ABS ACTA BIOLOGICA SIBIRICA
A journal on the biodiversity of Siberia and the adjacent lands

Acta Biologica Sibirica 12: 765–795 (2026)
doi: 10.5281/zenodo.21213015
http://journal.asu.ru

RESEARCH ARTICLE

Ground beetle (Coleoptera, Carabidae) spatial distribution in a meadow catena

Alexander G. Borisovskiy[1]

1 *Udmurt State University, 1/1 Universitetskaya St, Izhevsk, 426034, Russia*

Corresponding author: Alexander G. Borisovskiy (borisovscky.alexander@yandex.ru)

Academic editor: R. Yakovlev | Received 30 April 2026 | Accepted 2 June 2026 | Published 8 July 2026

http://zoobank.org/634085D5-0247-4AB9-B63E-D86F8CBDA48F

Citation: Borisovskiy AG (2026) Ground beetle (Coleoptera, Carabidae) spatial distribution in a meadow catena. Acta Biologica Sibirica 12: 765–795. https://doi.org/10.5281/zenodo.21213015

Abstract

The spatial distribution of ground beetle species in a meadow catena in Udmurtia was studied for the first time. The material was collected using pitfall traps, and the data were analyzed through multivariate statistical methods. Species distribution was examined across six catena positions: placor, eluvial, three transit positions, and the accumulative. Statistically significant differences were found in ground beetle community composition and structure among these positions. The most important factors determining the composition and structure of the ground beetle population in the studied catena were slope steepness, total projective vegetation cover, and the projective cover of mesoxerophytes. Species richness and abundance generally increased down the catena, peaking at the lowest, accumulative position. The most substantial shifts in ground beetle community composition and structure occurred at the boundaries between the accumulative position and the slope. The analysis of area-specific latitudinal groups of ground beetles demonstrated a clear trend: the number of boreal species escalates as one descends the catena.

Keywords

Forest zone, ground beetle population, habitats, indicator species, IndVal, slope, Udmurtia

Introduction

The spatial distribution of ground beetles (Coleoptera, Carabidae) across diverse biotopes and landscape elements is a widely studied topic. Given that ground beetle are significantly influenced by abiotic factors, particularly temperature and humidity (Thile 1977), shifts in composition of the ground beetle community can be observed along environmental gradients.

Southern-facing slopes, influenced by local geomorphological and edaphic factors, can develop natural complexes that mimic the landscape and ecological conditions of neighboring or distant natural zones (Kolomyts and Surova 2007). In these biotopes, communities can form that are typical of more southern natural zones (Chernov 1975; Alekhin 1986).

When considering slope habitats, several key aspects underscore their importance for study. Firstly, slopes constitute 90% of the land surface on plains, which themselves cover two-thirds of the Earth's terrestrial area (Mordkovich 2017). Secondly, in the southern part of Cis-Urals, much of the territory is arable, relatively natural habitats are often confined to slopes. Historically, these slopes were extensively grazed. However, recent factors have led to the abandonment of some pastures, including those on slopes, initiating the restoration of natural communities (Zhizhin et al. 2022).

This study investigates the distribution patterns of ground beetles across a series of meadow biotopes situated along the geomorphological profile of a ravine. This habitat sequence, exhibiting changing environmental conditions, can be described as a "catena" (Mordkovich et al. 1985). Catenas are typically characterized by increasing soil moisture and decreasing temperature as one descends the profile (Mordkovich et al. 1985). Moreover, hydrothermal conditions on slopes can diverge significantly from those in horizontal areas. Slope heat supply is heavily influenced by insolation exposure and steepness, leading to local temperature gradients that can surpass regional ones by hundreds of times. Slopes also possess unique mechanisms for redistributing atmospheric moisture, dictated by slope angle, shape, and soil composition. For instance, on straight loamy slopes, the soil at the base receives approximately 1.5 times more water than direct precipitation (Isachenko 1991). Moving from a horizontal area to a slope can result in increased aridity both at the top and bottom of the slope (Kolomyts and Surova 2007).

The principal aim of our investigation was to elucidate the distributional patterns of ground beetle species across the environmental gradient present on the catena. Furthermore, we sought to ascertain the existence of species complexes within the driest zones of the catena. To mitigate the confounding influence of forests, a treeless expanse dominated by meadow vegetation was chosen. It was hypothesized that within this selected area, ground beetle species indigenous to the open habitats of southern Udmurtia would manifest their capacity for habitat selection. In this scenario, the catena's sequence of biotopes functions as a representative model of the meadow habitats typical of this particular landscape.

Materials and methods

Object and study area

The study was conducted in the Western Cis-Urals, within the Karakulinsky administrative district of Udmurtia (Fig.1), situated 2 km northwest of the village of Cheganda. Botanically and geographically, this region falls within the broadleaf-spruce (subtaiga) forest subzone (Baranova et al. 2010). The Kama River valley, a transitional zone between forest and forest-steppe, lies 4 km southeast of the study site. Forest cover in the Karakulinsky district is notably sparse, at around 5%, with steppe meadows representing a characteristic vegetation type (Baranova 2002). A defining feature of the district's landscapes is its highly rugged relief; the total length of ravines exceeds 500 km (Podsosova 1972). The region experiences an average annual air temperature of +3.6°C, with July temperatures averaging +19.8°C. Average annual precipitation is 580 mm, with 180 to 190 mm occurring during the warm season (Rysin 2020). Data on average monthly temperature and precipitation were obtained from the Sarapul weather station (https://www.pogodaiklimat.ru), situated 55 km north of the study area. During May-September 2024, the average temperature was 15.66°C, closely matching the long-term average of 15.64°C for the same period. During the period of May to September 2024, 284 mm of precipitation was recorded, which is marginally below the long-term average of 292 mm for the same timeframe. Overall, the climate in 2024 aligned with long-term observations.

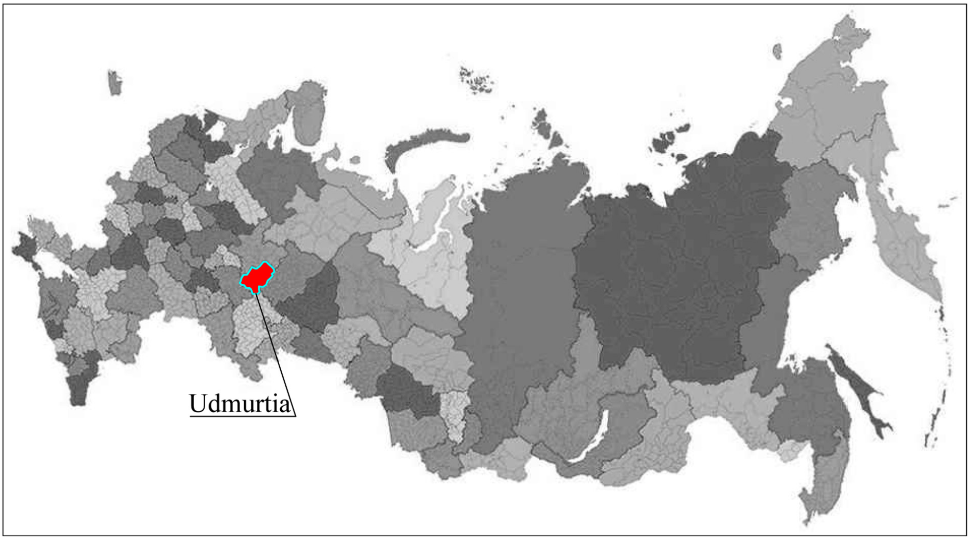

Figure 1. Udmurtia's location on the map of Russia.

This study took place in a treeless ravine section measuring 250 x 400 meters, centered at coordinates 55°58.52'N, 53°29.51'E. The ravine slopes within this area face south and southeast, with azimuths ranging from 151° to 188°.

The ravine is bordered by farmland, much of which is now abandoned. Within the study area, particularly on the slopes, are forested patches up to 300 x 800 meters, consisting of spruce (*Picea* sp.) and pine (*Pinus sylvestris* L.) stands.

The meadows have been fallow for the past two decades. Historically, the upper section of the area was arable land, with the ravine slopes and bottom serving as pasture. The area is now largely undisturbed. The elevation change across the study area, from northeast to southwest, is 50 meters. Loamy soils are prevalent. A temporary stream forms at the ravine bottom during snowmelt and heavy rainfall. Within the study area, a marshy zone at the ravine's base contains a permanent stream, measuring 30–50 cm in width and 5–10 cm in depth.

Fieldwork was conducted in the study area from May 9 to September 5, 2024, at 60 sampling sites (10x10 m). These sites were distributed across six habitat types, with 10 sites per type, arranged along a geomorphological gradient from the watershed to a swampy hollow at the ravine's base. Habitat typology followed the catena approach (Mordkovich et al. 1985; Mordkovich 2017). The identified habitat types (catena positions) were: watershed part, plakor position (PL); transition from interfluve to slope, eluvial position (EL); slope, with three transitional positions (TR1, TR2, TR3); and the hollow at the ravine's foot, an accumulative position (AK).

A single pitfall trap was deployed at the center of each site. Within each habitat type, traps were generally spaced 25 m apart. However, distances between some traps extended to 30–40 m to avoid areas with high concentrations of marmot (*Marmota bobak* (Müller, 1776)) burrows. Individual trap lines were typically separated by more than 25 m. The distance between the AK and TR lines was notably shorter, approximately 10 m. To ensure statistically independent samples, a minimum distance of 25 m was maintained between traps both within and between lines (Digweed et al. 1995).

The traps consisted of disposable 500 ml transparent plastic cups with an 87 mm opening diameter. Each trap contained 400 ml of 4% formalin, serving as both a preservative and kill agent. A small amount of liquid detergent was added to formalin to lower its surface tension. To protect the traps from various factors, steel covers (150.0 x 150.0 x 0.5 mm) on wire legs were positioned 3 cm above the soil surface. The collected animals were removed from the traps at 3–4 week intervals.

The following information was collected for each site. The geographic coordinates of the trap location were recorded using the GeoTracker mobile phone app, version 5.5.1.4624. The obtained data were plotted on a satellite image using the nakarte.me internet resource (Fig. 2). The elevation above sea level was determined using the same resource. Slope steepness was measured using the Construction Level mobile phone app, version 8.0. Azimuth was measured using the Compass mobile phone app, version 9.6.9.1.0.

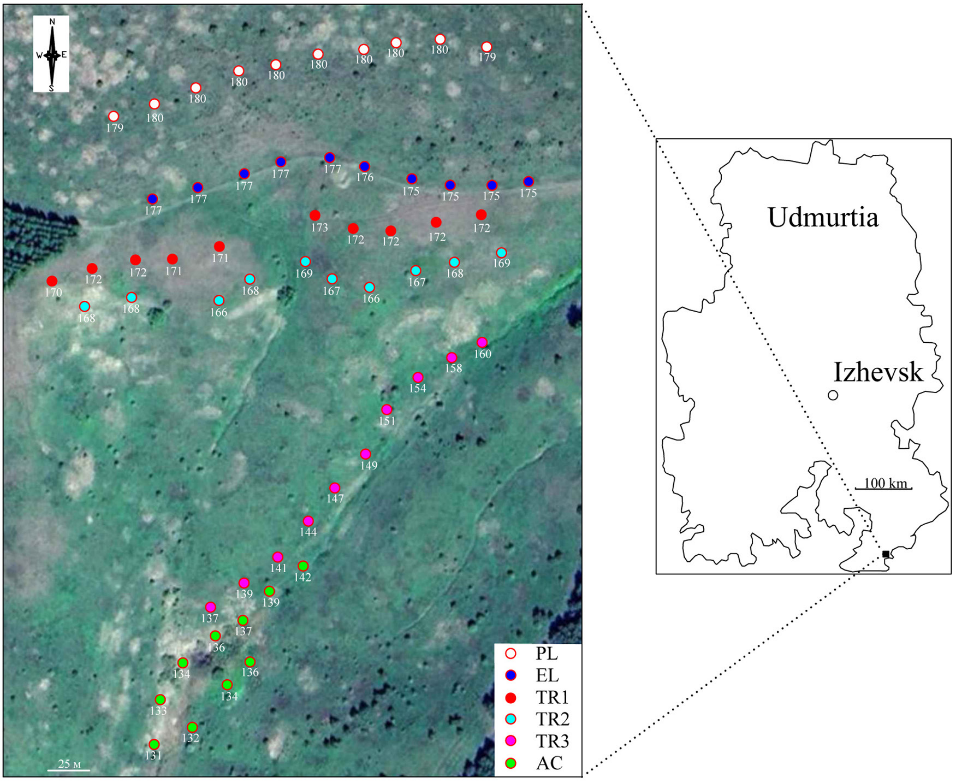

Figure 2. Map of the study area. Circles indicate the locations of pitfall traps at catena positions: PL – plakor position, EL – eluvial position, TR – transit position, AC – accumulative position. Numbers under the circles indicate altitude above sea level.

Data on vegetation at the sites were collected on August 6, 2024. The following data were taken (Lavrenko and Korchagin 1972): species composition of the community, TPC – total projective vegetation cover (%), number of vegetation layers, layer height (cm).

A general description of the sites by habitat type is given below.

Habitat 1, placor position (PL), horizontal area, 179–180 m ASL. Dry meadow. TPC is 90–100%. Three layers of herbaceous cover are distinguished. The first layer (15–20 cm) is dominated by *Fragaria viridis* Weston; the second (40–50 cm) – by *Origanum vulgare* L., *Trifolium pratense* L., *Festuca valesiaca* Gaudin; in the third (65–80 cm) – *Bromopsis inermis* (Leyss.) Holub, *Calamagrostis epigeos* (L.) Roth, *Hieracium umbellatum* L., *Stipa pennata* L. Single pine (*P. sylvestris*) and apple (*Malus domestica* (Suckow) Borkh.) trees aged 5–15 years are found. The general view of the habitat is shown in Figure 3.

Figure 3. General view of habitat 1, placor position (PL), 18.06.2024.

Habitat 2, eluvial position (EL), horizontal area, 175–177 m ASL. Dry meadow. TPC is 95–100%. In the first layer (15–20 cm) *F. viridis* dominates; in the second (40–50 cm) – *O. vulgare*, *T. pratense*, *F. valesiaca*, *Agrimonia asiatica* Juz., *Pimpinella saxifraga* L.; in the third (65–80 cm) – *B. inermis*, *C. epigeos*, *Galium album* Mill.

Habitat 3, transit position (TR1), slope, slope steepness – 12–20°, azimuth – 151–188°, 170–172 m ASL. Steppe meadow. TPC – 65–75% and 70–75%. In the first herbage layer (15–20 cm) *F. viridis* dominates; in the second (40–50 cm) – *O. vulgare*, *F. valesiaca*, *A. asiatica*; in the third (65–80 cm) – *S. pennata*.

Habitat 4, transit position (TR2), slope, slope steepness – 17–20°, azimuth – 156–188°, 166–169 m ASL. TPC from 75 to 100%. In the first herbage layer (15–30 cm), *F. viridis* dominates; in the second (40–60 cm) – *F. valesiaca*, *T. pratense*, *O. vulgare*, *A. asiatica*, *Carex praecox* Schreb.; in the third (65–100 cm) – *G. album*, *C. epigeos*, *Vicia tenuifolia* Roth, *S. pennata*, *Medicago falcata* L., *Centaurea scabiosa* L., *Silene nutans* L.

Habitat 5, transit position (TR3), slope, slope steepness – 5–14°, azimuth – 164–186°. The biotope is located at the bottom of the slope, along a hollow at the bottom of the ravine. The bottom of the ravine and the habitat under consideration located along it vary significantly in elevation above sea level. Due to this, the elevation of the sites within the line varies from 137 to 160 m. TPC is 100%. In the first herbage layer (15–20 cm) *F. viridis* dominates; in the second (40–60 cm) – *T. pratense*, *O. vulgare*, *A. asiatica*, *Pilosella caespitosa* (Dumort.) P.D. Sell & C. West, *Rhinanthus aestivalis* (N.W. Zinger) Schischk. & Serg.; in the third (65–100 cm) – *G. album*, *Lathyrus sylvestris* L., *M. falcata*, *Cichorium intybus* L., *C. scabiosa*. At positions TR1–TR2, there are single trees of *M. domestica* 2–4 m high. A general view of the slope positions (TR1, TR2, TR3) is shown in Figure 4.

Figure 4. General view of slope habitats (TR1, TR2, TR3), 18.06.2024.

Habitat 6, accumulative position (AC), moistened area bordering a swampy hollow at the bottom of the ravine. 131–142 m ASL. TPC is 100%. Communities have two or three layers. In the first layer (15–20 cm), *F. viridis* dominates in some areas; in the second tier (40–60 cm), *Carex acuta* L., *A. asiatica*, *Equisetum arvense* L., *O. vulgare*, *Stachys palustris* L., *T. pratense*; In the third layer (65–110 cm), *Rubus caesius* L., *Rumex confertus* Willd., *Galium aparine* L., *Calamagrostis canescens* (Weber) Roth, *G. album*, *B. inermis*, *Scirpus sylvaticum* L., and *Filipendula ulmaria* (L.) Maxim dominate. A general view of the accumulative position (AC) is shown in Figure 5.

Regarding the moisture conditions at the studied catena positions, the following can be noted. At the accumulative position (AC), due to the outflow of groundwater to the surface, the soil was very moist throughout the study season. The projective cover of hygrophilous plants here was 59±7.8%. At positions located higher up the catena, hygrophilous plants were practically absent. Positions PL, El, and TR are characterized by well-drained soils, and the soil there was almost always dry. It was slightly humid only in spring (May) and after heavy rains. Mesophytic plants (TPC = 38 ± 2.5%) and mesoxerophytes (TPC = 51 ± 1.6%) were present at these positions.

Figure 5. General view of the accumulative position (AC), 18.06.2024.

The projective cover of the indicator species *S. pennata* can also be used to estimate gradients in soil moisture and temperature within the studied habitats. This species, found in steppe environments, reaches the northern limit of its range in Udmurtia (Baranova 2012). Based on thermoclimatic scales (Tm), *S. pennata* thrives in conditions intermediate between "nemoral" and "sub-Mediterranean."On soil moisture scales (Hd), its optimal range lies between "middle steppe" and "meadow-steppe". For ombroclimatic aridity-humidity (Om), it prefers "subarid" conditions (Tsyganov 1983). Projective cover of *S. pennata* varies across catena positions: PL (single), EL (0.5 ± 0.5%), TR1 (34 ± 4.6%), TR2 (8±2.2%), TR3 (0.1 ± 0.1%), and AC (0%). Consequently, the warmest and driest conditions in these habitats are observed at the TR1 position.

All ground beetle species present in the studied area were identified by the author with the aid of special identification keys [Kryzhanovskiy 1965; Isaev 2002; Käfer Europas]. Scientific names of taxa are given in accordance with the Catalogue of Palaearctic Coleoptera [Löbl and Löbl 2017]. The correctness of identification of species was confirmed by B.M. Kataev (Zoological Institute of the Russian Academy of Sciences, St. Petersburg) and S.V. Dedyukhin (Udmurt State University, Izhevsk).

During the study period, a total of 6.360 trap-days were accumulated. Catches from each trap over the 106-day season were pooled into one sample (60 samples in total). In total, 4.065 ground beetles, representing 78 species, were captured in pitfall traps within the study area. To mitigate the influence of rare individuals, species with a total abundance of five or fewer specimens were excluded from the analysis. Consequently, data from 45 species and 3.994 specimens were utilized. Species nomenclature and arrangement follow the catalog of Palearctic Coleoptera (Löbl and Löbl 2017). The study area may contain two similar species, *Pterostichus nigrita* (Paykull, 1790) and *P. raeticus* Heer, 1837. Due to their morphological similarity (Angus et al. 2000), data for these species are combined under the designation *P. nigrita* aggr. In figures presenting ordination data for individual species, species names are represented by four- or five-letter abbreviations. In them, the first sign is the first letter of the generic name. The next three or four characters are the first letters of the species name.

Statistical analysis

Because the sampling effort was identical for all traps, untransformed data representing the number of ground beetles captured were used in the calculations.

Differences between samples were assessed using the Bray–Curtis index [Bray and Curtis 1957]. Nonmetric multidimensional scaling (NMDS) was employed for unconstrained ordination [Kruskal 1964]. The positions of individual species along environmental gradients (untransformed data) were estimated by fitting a smooth surface to the NMDS coordinates and empirical environmental factor values [Wood 2006]. Intergroup differences were evaluated using the nonparametric PERMANOVA method [Anderson 2001], followed by post hoc analysis.

To identify the influence of environmental factors (independent variables) on ground beetle assemblages (dependent variables), the dbRDA method (Legendre and Anderson 1999) was used. The following factors were used: slope steepness in degrees (Slope), elevation in meters (Elevation), number of plant species in the sites (Nsp); total projective vegetation cover (TPC); grass height in the sites (Height), projective cover of mesoxerophytes in the sites (Mesxer), projective cover of mesophytes in the sites (Mes), projective cover of *S. pennata* (Stipa).

The relationship between the predictors included in the analysis was assessed using the Spearman correlation coefficient (Rs). The height of the grass stand (Height) on the catena significantly decreases ($Rs = -0.93$, $p < 0.05$) with increasing altitude (Elevation). This indirectly confirms an increase in soil moisture down the catena. Moreover, the driest conditions in the entire habitat chain develop at the first and second transit positions (TR1 and TR2), since the projective cover of the dry conditions indicator species – feather grass (Stipa factor) positively correlates with the slope steepness (Slope): $Rs = 0.82$, $p < 0.05$. The sparse grass stand is also observed at these positions. This is indicated by the negative correlation between the Stipa factor and OPP: $Rs = -0.70$, $p < 0.05$.

To give equal weight to the independent variables, their values were logarithmized as $y' = \log(y+1)$. Collinearity between the independent variables was checked by calculating the Spearman correlation coefficient (Rs). The threshold value at which variables are correlated with each other was Rs > 0.6 (Zuur et al. 2010). The Akaike criterion (AIC) was used to assess the quality of the models.

The biotopic preferences of ground beetle species were identified using the indicator value method (IndVal) [Dufrêne and Legendre, 1997; De Cáseres and Legendre 2009]. The statistical significance of IndVal was assessed using a randomization procedure.

To assess the association of ground beetles with gradients of environmental factors (untranformed data), the TITAN (Thresold Indicator Taxa Analysis) algorithm proposed by Baker and King (2010) was used. This method (Bakker, 2026) is based on the calculation of IndVal values. IndVal values are scaled as z–scores according to the degree of deviation from the expected values by subtracting randomized permutations from the observed IndVal and dividing it by the permuted SD. As a result of the analysis, species are divided into a group with low values (z-) and a group with high values (z+). Species of the first group respond negatively (decrease in IndVal values) to increasing factor values (decreasers), while species of the second group respond positively (increasers). Bootstrapping is used to assess the statistical significance of the results ($p<0.05$). For this purpose, two metrics are calculated: purity and reliability. Purity refers to whether a species is consistently included in the z– or z+ group. Reliability refers to whether the species is a strong indicator of the group to which it is assigned. Only data for species with statistically significant results are included in the report.

The latitudinal component of species ranges was examined for 45 ground beetle species used in the analysis. The distribution of ground beetle species in the natural zones of the Palearctic was studied in a sector extending from the east of the East European Plain south to Iran. Information on the distribution of species is taken from general works on the territories under consideration (Kolesnikova et al. 2017; Löbl and Löbl 2017; Kozminykh 2025a, 2025b, 2025c, 2025d, 2026; Taxonomical list of ground beetles (Carabidae) of Russia; Kryzhanovsky et al. 1995). The following latitudinal groups of habitats have been identified (Dudko and Lyubechansky 2002): boreal group (species are distributed from the tundra to the steppe zone), subboreal humid (distributed no further north than the middle taiga and up to the steppe zone in the south), subarid group (distributed no further north than the forest-steppe), polyzonal group (distributed from the tundra to the semi-desert or further south).

PERMANOVA and post hoc analyses were conducted using PAST 4.11 (Hammer et al., 2001). All other calculations were performed in R 4.4.3 (R Core Team 2017) with the following packages: vegan v. 2.6-8 (dbrda(), ordistep(), anova.cca(), ordisurf()), indispecies v.1.7.15 (multipatt()), and TITAN2 v.2.4.4 (titan()).

Results

The list of species and the total number of captured ground beetles for each habitat type (catena positions) are given in Table 1. The original data are presented in Suppl. material 1: Table S1.

Table 1. The list of species and the total number of captured ground beetles on a meadow catena. Udmurtia, Karakulinsky district, vicinity of the village of Cheganda, 2024

Species	Number of captured specimens					
	PL	EL	TR1	TR2	TR3	AC
Leistus ferrugineus (Linnaeus, 1758)	-	-	-	1	-	3
Notiophilus germinyi Fauvel, 1863	-	-	-	-	2	-
Carabus hortensis Linnaeus, 1758	-	-	-	-	1	2
Carabus cancellatus Illiger, 1798	-	-	-	-	-	4
Carabus convexus Fabricius, 1775	-	-	-	-	-	1
Carabus estreicheri Fischer von Waldheim, 1820	1	-	-	-	1	-
Elaphrus uliginosus Fabricius, 1792	-	-	-	-	-	1
Bembidion biguttatum (Fabricius, 1779)	-	-	-	-	-	1
Bembidion guttula (Fabricius, 1792)	-	-	-	-	-	3
Bembidion mannerheimii C.R. Sahlberg, 1827	-	-	-	-	-	1
***Bembidion gilvipes* Sturm, 1825**	**-**	**-**	**-**	**-**	**1**	**37**
Bembidion articulatum (Panzer, 1796)	-	-	-	2	-	-
***Trechus rivularis* (Gyllenhal, 1810)**	**-**	**-**	**-**	**-**	**2**	**117**
***Trechus secalis* (Paykull, 1790)**	**-**	**-**	**-**	**3**	**13**	**66**
***Brachinus crepitans* Linnaeus, 1758**	**2**	**-**	**-**	**-**	**1**	**3**
Callistus lunatus (Fabricius, 1775)	-	-	-	-	-	1
Chlaenius costulatus (Motschulsky, 1859)	-	-	-	-	-	1
***Harpalus affinis* (Schrank, 1781)**	**3**	**1**	**-**	**1**	**3**	**-**
Harpalus distinguendus (Duftschmid, 1812)	-	-	-	2	1	-
***Harpalus latus* (Linnaeus, 1758)**	**-**	**1**	**2**	**6**	**10**	**52**
***Harpalus luteicornis* (Duftschmid, 1812)**	**18**	**2**	**9**	**2**	**5**	**4**
Harpalus pumilus Sturm, 1818	-	-	2	-	-	-
***Harpalus rubripes* (Duftschmid, 1812)**	**14**	**9**	**5**	**6**	**25**	**1**
Harpalus smaragdinus (Duftschmid, 1812)	-	-	2	-	-	-
***Harpalus subcylindricus* Dejean, 1829**	**26**	**6**	**15**	**11**	**-**	**-**
***Harpalus tardus* (Panzer, 1796)**	**5**	**1**	**5**	**17**	**9**	**6**
Harpalus zabroides Dejean, 1829	-	1	1	-	-	-
Harpalus calceatus (Duftschmid, 1812)	-	-	-	2	-	-
Harpalus griseus (Panzer, 1796)	-	-	-	-	1	-

Species	Number of captured specimens					
	PL	EL	TR1	TR2	TR3	AC
***Harpalus rufipes* (DeGeer, 1774)**	**85**	**96**	**25**	**45**	**76**	**12**
***Ophonus azureus* (Fabricius, 1775)**	**3**	-	-	**19**	**23**	-
***Ophonus laticollis* Mannerheim, 1825**	-	-	-	-	-	**8**
***Ophonus puncticollis* (Paykull, 1798)**	**25**	**10**	**21**	**52**	**58**	**4**
***Ophonus stictus* Stephens, 1828**	**8**	**3**	**1**	**10**	**1**	-
***Cymindis angularis* Gyllenhal, 1810**	**7**	**2**	**2**	**2**	**3**	**1**
***Microlestes maurus* (Sturm, 1827)**	**27**	**33**	**9**	**17**	**61**	**2**
Paradromius linearis (Olivier, 1795)	-	-	-	1	-	-
Philorhizus crucifer (Lucas, 1846)	1	-	-	-	-	-
***Syntomus truncatellus* (Linnaeus, 1761)**	**40**	**37**	**15**	**52**	**152**	**4**
Lebia cruxminor (Linnaeus, 1758)	-	-	-	-	-	1
***Badister bullatus* (Schrank, 1798)**	-	-	-	**3**	-	**7**
***Badister sodalis* (Duftschmid, 1812)**	-	-	-	-	**1**	**46**
***Masoreus wetterhallii* (Gyllenhal, 1813)**	**6**	**6**	**21**	**15**	**13**	**2**
Oodes helopioides (Fabricius, 1792)	-	-	-	-	-	3
Licinus depressus (Paykull, 1790)	-	-	-	-	1	3
Panagaeus bipustulatus Fabricius, 1775	-	-	-	-	-	2
Panagaeus cruxmajor (Linnaeus, 1758)	-	-	-	-	-	4
***Agonum fuliginosum* (Panzer, 1809)**	-	-	-	-	-	**22**
***Agonum viduum* (Panzer, 1796)**	-	-	-	-	**1**	**5**
***Anchomenus dorsalis* (Pontoppidan, 1763)**	-	-	-	-	**5**	**16**
***Oxypselaphus obscurus* (Herbst, 1784)**	-	-	-	-	-	**7**
Poecilus lepidus (Leske, 1785)	-	1	3	-	1	-
***Poecilus versicolor* (Sturm, 1824)**	**6**	-	**1**	**2**	**18**	**175**
Pterostichus macer (Marsham, 1802)	-	-	-	2	-	-
***Pterostichus vernalis* (Panzer, 1796)**	-	-	-	-	-	**12**
Pterostichus melanarius (Illiger, 1798)	-	-	-	-	-	4
***Pterostichus diligens* (Sturm, 1824)**	-	-	-	-	-	**86**
***Pterostichus strenuus* (Panzer, 1796)**	-	-	-	-	-	**11**
***Pterostichus niger* (Schaller, 1783)**	-	-	-	**1**	**2**	**165**
***Pterostichus minor* (Gyllenhal, 1827)**	-	-	-	-	-	**29**
***Pterostichus nigrita* aggr.**	-	-	-	-	-	**29**
***Calathus fuscipes* Goeze, 1777**	**172**	**36**	**19**	**52**	**43**	**1**
***Calathus ambiguus* (Paykull, 1790)**	**2**	**1**	**4**	**5**	-	-
***Calathus erratus* (C.R. Sahlberg, 1827)**	**1**	**6**	**48**	**48**	**7**	-
***Calathus melanocephalus* (Linnaeus, 1758)**	**31**	**14**	**12**	**21**	**97**	**15**

Species	Number of captured specimens					
	PL	EL	TR1	TR2	TR3	AC
Synuchus vivalis (Illiger, 1798)	-	-	-	-	-	1
***Amara aenea* (DeGeer, 1774)**	**1**	**3**	**4**	**1**	**5**	**-**
***Amara communis* (Panzer, 1797)**	**9**	**1**	**-**	**1**	**10**	**173**
***Amara convexior* Stephens, 1828**	**10**	**3**	**-**	**11**	**38**	**33**
Amara curta Dejean, 1828	-	-	2	-	-	-
Amara eurynota (Panzer, 1796)	-	1	-	-	-	-
Amara montivaga Sturm, 1825	-	-	-	-	1	-
***Amara nitida* Sturm, 1825**	**-**	**-**	**-**	**-**	**-**	**6**
***Amara bifrons* (Gyllenhal, 1810)**	**5**	**2**	**22**	**6**	**5**	**1**
Amara apricaria (Paykull, 1790)	-	-	-	-	-	1
***Amara aulica* (Panzer, 1796)**	**1**	**-**	**1**	**4**	**23**	**2**
***Amara taurica* (Motschulsky, 1844)**	**-**	**1**	**9**	**2**	**-**	**-**
***Amara equestris* (Duftschmid, 1812)**	**17**	**14**	**215**	**359**	**71**	**1**
Specimens in total	526	291	475	784	791	1205
Trap-days in total	1060	1060	1060	1060	1060	1060
Species in total	27	26	27	35	39	54

Notes: Species included in the analysis are highlighted in bold. For descriptions of habitats (catena positions) PL, EL, TR1, TR2, TR3, and AC, see the text.

Species richness and abundance of ground beetles in catches (Table 1) tend to increase downslope, from the eluvial (EL) to the accumulative (AC) positions. When moving from the eluvial position (EL) to the placor position (PL), a slight increase in the number of ground beetles is also observed.

We analyzed the relationship between all studied predictors (Slope, Elevation, Nsp, TPC; Height, Mesxer, Mes, Stipa) and species richness (S) and specimen count (N) using Spearman's rank correlation coefficient (Rs). Two analyses were performed: one including all catena positions, and another excluding the upland position (PL).

In the first analysis, a significant ($p < .05$) negative correlation was found between species richness (S) and Elevation ($Rs = -0.60$), and between specimen count (N) and Elevation ($Rs = -0.64$). A moderate positive correlation was observed between both S and N, and grass height (Height) ($Rs = 0.60$ and $Rs = 0.65$, respectively).

When excluding the placor position (Pl) from the data set, the strength of the relationship increases in all the cases considered ($Rs = -0.70, -0.77, 0.71, 0.76$). All other correlations between S and N and the remaining predictors were either less than 0.5 or statistically insignificant.

Given the negative correlation between Height and Elevation (Rs = −0.93), our analysis confirms the statistically significant trend of increasing species richness and ground beetle abundance as elevation decreases down the catena.

The non-metric multidimensional scaling (NMDS) method was used to ordinate sixty samples onto two axes, with the results depicted in Figure 6.

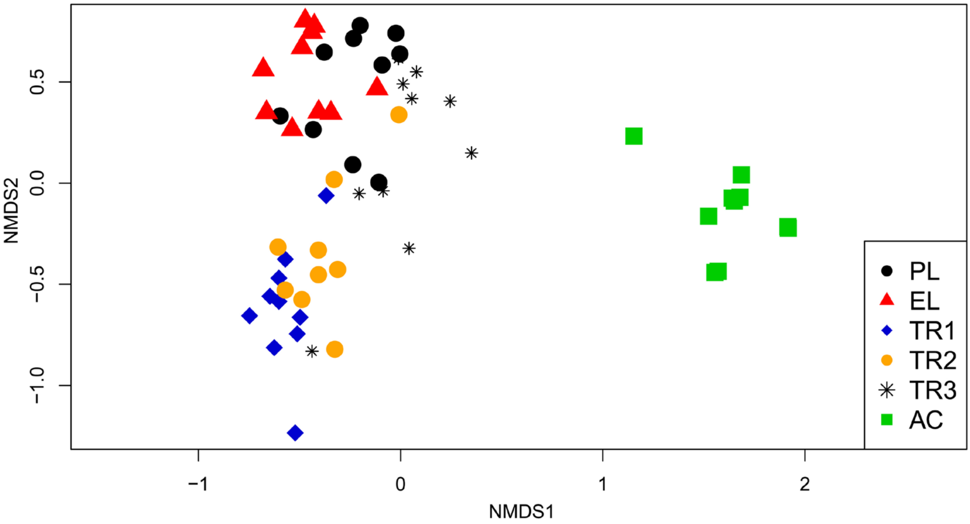

Figure 6. NMDS ordination diagram of ground beetle assemblages (Coleoptera, Carabidae) based on the Bray-Curtis distance (stress = 0.08, k = 4). For descriptions of habitats (catena positions) PL, EL, TR1, TR2, TR3, AC, see text.

Ordination results (Figure 6) clearly divide the dataset into two clusters: samples from the accumulative position (AC) and all other locations. This differentiation is primarily driven by significant differences in ground beetle populations across the studied habitats. Of the 45 species analyzed (Table 1), 9 were exclusive to the accumulative position. An additional 9 species were predominantly found there, with only single specimens observed in two adjacent habitats. The remaining 27 species exhibited broader distribution across the catena's habitats.

Ground beetle samples from positions PL to TR3 form a single cluster, though some separation based on catena position is evident (Figure 6). TR1 and TR2 samples generally form a distinct group.

Differences between samples grouped by the "catena position" factor were assessed using the PERMANOVA method. The results of the analysis show that the composition of the ground beetle population at different positions of the studied catena differs statistically significantly ($p < 0.001$). Post-hoc pairwise comparisons indicated significant differences ($p < 0.05$) between all biotope pairs, with the exception of the TR1–TR2 comparison (Table 2).

Table 2. Results of pairwise comparisons of ground beetle samples across catena positions (p-values with Bonferroni correction). PERMANOVA, Bray–Curtis index

	PL	EL	TR1	TR2	TR3	AC
PL	–	0.006	0.0015	0.0015	0.0015	0.0045
EL	0.006	–	0.0015	0.0015	0.0015	0.0015
TR1	0.0015	0.0015	–	0.114	0.0015	0.0015
TR2	0.0015	0.0015	0.114	–	0.0315	0.0015
TR3	0.0015	0.0015	0.0015	0.0315	–	0.0015
AC	0.0045	0.0015	0.0015	0.0015	0.0015	–

Beyond the catena position factor, the influence of several environmental variables on the ground beetle population was analyzed using dbRDA. Initially, all independent variables were included: Slope, Elevation, Nsp, TPC, Height, Mesxer, Mes, and Stipa. The original data on independent variables are presented in Suppl. material 2: Table S2. Significant Spearman correlations ($p < 0.05$) exceeding the threshold of $Rs > 0.6$ were identified between TPC and Stipa ($Rs = -0.70$), Height and Elevation ($Rs = -0.93$), and Steepness and Stipa ($Rs = 0.82$). According to the result, Stipa and Height were removed from the initial model.

The model underwent further optimization using the ordistep() function. This function's algorithm first conducts a global test with all explanatory variables. If significant, it proceeds to select variables from the global model based on the Akaike criterion and adjusted R^2 (R^2adj) (Borcard et al. 2018). Applying ordistep() to our data resulted in a final model retaining three factors: Slope, TPC, and Mesxer. The adjusted R^2 of 0.43 suggests moderate explanatory power. A global test of the model, performed with anova.cca(), confirmed its statistical significance (Pr(>F) =0.001; 999 permutations). Three constrained ordination axes were found to be statistically significant (Pr(>F) = 0.001; based on 999 permutations). Together, these three axes explained 45.7% of the total variance. Specifically, dbRDA1 accounted for 57.5% of this explained variance, dbRDA2 for 32.0%, and dbRDA3 for 10.5%. An independent test assessing the influence of each factor confirmed a statistically significant effect (Pr(>F) = 0.001) of the variables on the ground beetle population structure. The dbRDA ordination results for the first two axes are illustrated in Figure 7.

The constrained ordination analysis (Figure 7) reveals a negative relationship between the ground beetle population composition and structure in the most humid habitat (AC) and the proportion of mesoxerophytes (Mesxer). This finding is entirely expected, given that the proportion of mesoxerophytes was near zero in the accumulative position of the catena. This factor exerted a relatively minor influence on samples from other habitats.

The Slope and TPC factors have opposite effects on ground beetle population structure. The structure of most samples from positions TR1 and TR2 is primarily determined by the Slope factor. Similarly, the total projective cover (TPC) significantly influences the composition of a significant portion of samples from positions PL, EL, and TR3.

We employed the TITAN algorithm to track the ground beetle population response to environmental changes, specifically examining the influence of Elevation, TPC, and Slope factors. The aggregated results for the entire ground beetle population are illustrated in Figures 8–10.

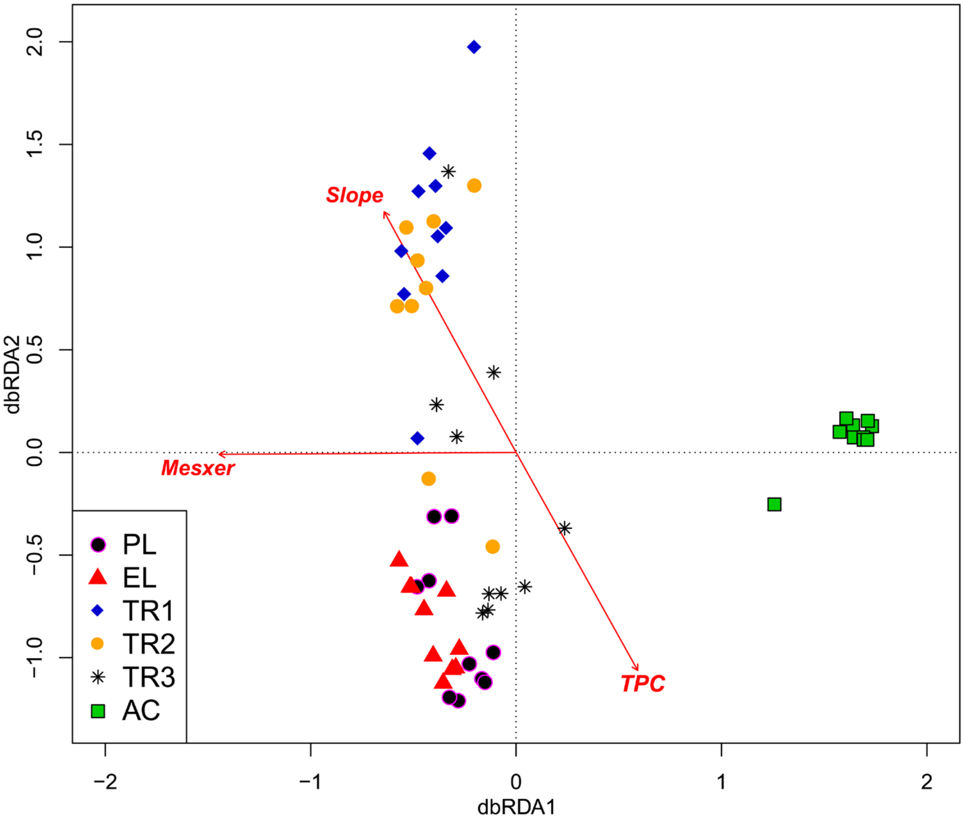

Figure 7. Ordination diagram (dbRDA) of ground beetle samples on a meadow catena based on the Bray-Curtis distance (R^2adj = .43). For a description of habitats (catena positions) PL, EL, TR1, TR2, TR3, AC and an explanation of the factor names (Slope, TPC, Mesxer), see the text.

In this study, changes in Elevation are analogous to alterations in catena positions. The presented graphs (Figure 8) reveal that species exhibiting a negative response to increasing elevation (decreasers) experience the largest cumulative changes within the Elevation range up to 150 meters, specifically from the accumulative (AC) to the third transit (TR3) positions. As Elevation further increases, the sum of changes for this ground beetle group smoothly declines to zero. Species that respond positively to rising catena elevations (increasers) demonstrate considerably smaller total responses along the gradient. Their responses are generally uniform across the studied elevation range, with somewhat higher sums of change observed in the segments from 131 to 140 m (AC to TR3) and from 165 m to 175 m (TR2 and TR1).

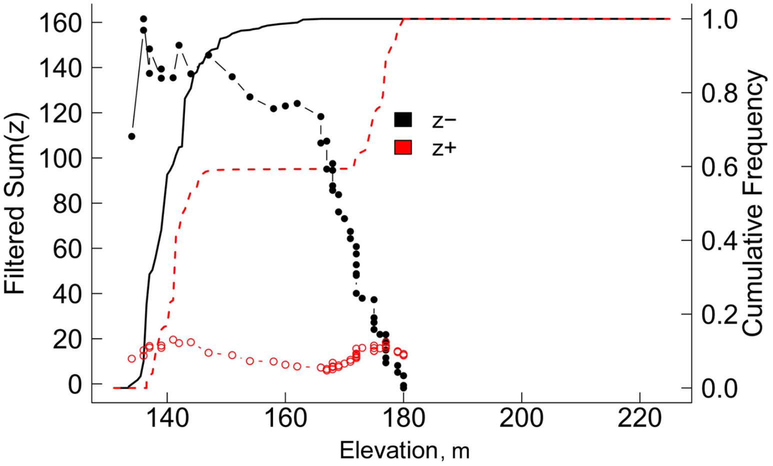

Figure 8. Ground beetle population response to Elevation changes in a meadow catena. TITAN method. Circles represent summed z-scores for species with increasing (z+) and decreasing (z–) IndVal values. Solid and dashed lines are cumulative frequency distributions of sum(z–) and sum(+) maxima.

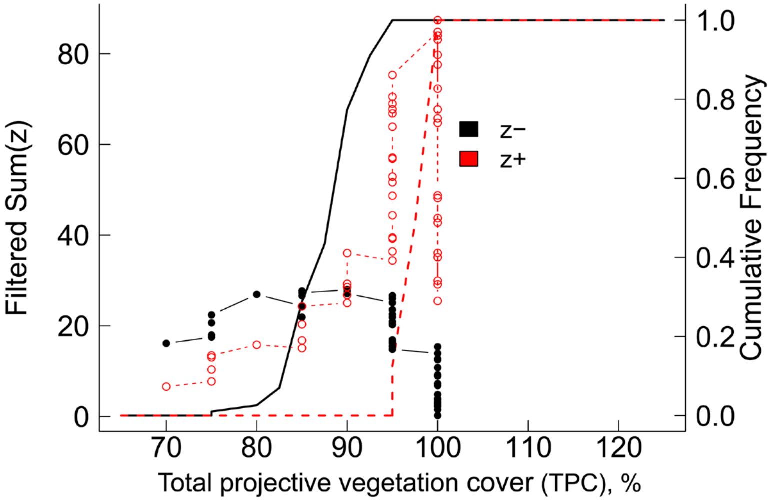

Figure 9. Ground beetle population response to changes in total projective vegetation cover (TPC) in a meadow catena. TITAN method. See Figure 7 for legend.

The greatest overall response of ground beetles to an increase in TPC values is observed in the increasers group with a factor value of 95–100% (Fig. 9). The results indicate that, regardless of catena position, the most significant changes in the composition or structure of the ground beetle population occur at the transition from areas with relatively sparse grass cover to areas with a surface maximally covered by grass cover.

The maximum effect of slope steepness (Figure 10) on the structure and composition of ground beetle population occurs at the transition from horizontal sections to slopes (i.e., from AC to TR3 and from TR1 to EL). In this case, the sum of changes for decreaser species is significantly greater. With further increases in slope steepness, the sum of changes for increasers and decreasers gradually decreases, and this process occurs generally in parallel for the groups under consideration.

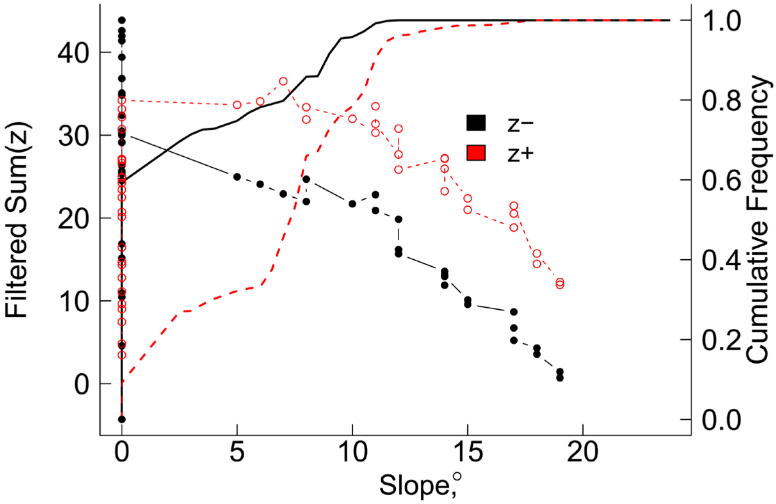

Figure 10. Ground beetle population response to changes in slope steepness in a meadow catena. TITAN method. See Figure 7 for legend.

Differentiation of individual species along gradients of environmental conditions can be visualized using the ordisurf() function. Function ordisurf() fits a smooth surface for given variable and plots the result on ordination diagram (NMDS ordination). The results of species distribution along the gradients of the Elevation, TPC, and Slope factors are presented in Figures 11, 12, and 13.

The ordination results show the distribution of species across the environmental gradients under consideration. Three more or less distinct groups of ground beetles can be identified. A group of 10 species is quite clearly defined, with the highest abundance on slopes with steepness from 10° to 16° with relatively sparse grass cover (TPC from 76 to 94%): *H. tardus*, *O. puncticollis*, *O. azureus*, *O. stictus*, *M. wetterhallii*, *C. ambiguus*, *C. erratus*, *A. bifrons*, *A. taurica*, *A. equestris*. This group of species is primarily characteristic of positions TR1 and TR2 (elevation from 155 to 175 m).

At the opposite ends of the gradients of the factors under consideration, at points with a horizontal surface and maximum projective grass cover (100%), 8 species are also located separately: *A. fuliginosum*, *O. obscurus*, *P. vernalis*, *P. diligens*, *P. strenuus*, *P. niger*, *P. minor*, *P. nigrita* aggr. All these species are characteristic of the most humid accumulative position (AC).

The remaining 27 species out of 45 included in the analysis gravitate toward sites with intermediate values of the factors examined. Some of them, under the conditions examined, do not exhibit a pronounced topical preference and are distributed more or less evenly across the catena: *H. latus*, *H. luteicornis*, *H. rubripes*, *H. rufipes*, *M. maurus*, *S. truncatellus*, *C. fuscipes*, and *C. melanocephalus*. Of particular note is *H. subcylindricus*, a species that prefers the uppermost positions of the catena but is also found on slopes and horizontal areas. The remaining species either gravitate toward the lowermost positions of the catena or are represented by a small number of individuals, making it difficult to clearly characterize their preferences.

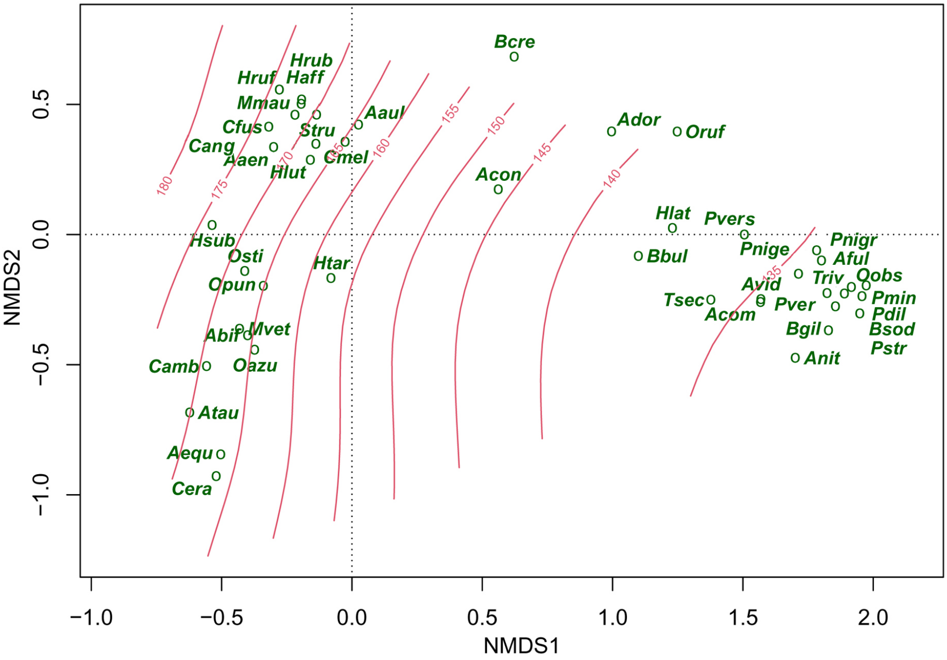

Figure 11. NMDS ordination of ground beetle species, with smooth surface for the Elevation factor (m).

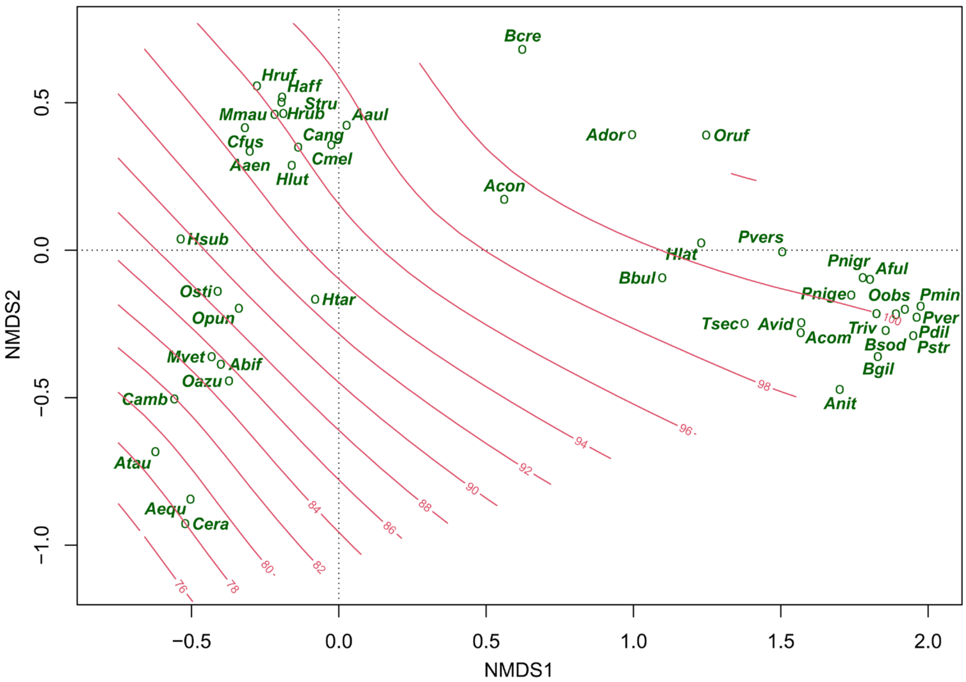

Figure 12. NMDS ordination of ground beetle species, with smooth surface for the TPC factor, %.

The distribution of ground beetle species in the studied conditions can be further refined using a procedure for identifying species indicative of the studied habitats (catena positions). The results of calculating the indicator value index (IndVal) are presented in Table 3. The table includes only statistically significant results for 35 of the 45 species included in the analysis.

Table 3. Results of calculating the indicator value index (IndVal) for ground beetle species on the meadow catena. Udmurtia, Karakulinsky district, vicinity of the village. Cheganda, 2024

Species	IndVal value	p-value
	Plakor position (PL)	
Calathus fuscipes	0.73	0.001
Harpalus luteicornis	0.64	0.001
Harpalus subcylindricus	0.56	0.029
	Eluvial position (EL)	
Harpalus rufipes	0.53	0.037

Species	IndVal value	p-value
Transit position 1 (TR1)		
Amara taurica	0.72	0.001
Calathus erratus	0.66	0.009
Masoreus wetterhallii	0.52	0.042
Transit position 2 (TR2)		
Amara equestris	0.73	0.001
Harpalus tardus	0.60	0.003
Transit position 3 (TR3)		
Syntomus truncatellus	0.71	0.001
Calathus melanocephalus	0.68	0.001
Amara aulica	0.67	0.002
Microlestes maurus	0.61	0.005
Amara convexior	0.60	0.004
Harpalus rubripes	0.58	0.008
Ophonus puncticollis	0.55	0.027
Ophonus azureus	0.51	0.040
Accumulative position (AC)		
Trechus rivularis	0.99	0.001
Pterostichus niger	0.99	0.001
Agonum fuliginosum	0.95	0.001
Amara communis	0.94	0.001
Bembidion gilvipes	0.94	0.001
Pterostichus vernalis	0.93	0.001
Trechus secalis	0.90	0.001
Badister sodalis	0.88	0.001
Poecilus versicolor	0.84	0.001
Pterostichus diligens	0.84	0.001
Pterostichus minor	0.77	0.001
Harpalus latus	0.76	0.001
Pterostichus nigrita aggr.	0.71	0.001
Oxypselaphus obscurus	0.71	0.001
Pterostichus strenuus	0.63	0.003
Agonum viduum	0.58	0.010
Amara nitida	0.55	0.024
Badister bullatus	0.53	0.022

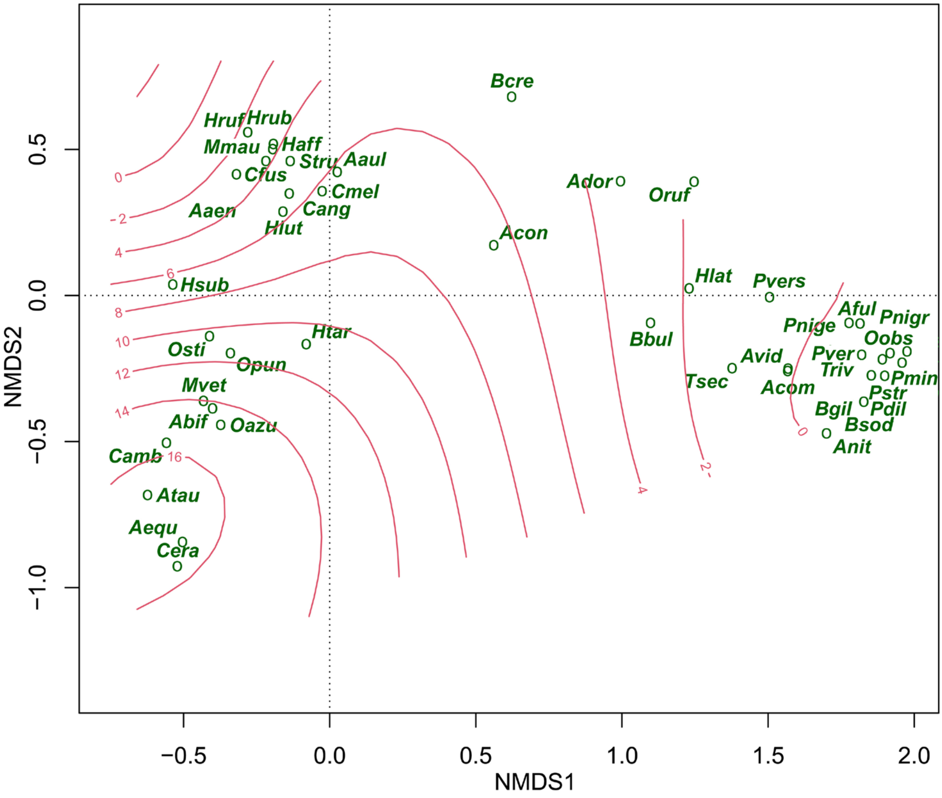

Figure 13. NMDS ordination of ground beetle species, with smooth surface for the Slope factor, °.

When calculating IndVal, the most significant result is selected from the entire data typology. In our case, the IndVal calculation results practically coincide with the maximum total species abundance in the range of studied habitats (Table 1). Among the species included in the analysis, with a single exception, the total abundance of each species at different positions in the catena differs from all others.

The results of the analysis of the belonging of 45 studied species of ground beetles to latitudinal groups of species ranges are presented in Table 4. The original data are presented in Suppl. material 3: Table S3.

The results show a pronounced trend of increasing boreal species abundance down the catena. In the subboreal humid group, despite a general increase in species abundance down the catena, there is a sharp decline in species richness at positions EL and TR1. Polyzonal species show no trend of increasing abundance, but their abundance also decreases at positions EL and TR1. Subarid species are found only in the driest habitats, from PL to TR2.

Table 4. Latitudinal groups of ground beetle species ranges in meadow catena positions. Udmurtia, Karakulinsky district, environs of the village of Cheganda, 2024

Latitudinal group of species ranges	Position of catena, number of species					
	PL	EL	TR1	TR2	TR3	AC
Boreal	1	2	2	2	4	8
Subboreal humid	11	9	8	12	15	17
Subarid	1	2	2	2	–	–
Polyzonal	12	10	10	13	12	12

Discussion

As shown above, the habitats we examined were previously used for agricultural purposes. The most transformed sites were those in the plakor (PL) position, which had previously been used as arable land. Currently, the process of forming a meadow community here has apparently progressed quite far. This is confirmed by the fact that some species of ground beetles recorded in the catena (for example, *H. rufipes* and *M. maurus*), often abundant in agricultural fields (Aleksanov and Alekseev 2019; Borisovskiy 2025), do not reach the maximum abundance at this position (IndVal value, see Table 3).

Our understanding of the spatial distribution of ground beetles on catenas and slopes within the forest zone is limited. Existing research has identified some ground beetle species in steppe and meadow environments situated on slopes in regions such as Perm Krai (Kozminykh 2003; 2013), Samara Oblast (Leontyeva and Krivopalova 1999), Altai Krai (Bespalov et al. 2008), Mordovia, and Ulyanovsk Oblast (Aleksanov et al. 2022). However, these investigations typically focused on discrete steppe and meadow habitats, neglecting the influence of environmental gradients that characterize catenas. Additionally, some studies incorporated areas with a mosaic of open habitats interspersed with forest biotopes. While these approaches successfully revealed species affiliations with particular biotopes, they did not elucidate specific distribution patterns along these environmental gradients.

Ground beetle distribution patterns in steppe catenas across southern Siberia and Kazakhstan have been extensively documented (Lyubechansky et al. 1997; Mordkovich and Lyubechansky 1998; Mordkovich et al. 1985, 2020, 2022). Research indicates that within steppe zones, eluvial positions of catenas experience moisture deficit, while accumulative positions exhibit excess moisture. Consequently, peak species richness and abundance of ground beetles were observed at the middle positions of these catenas, with a gradual decline in both metrics towards the upper and lower ends. In contrast, studies of Siberian forest zones (specifically the birch-aspen forest subzone) reveal that the highest concentrations of species diversity and abundance occur at the uppermost catena position (EL), where optimal moisture levels coincide with fairly high temperatures.

Previous studies on ground beetle differentiation in catenas have focused on species distribution within individual positions. Our findings reveal significant shifts in ground beetle population structure along the geomorphological profile of a catena. In most instances, ground beetle populations at distinct positions exhibit statistically significant differences (Table 2), aligning with established patterns observed in steppe catenas (Lyubechansky et al. 1997; Mordkovich et al. 1985; Mordkovich et al. 2020).

In the catena we studied, as we move down the profile, we generally observe an increase in the number of species and abundance of ground beetles (Table 1). The change in species composition across the habitats examined is not absolute. Thirteen of the 45 ground beetle species (29%) were present in all catena positions. In the steppes, where conditions are more contrasting, the ground beetle population composition at the extreme ends of the catenae sometimes differs completely (Lyubechansky et al. 1997; Mordkovich et al. 1985).

A trend toward an increasing number of boreal species was noted as we proceeded down the catena (Table 3). This finding aligns with observations from the steppe catenas (Mordkovich 2020).

In our study examined the ground beetle population in the upland position (PL). This position has typically not been considered in studies of ground beetles in catenas. If PL is excluded from consideration, a decrease in abundance and species diversity occurs in the upper catena positions (TR1 and EL), as was observed in steppe catenas (Mordkovich et al. 1985).

As noted above, in steppe catenas, the peak in diversity and abundance occurs in the middle positions of the catenas (Mordkovich et al. 1985). In the catena we studied, however, the maximum species diversity occurs in the accumulative position (AC). At the transition from the accumulative position to the slope in the catena we studied, in most cases the greatest changes in the composition and structure of the ground beetle population are observed (Figures 8–10). Moreover, the number of ground beetle species noted here in our case exceeds the species richness indicated for the accumulative positions of catenas studied in Siberia and Kazakhstan (Mordkovich et al. 1985): 53 species versus 46. Moreover, 18 species are statistically significant indicators of this position (Table 2), and 8 of the 45 species included in the analysis are noted only here.

The distribution patterns of ground beetle abundance and species richness in our studied catena diverge significantly from those documented in southern Siberia and Kazakhstan (Mordkovich et al. 1985). A probable explanation for these observed differences lies in the substantial elevation variation (50 m) and steep slopes (up to 20°) present in our study area. This contrasts sharply with the catenas investigated in Siberia and Kazakhstan, which were characterized by considerably less pronounced elevation differences. For example, the Shortandy catena recorded an elevation change of a mere 4.5 m across 1,400 m (Mordkovich et al. 1985). Another defining characteristic of steppe catenas is the obligatory presence of solonetzic soilsat in TR positions, exhibiting a specific moisture regime. Such soils were absent in the catena we examined.

In addition to the "position of catena" factor, our investigation extended to other variables hypothesized to influence the species composition and structure of ground beetle populations. The quantitative variable "Elevation" served as an analogue to the qualitative "catena position," given that nearly all catena positions within the study area are situated at distinct elevations. Our analysis revealed that "elevation above sea level" does not rank among the top three factors most predictive of ground beetle population composition and structure. However, the factors Slope, Mesxer, and TPC demonstrated the most significant influence on the composition of ground beetle assemblages along the catena. Different factors exert the greatest influence on ground beetle population structure at different catena positions. Thus, it can be concluded that the structure of ground beetle assemblages on the catena is determined by a number of factors, the influence of which varies at different positions.

One of the goals of our study was to identify the presence of a specific, narrowly localized species complex on the slope. By comparing the NMDS ordination results (Figures 11–13) with the IndVal calculation results (Table 2), we identified five species that characterize the steepest, sparsely vegetated catena positions: *H. tardus*, *M. wetterhallii*, *C. erratus*, *A. equestris*, and *A. taurica*. We initially hypothesized that these steepest (dry) catena sections (TR1, TR2) would host a number of species with a "southern" distribution, similar to observations in steppe catenas (Mordkovich et al. 2020). However, only one species from this subarid category, *A. taurica*, proved characteristic of positions TR1 and TR2 (Figures 11–13 and Table 2). The other four species are widely distributed across natural zones and belong to polyzonal and subboreal humid groups (Table 3). While these four species, based on their highest abundance, formally indicate (IndVal value, table 2) the driest habitats within our study area, they are quite eurytopic and occur throughout almost the entire catena profile (Table 1). Therefore, unlike in steppe catenas (Mordkovich et al. 2020), our studied catena exhibits only one subarid species in its driest botopes.

Conclusion

As a result of the research, statistically significant differences in the composition and structure of the ground beetle population at different positions of the studied catena were revealed. Slope steepness (Slope), total projective cover (TPC), and the proportion of mesoxerophytes in the herbage (Mesxer) were the primary drivers of species composition and population structure. Ground beetle species richness and abundance generally increased down the catena, peaking at the lowest, accumulative position. The fewest ground beetle species were found at the upper catena positions: eluvial and the first transit. These observed patterns of species distribution and abundance shifts along the catena diverge from previously documented trends in Siberian and Kazakh steppe catenas.

Ground beetle composition and structure undergo their most significant overall changes with increasing elevation at the transition from accumulative positions (AC) to slopes (TR3). Similarly, ground beetles exhibit their strongest overall responses to rising TPC values when moving from areas with sparse grass cover (TPC up to 90%) to those with 95–100% TPC.

Analysis of the latitudinal distribution of ground beetle species revealed a trend: the number of boreal species increases down the catena. Five indicator species were found on the driest and steepest slope sections, with only one of these being subarid.

Acknowledgements

The author thanks B.M. Kataev (Zoological Institute of the Russian Academy of Sciences, St. Petersburg) and S.V. Dedyukhin (Udmurt State University, Izhevsk) for their expertise in species identification, including confirmations and corrections. Gratitude is also extended to T.V. Borisovskaya (Udmurt State University, Izhevsk) for her valuable assistance in describing habitats, and to D.A. Adakhovsky (Udmurt State University, Izhevsk) for his support during fieldwork.

The study was carried out with the financial support of the Ministry of Science and Higher Education of the Russian Federation within the framework of the state assignment FEWS-2024-0011 "Biodiversity of natural ecosystems of the Trans-Volga-Ural region: the history of its formation, modern dynamics and ways of protection".

References

Alekhin VV (1986) Theoretical problems of phytocenology and steppe studies. Moscow State University, Moscow, 216 pp. [In Russian]

Aleksanov VV, Alekseev SK (2019) Cadaster of ground beetles (Coleoptera, Carabidae) of the urban district of Kaluga City. LLC Print, Izhevsk, 276 pp. [In Russian]

Aleksanov V, Alekseev S, Ruchin A, Lukiyanov S, Lobachev E, Esin M, Ershkova E (2023) Comparative analysis of the beetle fauna (Coleoptera: Carabidae) of small steppe plots in the forest-steppe zone. E3S Web of Conferences 431: 1–12. https://doi.org/10.1051/e3sconf/202343101028

Anderson MJ (2001) A new method for non-parametric multivariate analysis of variance. Austral Ecology 26: 32–46. https://doi.org/10.1111/j.1442-9993.2001.01070.pp.x

Angus RB, Brown RE, Bryant LJ (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

Baker ME, King RS (2010) A new method for detecting and interpreting biodiversity and ecological community thresholds. Methods in Ecology and Evolution 1: 25–37. https://doi.org/10.1111/j.2041-210X.2009.00007.x

Baranova OG (2002) Local flora of Udmurtia: analysis, synopsis, protection: Textbook. Udmurt State University, Ishevsk, 199 pp. [In Russian]

Baranova OG, Egorov IE, Sturman VI (2010) On the south limit of taiga in the western part of pre-Urals. Bulletin of Udmurt University. Series Biology. Earth Sciences 1: 58–69. [In Russian]

Baranova OG (2012) Feather grass – *Stipa pennata* L. In: Red Book of the Udmurt Republic. Perfektum, Cheboksary, 261. [In Russian]

Bespalov AN, Ivanov SB, Dudko RYu, Lyubechanski II (2008) Structure of the ground beetle community (Coleoptera, Carabidae) in the forest-steppe landscapes of the lower Biya river valley (Altai Province). Altai Zoological Journal 2: 3–19. [In Russian]

Borisovskiy AG (2025) Ecological grouping of ground beetles (Carabidae, Coleoptera) by biotopic preferences in the forest-meadow landscape of Udmurtia. Ecosystem Transformation 8(4): 65–92. https://doi.org/10.23859/estr-240501 [In Russian]

Bray JR, Curtis JT (1957) An ordination of the upland forest communities of Southern Wisconsin. Ecological Monographs 27: 325–349.

Chernov YI (1975) Natural zonation and fauna of the land. Mysl', Moscow, 222 pp. [In Russian]

De Cáceres M, Legendre P (2009) Associations between species and groups of sites: indices and statistical inference. Ecology 90: 3566–3574. https://doi.org/10.1890/08-1823.1

Digweed SC, Currie CR, Carcamo HA, Spence JR (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.

Dudko RYu, Lyubechanskii II (2002) Fauna and zoogeographic characteristics of ground beetles (Coleoptera, Carabidae) of the Novosibirsk region. Euroasian Entomological Journal 1(1): 30–45. [In Russian]

Dufrêne M, Legandre P (1997) Species assamblages 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 DAT, Ryan PD (2001) PAST: Paleontological Statistics Software Package for Education and Data Analysis. Palaeontologia Electronica 4(1): 1–9.

Isachenko AG (1991) Landscape science and physical-geographical zoning. Vysshaya shkola, Moscow, 366 pp. [In Russian]

Isaev AYu. (2002) Key of Coleoptera of the Middle Volga Region (Part 1 – Adephaga and Myxophaga). Nature of the Ulyanovsk region 10: 1–80. [In Russian]

Lavrenko EM, Korchagin AA (eds) (1972) Field geobotany. Nauka, Leningrad, 336 pp. [In Russian]

Käfer Europas: https://coleonet.de/coleo/texte/carabidae.htm (Accessed on 01.04.2026).

Kolesnikova AA, Dolgin MM, Konakova TN (2017) Ground beetles (Coleoptera, Carabidae). Fauna of the European northeast of Russia. Vol. VIII. Part 4. Institute of Biology of the Kola Science Center of the Ural Branch of the Russian Academy of Sciences, Syktyvkar, 340 pp. [In Russian]

Kolomyts EG, Surova NA (2007) Forest ecosystems of Samarskaya Luka under the coming global warming (Structure functional analysis and prognosis). Samara Luka 3(21): 372–430. [In Russian]

Kozminykh VO (2003) Composition and distribution of beetles (Insecta, Coleoptera) in the biotopes of the Lunezhskie Gory natural landscape monument (Perm Region). In: Environmental problems of protected areas in Russia. Publishing House of the Institute of Ecology of the Volga Basin of the Russian Academy of Sciences, Tolyatti, 204–210. [In Russian]

Kozminykh VO (2013) Beetles (Insecta, Coleoptera) of the Perm area. Part 12. Structure of beetle communities in the nature territory "Ergach". In: Innovations in Science. A collection of articles from the XXVIII International Scientific and Practical Conference 28. Novosibirsk, 50–66. [In Russian]

Kozminykh VO (2025a) The Catalogue of Beetles (Coleoptera) of the Urals and adjacent territories (to the 200th anniversary of scientific research in the Urals Region). II. Ground beetles (Carabidae), 3rd communication. Eversmannia 81: 23–64. [In Russian]

Kozminykh VO (2025b) The Catalogue of Beetles (Coleoptera) of the Urals and adjacent territories (to the 200th anniversary of scientific research in the Urals Region). II. Ground beetles (Carabidae), 4th communication. Eversmannia 82: 14–58. [In Russian]

Kozminykh VO (2025c) The Catalogue of beetles (Coleoptera) of the Urals and adjacent territories (to the 200th anniversary of scientific research in the Urals Region). II. Ground beetles (Carabidae), 5th communication. Eversmannia 83, 3–45. [In Russian]

Kozminykh VO (2025d) The Catalogue of beetles (Coleoptera) of the Urals and adjacent territories (to the 200th anniversary of scientific research in the Urals Region). II. Ground beetles (Carabidae), 6th communication. Eversmannia 84: 49–82. [In Russian]

Kozminykh VO (2026) The Catalogue of beetles (Coleoptera) of the Urals and adjacent territories (to the 200th anniversary of scientific research in the Urals Region). II. Ground beetles (Carabidae), 7th communication. Eversmannia 85: 8–498. [In Russian]

Kruskal JB (1964) Nonmetric multidimensional scaling: a numerical method. Psychometrika 29: 115–129.

Kryzhanovskiy OL (1965) Family Carabidae – ground beetles. In: Key of insects of the European part of the USSR. Vol. 2. Nauka, Moscow, Leningrad, 29–77. [In Russian]

Kryzhanovskij OL, Belousov IA, Kabak II., Katae BM, Makarov KV, Shilenkov VG (1995) A checklist of the ground beetles of Russia and adjacent lands (Insecta, Coleoptera, Carabidae). Pensoft Publishers, Sofia–Moscow, 271 pp.

Legendre P, Anderson MJ (1999) Distance-based redundancy analysis: testing multispecies responses in multifactorial ecological experiments. Ecological Monographs 69:1–24.

Leontyeva OV, Krivopalova SA (1999) Carabid complexes (Coleoptera, Carabidae) of the watershed slope habitats in the north-east of Samara region. Izvestia of Samara Scientific Center of the Russian Academy of Sciences 2: 193–200. [In Russian]

Löbl I, Löbl D (Eds) (2017) Catalogue of Palaearctic Coleoptera. Archostemata – Myxophaga – Adephaga. Vol. 1. Brill Publ., Leiden, Boston, 1443 p.

Lyubechansky II, Smelyansky IE, Legalov AA, Dudko Ryu (1997) Population of terrestrial invertebrates of the steppe catena in the Trans-Volga region. In: Eurasian Steppes: Conservation of Natural Diversity and Monitoring of Ecosystem Conditions. Proceedings of the International Symposium. Orenburg, 109–110. [In Russian]

Mordkovich VG, Shatokhina NG, Titlyanova AA (1985) Steppe catenas. Nauka, Novosibirsk, 117 pp. [In Russian]

Mordkovich VG, Lyubechansky II (1998) Zonal-catena order of ecological ordination in carabids (Coleoptera, Carabidae) from the West Siberian plain. Advances in Current Biology 118(2): 205–215. [In Russian]

Mordkovich VG (2017) Interconnectedness between ecological successions and catenary arrangement of space. Journal of General Biology 78(2): 32–46. [In Russian]

Mordkovich VG, Khudyaev SA, Dudko RYu, Lyubechansky II (2020) Zoological Indication of Climate Change in the Central Kazakh Steppe Compared to the Middle of the 20th Century Using the Example of Carabid and Tenebrionid Beetles. Contemporary Problems of Ecology 13(5): 443–468. https://doi.org/10.1134/S1995425520050078

Mordkovich VG, Dudko RYu, Khudyaev SA, Lyubechansky II (2022) Changes in ground beetle communities (Coleoptera: Carabidae, Tenebrionidae) in mountain depressions of the Tuva and Altai over 60 years: trend or fluctuation? Contemporary Problems of Ecology 15(6): 579–596. https://doi.org/10.1134/S1995425522060099

Podsosova TK (1972) Relief. In: Nature of Udmurtia. Udmrtia, Izhevsk, 37–64. [In Russian]

Taxonomical list of ground beetles (Carabidae) of Russia: http://www.zin.ru/Animalia/Coleoptera/eng/car_rus.htm (Accessed on 01.04.2026).

Tsyganov DN (1983) Phytoindication of ecological regimes in the subzone of coniferous-broadleaf forests. Nauka, Moscow, 197 pp. [In Russian]

Zhizhin CM, Zalesov SV, Magasumova AG (2022) Agricultural land change in Udmurt Republic. Forestry Bulletin 26(3): 47–53. [In Russian]

R Core Team (2017) R: A Language and Environment for Statistical Computing. http://www.R-project.org/

Rysin II (2020) Climate. In: Atlas of the Udmurt Republic. Moscow–Izhevsk, 68–75. [In Russian]

Thiele HU (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 pp.

Wood SN (2006) Generalized Additive Models: An Introduction with R. Chapman, Hall/CRC, 410 pp.

Zuur AF, Ieno EN, Elphick CS (2010) A protocol for data exploration to avoid common statistical problems. Methods of Ecology and Evolution 1: 3–14. https://doi. org/10.1111/j.2041-210X.2009.00001.x

Supplementary material 1

Table S1. Number of captured ground beetles

Author: Alexander G. Borisovskiy
Data type: table

Link: https://journal.asu.ru/biol/article/view/19828/16908

Supplementary material 2

Table S2. Environmental variables

Author: Alexander G. Borisovskiy
Data type: table

Link: https://journal.asu.ru/biol/article/view/19828/16909

Supplementary material 3

Table S3. Latitudinal groups of ground beetle species ranges

Author: Alexander G. Borisovskiy
Data type: table

Link: https://journal.asu.ru/biol/article/view/19828/16910