging and characteristic of more southern regions (*Harpalus zabroides*), attracted attention in two biotopes (Nos. 8 and 9). In terms of breeding season, summer and spring-summer species predominate.

Among meadow steppe inhabitants, 14 dominant species were identified, of which 3-5 species dominate in one biotope. There are no common dominants for all 5 biotopes. Due to the great dissimilarity of the species structure, the meadow steppe population is considered on the basis of individual biotopes.

Levzhensky hillsides have extremely high total abundance of beetles and species richness of beetles. The number of species is twice as high as the average for meadow-steppe biotopes and three times higher than the average for all biotopes surveyed. Total abundance is 2.2 times higher than the average for meadow-steppe habitats and almost 5 times higher than the average for all habitats. The population structure is remarkable for the dominance of meadow-field species with significant participation of forest species. There are two superdominant species which are *Poecilus versicolor* and *Poecilus cupreus* - burrowing zoophages stratobionts with spring-summer reproduction. The first species is typical for open biotopes of the Russian forest-steppe [12,13] and for meadows of the forest belt [32,33]. The second species is more peculiar to agrocenoses [34,35]. The significant participation of the typically forest *Limodromus assimilis* - litter-live zoophage stratobiont with spring-early summer reproduction, depending on the presence of forest litter and moderately moist soil [36], draws attention. The hygrophilous species *Limodromus krynickii, Pterostichus anthracinus, Pterostichus nigrita* occur with low numerical abundance. The greatest diversity of beetles from genus *Bembidion* was also recorded.

Endova site (No. 2) has the superdominance of *Harpalus rufipes*, a field species particularly characteristic of disturbed lands. Another field beetle *Harpalus griseus* is also dominant. Along with them the zoophagous stratobiont litter-cracker *Microlestes maurus* dominates. *Poecilus cupreus* was subdominant. A similar population structure was found at Drakino site (No. 4), only the dominant species *are Microlestes minutulus* and *Poecilus versicolor*, related to the above-mentioned species. Selishchi (No. 3) is remarkable for the predominance of large beetles (zoophages epigeobionts) *Carabus convexus* and *Carabus stscheglowi*. While the first species is characteristic of a wide range of habitats of different natural zones, the second is a typical inhabitant of the forest-steppe zone [37]. In No. 5 is more similar in species structure to calcareous steppe and also has a low total abundance of beetles.

Analysis of indicator values allowed us to identify 9 species associated with meadow steppe sites (Table 5). Most of them are xerophiles and mesoxerophiles (except *Anisodactylus binotatus* and *Bembidion properans*). No species was found to be meaningfully gravitating towards calcareous steppe. Even *Callistus lunatus*, considered a typical calcophile, was less common in calcareous steppe than in meadow steppe.

Table 5. Indicator values of ground beetle species for the meadow steppe biotope group (only statistically significant results are given).

Species	A	B	stat	p.value
Anisodactylus binotatus	1	0.6	0.78	0.04
Anisodactylus nemorivagus	1	0.6	0.78	0.03
Bembidion properans	1	0.6	0.78	0.045
Calathus erratus	0.88	0.8	0.84	0.05
Cicindela campestris	0.83	0.6	0.71	0.045
Harpalus distinguendus	0.96	0.8	0.88	0.03
Harpalus smaragdinus	0.98	1	0.99	0.005
Microlestes minutulus	0.85	1	0.92	0.035
Poecilus lepidus	1	0.6	0.78	0.025

A is the probability of belonging of a given species to a biotope of a given type, B is the probability of finding a given species in a biotope of a given type.

At the same time, in some localities in calcareous steppe, several rare for the region species were found: *Brachinus crepitans* (No. 12), *Harpalus calathoides* (No. 10), *Cymindis humeralis* (No. 6), *Pterostichus macer* (No. 12). They are considered a characteristic of steppes, wastelands and other atypical habitats

4 Discussion

Low total abundance and reduced species richness combined with low individual species abundance and high community evenness indicates that calcareous steppe is less favourable for beetles than meadow steppe, despite its high floristic species richness. This result correlates with other studies that meadow floristic richness alone is not a predictor of species diversity of beetles [38]. Apparently, calcareous rocky outcrops with relatively sparse vegetation cover provide poor refuges for beetles. The lack of foraging habitat may also have a significant impact due to the unfavourable nature of such habitats for soil invertebrates. The chalk is a particularly extreme environment for invertebrates, with its relatively cool thickness and high surface temperatures and moisture deficit [39].

The obtained results suggest that the most adapted to calcareous rocky outcrops are myxophytophagous geochortobionts and zoophagous litter-and-crevice-dwelling stratobionts. Representatives of the latter group by virtue of small size and other morphological features easily penetrate into the soil and rock thickness through cracks, escaping from overheating and drying. Species of the first group are also well adapted to vertical migrations, capable of both digging and climbing plants. The ability to satisfy food requirements entirely through plant food also favours the adoption of such extreme conditions by myxophytophagous species. Another feature of species dominating calcareous rocky outcrops is the ability to fly. On the contrary, there are many flightless beetles among meadow steppe dominants poorly penetrating calcareous rocky outcrops, which depend significantly on the availability of shelters in a particular biotope in the form of forest litter, rags, felt, turf, and under more severe conditions burrow into the soil (*Poecilus, Pterostichus*) or hide under the bark of deadwood (*Limodromus*). The ratio of myxophytophagous and zoophagous species as such does not allow us to separate the studied community types, since the predominance of myxophytophagous species is a feature of the most diverse grasslands [40]. At the same time, it should be noted that the full realisation of life cycles of individual beetle species in these habitat types requires further study.

The results obtained allow us to consider meadow-steppe biotopes with a diverse range of life forms and ecological groups of beetles as the "indigenous element" of the studied natural zone. This coincides with the results of analyses of the forest-steppe zone in Western Siberia, where meadow communities were identified as the "indigenous element" [14]. Steppe grass communities on calcareous rocky outcrops can be considered as derived intrazonal communities, different from both meadow communities of their natural zone and zonal communities of the true steppe. At the same time, despite the low species richness, calcareous rocky outcrops are of significant importance for the conservation of regionally rare species.

5 Conclusion

As a result, 104 species of beetles from 6 subfamilies were found in 14 biotopes. In meadow steppe (in 5 biotopes) 91 species of beetle species were found, in calcareous steppe 64 species were found (in 9 biotopes). Numerical abundance and species richness of beetles were significantly higher in some meadow steppe plots than in calcareous steppe plots. Nine meadow steppe indicator species were identified that are associated mainly or exclusively with this type of grassland, and no indicator species for calcareous steppe. *Harpalus rubripes* dominates in calcareous steppe, while the dominance structure is not similar in different meadow steppe. Harpalus-like mixedophytophagous geohortobionts and zoophagous litter-and-crevice-dwelling stratobionts with summer and spring-summer reproduction are characteristic inhabitants of calcareous steppe. In meadow steppe the spectrum of life forms and types of life cycles are more diverse. Regionally rare species are confined to certain calcareous steppe.

6 Acknowledgements

This research was funded by the Russian Science Foundation, grant number 22-14-00026.

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