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Diversity and altitudinal structure of darkling beetles (Tenebrionidae) in the Zarafshan Valley, Uzbekistan

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Abstract. *Umirzokova MS, Alimova LKH, Akramov IB, Rakhimov MR, Khamzaev RA, Sayfullayev GM, Daminov MA, Urazova RS, Safarova MS, Usanov UN, Baysariyev SU, Oljayev DN, Arepbaev IM, Khalimov FZ. 2026. Diversity and altitudinal structure of darkling beetles (Tenebrionidae) in the Zarafshan Valley, Uzbekistan. Biodiversitas 27 (4): d270411. https://doi.org/10.13057/biodiv/d270411.* Darkling beetles (Tenebrionidae) are a major component of arid and semi-arid ecosystems and are widely used as indicators of environmental conditions, particularly under increasing aridization in Central Asia. The present study aims to assess species diversity, taxonomic structure, and altitudinal patterns of Tenebrionidae assemblages in the Zarafshan Valley, one of the most biogeographically heterogeneous regions of Uzbekistan. Sampling was conducted in 2022-2024 across 30 localities representing different elevations and vegetation types. Beetles were collected using pitfall traps, light traps, and manual sampling. Uzbekistan, using standardized sampling across 30 sites (2022-2024). A total of 84 species belonging to 36 genera, 17 tribes, and 4 subfamilies were recorded, including 1 genus newly reported for Central Asia and 11 species newly recorded for Uzbekistan. Community structure was characterized by high diversity (Shannon H′: 3.67; Simpson 1-D: 0.96) and low dominance (D: 0.04), indicating a relatively balanced assemblage. Multivariate analyses revealed significant compositional differentiation along the elevational gradient (PERMANOVA: R^2: 0.176, p: 0.009), with a strong association between elevation and community structure in PCA ordination (R^2: 0.492, p: 0.002). Overall, the results support a pattern of continuous, gradient-driven restructuring of Tenebrionidae communities rather than sharply defined altitudinal belts. These findings provide a quantitative baseline for monitoring climate-driven changes in arid insect communities and highlight the importance of integrating environmental variables in future studies to clarify the mechanisms underlying elevational patterns.

Keywords: Central Asia, community turnover, darkling beetles, elevational gradient, new records

INTRODUCTION

The Palaearctic region, particularly Central Asia, is one of the key areas for the formation of beetle diversity in desert ecosystems. Within this region, the family Tenebrionidae Latreille, 1802 occupies a leading position in both species' richness and ecological significance. Darkling beetles are a major component of the fauna of many arid and semi-arid ecosystems worldwide (Raś 2022; Szara 2025). They contribute to the functioning of dry habitats through organic matter decomposition, soil formation, trophic interactions, and the maintenance of ecosystem stability (Kamiński et al. 2021; Cheli 2022). Because of their high sensitivity to environmental changes, darkling beetles are widely recognized as characteristic elements of arid ecosystems and have long served as model organisms for studying ecological adaptation to desert conditions (Nabozhenko and Chigray 2022; Zhao 2025).

Recent studies show that Central Asia is experiencing pronounced climate change, including rising air temperatures, shifts in moisture regimes, and major hydrological changes across inland arid regions (Chen et al. 2019; Yao et al. 2022). These trends are expected to strongly affect the structure and functioning of arid and semi-arid ecosystems, including insect communities (IPCC 2021).

The Zarafshan Valley, which includes mountainous, foothill, and desert-steppe landscapes of Uzbekistan, is one of the most biogeographically heterogeneous regions of Central Asia (Alikulov et al. 2023). In recent years, the biodiversity of invertebrates in this region has been actively studied (Kudratov et al. 2024; Shodmonov and Fomichev 2025; Uralov et al. 2025), including its entomofauna (Rakhimov 2023; Medetov et al. 2024). Nevertheless, the

Tenebrionidae fauna of the valley remains insufficiently investigated, and available information is often fragmented or based on isolated and outdated records (Pirnazarov 1973; Khamraev 2003).

Although the Catalog of Palaearctic Coleoptera (Löbl and Smetana 2008), updated in its revised second edition (Iwan et al. 2020), provides a comprehensive taxonomic framework, many species have not been recently confirmed for Uzbekistan or still require revision of their distribution ranges. Recent studies have reported new species records, clarified distribution patterns, and shown that the desert and mountain ecosystems of the Zarafshan Valley represent important centers of local endemism and biodiversity refugia (Chigray et al. 2022; Mamanov et al. 2024).

Despite the availability of classical catalogs and recent faunistic studies, contemporary spatially standardized surveys covering the full elevational gradient of the Zarafshan Valley are still lacking. Most earlier data are based on non-comparable sampling efforts, limiting the assessment of gradient-driven community structuring under current environmental conditions. Elevational gradients act as composite environmental filters by integrating changes in temperature, moisture, soil structure, and vegetation complexity (Lomolino 2001; Körner 2007). In semi-arid mountain systems, such gradients are usually associated with gradual species turnover rather than sharply defined ecological zonation. In addition, β-diversity may increase toward higher elevations because environmental conditions become more heterogeneous over shorter spatial scales. Upper elevational zones often combine stronger microclimatic contrasts, greater variation in slope exposure, patchier vegetation, and increased habitat heterogeneity, all of which can enhance compositional dissimilarity among local assemblages.

There remains a lack of standardized, gradient-wide surveys encompassing the region's full elevational range. This limits evaluation of how community composition, diversity, and β-diversity respond to continuous environmental variation, constrains robust inference on gradient-driven community structuring, and hampers detection of ecological patterns associated with environmental filtering. Addressing this gap is essential to establish a consistent quantitative framework for assessing biodiversity patterns and to provide a baseline for monitoring climate-driven changes in arid and semi-arid insect communities. Therefore, the objectives of the present study were to determine the species composition of the Tenebrionidae fauna in the Zarafshan Valley, to analyze its taxonomic structure, and to evaluate the effect of the elevational gradient on community composition.

MATERIALS AND METHODS

Study area

The material was collected during the period 2022-2024 across various habitats of the Zarafshan Valley (Figure 1, Table 1).

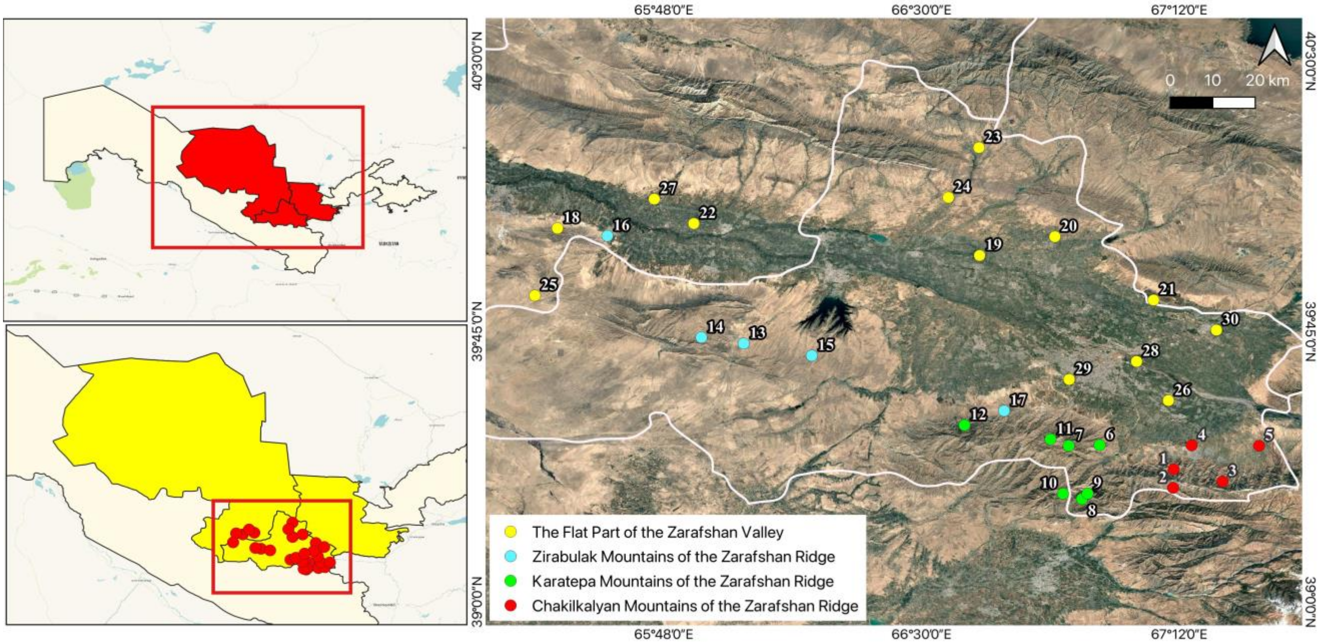

Figure 1. Location of the study sites in the Zarafshan Valley, Uzbekistan. 1. Kamongaron; 2. Saridukan Pass; 3. Qumbelsay Village; 4. Yalpoktepa Village; 5. Chep Village; 6. Yetti Uyli River; 7. Sevasay; 8. Amankutan Village, Yulsay River; 9. Amankutan Village, Bulbulzorsay River, vicinity of Leva Cave; 10. Takhtakoracha Pass; 11. Kemkutan Mountain, Agalyk Village; 12. Hazrati Dovud; 13. Ingichka; 14. Ostonabobo Village; 15. Nurdum Village; 16. Ziyadin Town; 17. Sazagan Village; 18. Gurugli Village; 19. Birlashgan Village; 20. Baxrin Village; 21. Kungrat Village; 22. Durman Village; 23. Kuralas Village; 24. Tulabosti Village; 25. Karnabchul Desert; 26. Talliata Village; 27. Kuchi Village; 28. Zarafshan National Park; 29. Botanical Garden of Samarkand State University; 30. Sabalak Village

Table 1. Biogeographical characteristics of the collection sites

Elevation class (m asl)	Sampling site number	Climate and vegetation of sampling sites
Low (≤697)	13, 15, 16, 18, 19, 20, 22, 24, 25, 27	Dry steppe to semi-desert/desert climate, steppes and semi-deserts with ephemeral grasses and ephemeroids, rainfed or irrigated agroecosystems. Annual precipitation is typically ~200-300 mm
Middle (697-1,050)	5, 6, 7, 14, 17, 21, 23, 26, 28, 29, 30	Dry low-mountain/foothill climate, hot summers and mild winters, steppe vegetation with ephemeral grasses and shrubs. Annual precipitation is typically ~250-350 mm
High (>1,050)	1, 2, 3, 4, 8, 9, 10, 11, 12	Mountain climate, moderately warm to warm summers and generally cooler winters compared with lower elevations. Vegetation includes mountain steppe and juniper woodlands/stands on slopes. Annual precipitation is typically ~300-550 mm, varying locally with exposure and topography

Note: Elevation classes correspond to tertiles derived from elevation quantiles (n: 30 sites). Breakpoints were q33 ≈ 696.7 m asl (rounded to 697 m asl) and q66: 1,050 m asl; sites at 1,050 m asl were assigned to the middle tertile. M asl: meters above sea level

Geographical coordinates of the collecting sites

Chakilkalyan Mountains of the Zarafshan Ridge

Zarafshan Ridge, Kamongaron (39°22'05"N, 67°11'06"E; h: 1,550 m asl); Zarafshan Ridge, Saridukan Pass (39°19'00"N, 67°11'00"E; h: 2,200-2,600 m asl); Zarafshan Ridge, Qumbelsay Village (39°20'04"N, 67°19'04"E; h: 1,400 m asl); Samarkand Region, Urgut District, Yalpoktepa Village (39°26'04"N, 67°14'02"E; h: 900 m asl); and Samarkand Region, Urgut District, Chep Village (39°26'00"N, 67°25'00"E; h: 1,050 m asl).

Karatepa Mountains of the Zarafshan Ridge

Zarafshan Ridge, Yetti Uyli River (39°26'07"N, 66°59'02"E; h: 1,050 m asl); Zarafshan Ridge, Sevasay (39°26'00"N, 66°54'00"E; h: 1,500 m asl); Zarafshan Ridge, Amankutan Village, Yulsay River (39°17'09"N, 66°56'09"E; h: 1,700 m asl); Zarafshan Ridge, Amankutan Village, Bulbulzorsay River, vicinity of Leva Cave (39°18'03"N, 66°57'04"E; h: 1,460 m asl); Zarafshan Ridge, Takhtakoracha Pass (39°18'02"N, 66°53'03"E; h: 1,800 m asl); Zarafshan Ridge, Kemkutan Mountain, Agalyk Village (39°27'05"N, 66°51'02"E; h: 1,550 m asl); and Zarafshan Ridge, Hazrati Dovud (39°29'26"N, 66°37'00"E; h: 1,144 m asl).

Zirabulak Mountains of the Zarafshan Ridge

Samarkand Region, Nurabad District, Ingichka (39°43'01"N, 66°01'01"E; h: 650 m asl); Samarkand Region, Nurabad District, Ostonabobo Village (39°44'2"N, 65°54'8"E; h: 720 m asl); Samarkand Region, Nurabad District, Nurdum Village (39°41'00"N, 66°12'07"E; h: 570 m asl); Samarkand Region, Pakhtachi District, Ziyadin Town (40°00'56"N, 65°38'49"E; h: 455 m asl); and Samarkand Region, Nurabad District, Sazagan Village (39°31'49"N, 66°43'28"E; h: 825 m asl).

The Flat Part of the Zarafshan Valley

Samarkand Region, Paxtachi District, Gurugli Village (40°02'12"N, 65°30'41"E; h: 540 m asl); Samarkand Region, Payarik District, Birlashgan Village (39°57'40"N, 66°39'28"E; h: 540 m asl); Samarkand Region, Payariq District, Baxrin Village (40°00'48"N, 66°51'44"E; h: 620 m asl); Samarkand Region, Chelak District, Kungrat Village (39°50'15"N, 67°07'49"E; h: 720 m asl); Samarkand Region, Narpay District, Durman Village (40°02'59"N, 65°52'54"E; h: 407 m asl); Samarkand Region, Kushrabad District, Kuralas Village (40°15'37"N, 66°39'22"E; h: 745 m asl); Samarkand Region, Kushrabad District, Tulabosti Village (40°07'19"N, 66°34'23"E; h: 635 m asl); Samarkand Region, Nurabad District, Karnabchul Desert (39°51'00"N, 65°27'00"E; h: 420 m asl); Samarkand Region, Taylak District, Talliata Village (39°33'32"N, 67°10'14"E; h: 769 m asl); Navoi Region, Khatirchi District, Kuchi Village (40°07'03"N, 65°46'27"E; h: 420 m asl); Samarkand Region, Jambay District, Zarafshan National Park, Sector 1 (39°40'02"N, 67°05'03"E; h: 750 m asl); Samarkand Region, Botanical Garden of Samarkand State University (39°37'02"N, 66°54'04"E; h: 750 m asl); and Samarkand Region, Bulungur District, Sabalak Village (39°45'15"N, 67°18'04"E; h: 760 m asl).

Habitat types at each sampling site were assigned based on field observations and regional vegetation descriptions. Vegetation was identified in situ according to dominant plant communities and physiognomic structure (e.g., desert-steppe, foothill steppe, mountain steppe, juniper woodland), with reference to published regional sources. Sites were classified into habitat categories based on dominant vegetation and environmental context (elevation, slope, land use). These categories correspond to the generalized vegetation and climate descriptions presented in Table 1 and were used for descriptive purposes only.

Sampling, preservation, and identification

Insects were collected using pitfall traps (Barber 1931; Heydemann 1955), standardized soil excavations, light traps (Alimova et al. 2024), and hand collecting. Sampling was conducted during three consecutive years (2022-2024) at 30 sites distributed along the elevational gradient. At each site, five visits per year were carried out: two in spring (April-May), two in summer (June-July), and one in autumn (September). Each visit lasted 3-4 days. In total, each site was sampled during 15 visits over the three years (5 visits × 3 years), ensuring a fully standardized and comparable sampling effort across sites. The sampling design and effort were identical across all sites and years. During each visit, five Barber-Heydemann pitfall traps were installed along a linear transect at 25 m intervals and remained active for the entire visit period. One light trap was operated for two nights per visit (18:00-23:00). Additionally, 5 standardized soil excavations (0.5×0.5×0.5 m) were performed manually at each site. Pitfall traps primarily capture actively moving epigeic adults, while light traps sample nocturnally active flying species. Soil excavations, therefore, complement these methods by detecting species that remain concealed in soil microhabitats or exhibit limited surface activity. Because sampling effort was consistent among sites, abundance values were directly comparable without additional standardization. As summarized in Table 2, complementary sampling methods were used to target distinct ecological strata and functional groups, ensuring comprehensive coverage of both epigeic and cryptic Tenebrionidae taxa.

Specimens were fixed in ethyl acetate ($C_4H_8O_2$) for 3-5 hours and subsequently mounted on entomological pins or preserved in cotton-lined boxes. Species identification was performed using the keys of Medvedev and Nepesova (1985) and Abdurakhmanov and Nabozhenko (2011). Identification of *Gnaptor spinimanus* was additionally based on detailed examination of diagnostic morphological characters following Medvedev (2001) and Chigray et al. (2015), including body proportions, pronotal morphology, elytral sculpture, and male genital structures. Determinations were independently verified by M. Nabozhenko (Russia), a specialist in Tenebrionidae taxonomy. Taxonomic nomenclature follows the revised and updated second edition of the Catalog of Palaearctic Coleoptera (Iwan et al. 2020). All examined specimens are deposited in the entomological collection of Samarkand State University.

Voucher specimens and verification. Specimens are organized by locality and date of collection and are available for examination upon request. For taxa newly recorded from Uzbekistan, full locality data (coordinates, elevation, date, and collector) are provided in the text.

Data analysis

The degree of dominance was assessed according to the Renkonen scale (Renkonen 1944), distinguishing dominant (>5%), subdominant (2-5%), low-abundance (1-2%), and rare (<1%) species.

Biodiversity was evaluated using the Margalef, Shannon, Menhinick, Shannon evenness, Simpson, and Berger-Parker indices. Similarity between communities was assessed using the Chekanovsky-Sørensen and Jaccard coefficients.

Grouping of sampling sites by elevation

To assess the effect of elevation, all sampling sites were grouped according to altitude. The elevational range was divided into three tertiles based on elevation quantiles, resulting in three elevation groups: low, middle, and high. The exact breakpoints corresponded to the 33rd and 66th percentiles (q33 ≈ 696.7 m; q66: 1050 m). Sites at exactly 1050 m were assigned to the middle tertile. This classification was used exclusively as an analytical framework to compare patterns of community structure along the elevational gradient and does not imply discrete ecological boundaries. The use of tertiles ensures a balanced distribution of sampling sites across elevation groups and allows statistically comparable analyses.

Data matrix preparation

For statistical analyses, the sampling unit was the individual sampling site (n: 30). For each site, species abundances were pooled across all sampling visits and across all three study years (2022-2024) to characterize site-level community structure and reduce short-term temporal variability. Because sampling effort was fully standardized across sites, pooling does not introduce bias related to unequal sampling intensity. Thus, the resulting “site×species” matrix represents the cumulative abundance of each species recorded at each site during the entire study period. All sampling methods were integrated into this matrix. To reduce the influence of double zeros and to ensure ecological interpretability of Euclidean-based ordination methods, the abundance matrix was subjected to Hellinger transformation (Legendre and Gallagher 2001). This transformation minimizes the disproportionate effect of rare species while preserving community structure information.

Table 2. Linkage between sampling methods and target taxa in Tenebrionidae survey

Sampling method	Target taxa / Functional group	Ecological stratum	Detection strength	Limitations	Contribution to the dataset
Pitfall traps (Barber-Heydemann)	Epigeic, actively moving beetles (ground-dwelling adults)	Surface/soil interface	High efficiency for abundant, mobile taxa, standardized abundance data	Underrepresents low-mobility and cryptic species	Core dataset for community structure and dominance
Light traps	Nocturnal and flying species	Above-ground/ aerial	Effective for detecting dispersive and phototactic taxa	Biased toward phototactic species, limited for ground specialists	Complements taxonomic completeness
Soil excavation (manual)	Cryptic, low-mobility, soil-dwelling taxa	Subsurface/ upper soil layer	Detects hidden or inactive species not captured by traps	Labor-intensive, limited spatial coverage	Enhances detection of rare and cryptic taxa
Hand collecting	Opportunistic taxa across habitats	All strata (microhabitats)	Flexible, useful for targeted or rare species	Non-standardized, potential collector bias	Supplementary records and rare taxa confirmation

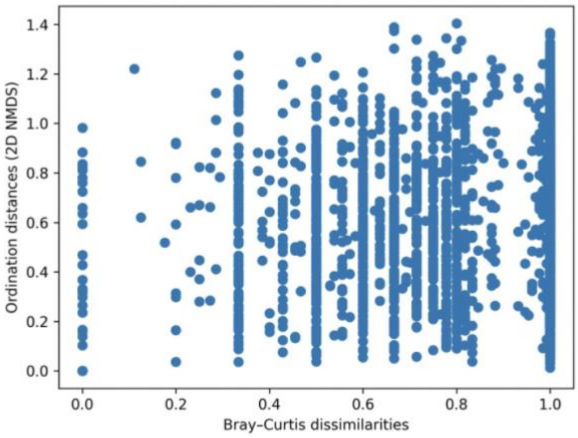

Figure 2. Shepard diagram of the two-dimensional non-metric multidimensional scaling (2D NMDS) based on Bray-Curtis dissimilarity, showing the relationship between observed dissimilarities and ordination distances

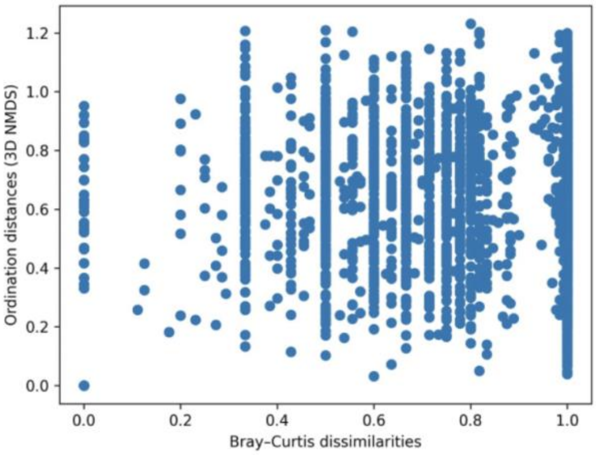

Figure 3. Shepard diagram of the three-dimensional non-metric multidimensional scaling (3D NMDS) based on Bray-Curtis dissimilarity, showing the relationship between observed dissimilarities and ordination distances

Ordination analysis

To identify the main linear gradients in community structure, principal component analysis (PCA) was applied to the Hellinger-transformed species matrix. To analyze non-linear patterns of variation in community composition, non-metric multidimensional scaling (NMDS) was performed using the Bray-Curtis dissimilarity index (Bray and Curtis 1957; McCune and Grace 2002) in R with the vegan package (Oksanen et al. 2025). Both two-dimensional and three-dimensional solutions were explored. Goodness-of-fit of the ordinations was evaluated using stress values, and diagnostic plots are provided in Figure 2 and Figure 3.

Relationship between ordinations and elevation

The relationship between ordination configuration and elevation was assessed using the envfit procedure implemented in the vegan package. The statistical significance of fitted vectors was tested using 999 permutations. The coefficient of determination (R^2) was used to quantify the proportion of variation in ordination space explained by elevation.

Comparison of altitudinal groups

Differences in community composition among elevational groups were tested using permutational multivariate analysis of variance (PERMANOVA; Anderson 2001), implemented with the adonis2 function (vegan package) based on the Bray-Curtis dissimilarity matrix. The analysis included: pseudo-F statistics, degrees of freedom (df), R^2 values (effect size), and permutation-based p-values (999 permutations). When appropriate, pairwise comparisons among elevational groups were conducted. To control for multiple testing, p-values were adjusted using the false discovery rate (FDR) correction (Benjamini and Hochberg 1995).

Test of homogeneity of dispersions

To evaluate whether group differences detected by PERMANOVA could be influenced by heterogeneity of dispersion (β-diversity), homogeneity of multivariate dispersions was assessed using the betadisper function (vegan package), followed by permutation testing (permutest, 999 permutations) (Anderson and Walsh 2013). This procedure estimates distances of sampling sites to group centroids in principal coordinates space derived from the Bray-Curtis dissimilarity matrix.

Indicator species analysis

To identify species significantly associated with specific elevational groups, indicator value analysis (IndVal) was performed using the multipart function in the indicspecies package (Dufrêne and Legendre 1997). Statistical significance of indicator values was assessed using permutation tests (999 permutations). To account for multiple comparisons, p-values were adjusted using the false discovery rate (FDR) procedure (Benjamini and Hochberg 1995).

RESULTS AND DISCUSSION

Taxonomic composition

A total of 84 species of darkling beetles recorded in the biocenoses of the Zarafshan Valley belong to four subfamilies of the family Tenebrionidae: Pimeliinae, Tenebrioninae, Diaperinae, and Alleculinae. In terms of species richness, the subfamily Tenebrioninae clearly predominates, comprising 59% of all recorded species (50 species). The contribution of the subfamily Pimeliinae is slightly lower, accounting for 36% of the tenebrionid fauna (30 species) (Figure 4.A). The contribution of representatives of different subfamilies to the tenebrionid fauna in terms of individual abundance shows a largely similar pattern (Figure 4.B).

The contribution of different tribes to the tenebrionid fauna was also analyzed in terms of species richness and individual abundance. In terms of species diversity, the tribes Blaptini, Pimeliini, and Opatrini show a clear predominance within the tenebrionid fauna (Figure 5). In contrast, the tribes Adesmiini, Alphitobiini, Zophosini, Dissonomini, Pedinini, Triboliini, and Diaperini make the smallest contribution to the fauna, each being represented by only a single species, accounting for 1.2% of the total fauna per tribe.

When the contribution of different tribes is considered in terms of individual abundance, the pattern changes slightly. Although the composition of the dominant tribes remains the same, their relative ranking differs. In terms of individual abundance, the contribution of the tribes Opatrini and Pimeliini increases (accounting for 23.7% and 23.0%, respectively), reaching levels comparable to that of the tribe Blaptini (23.1%), which shows clear dominance in species richness.

The 84 species of darkling beetles recorded in the biocenoses of the Zarafshan Valley belong to 36 genera. The contribution of different genera to the tenebrionid fauna in terms of species richness and individual abundance is presented in Table 3. In terms of species richness, a clear predominance is observed for the genus *Prosodes*. Notably, this genus comprises approximately 225 species and subspecies worldwide, the majority of which are endemic to Central Asia. Considering this, the number of *Prosodes* species recorded in the present study appears relatively low, indicating the need for continued and more intensive future investigations.

At the same time, most records of representatives of this genus are based on studies conducted in the mid-20th century. Therefore, the relatively low number of recorded *Prosodes* species may reflect changes in species occurrence compared with earlier records. Despite its relatively high species richness, the contribution of the genus *Prosodes* in terms of individual abundance is comparatively lower, accounting for only 9% of all collected specimens.

The dominance of *Prosodes* in terms of individual abundance is primarily driven by high population densities of *Prosodes oblonga*, *Prosodes nuratensis*, *Prosodes staudingeri*, *Prosodes ballionis*, and *Prosodes obliquesulcata*. In contrast, species such as *Prosodes kataevi*, *Prosodes chigrayi*, *Prosodes pygmaea pygmaea*, and *Prosodes sogdiana* were represented by extremely few individuals, with only a single specimen recorded during the study. Assessing the current population status of these species requires targeted investigations and is of particular importance for the development of effective conservation measures.

The genera *Stalagmoptera* and *Blaps* also belong to the dominant genera in the tenebrionid fauna. The high contribution of the genus *Stalagmoptera* in terms of individual abundance is primarily driven by high population densities of *Stalagmoptera intermedia*, *Stalagmoptera laticollis*, and *Stalagmoptera tuberculatocostata*. Populations of species belonging to the genus *Blaps* show relatively similar densities; however, *Blaps medvedevi* is a very rare species and was recorded by only a single specimen during the present study.

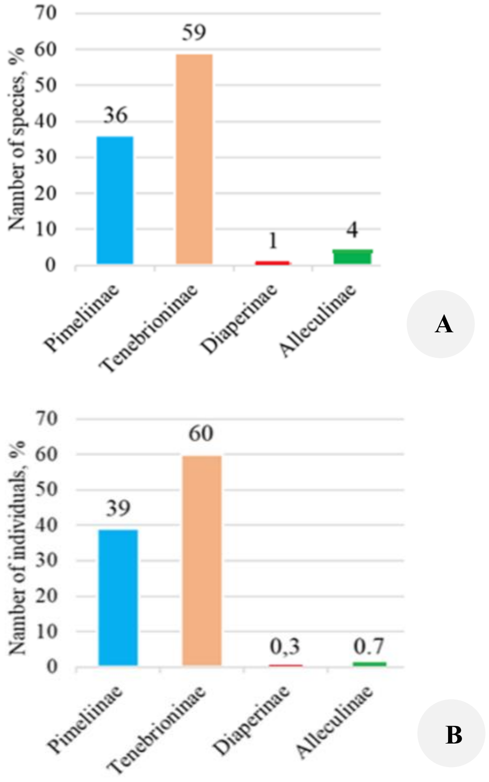

Figure 4. Contribution of Tenebrionidae subfamilies to species richness (A) and relative abundance (B) in the Zarafshan Valley

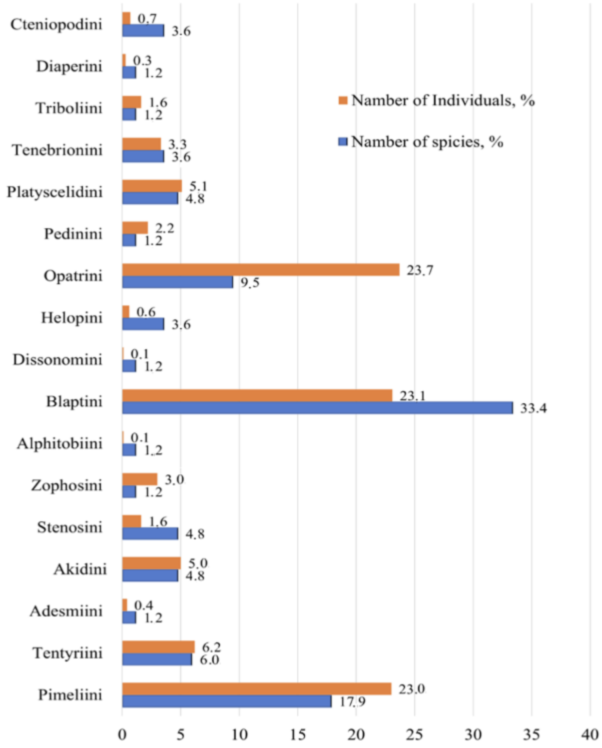

Figure 5. Contribution of Tenebrionidae tribes to species richness and relative abundance

Table 3. Contribution of different genera to the tenebrionid fauna in terms of species richness and individual abundance

Genera	Species richness (n)	Species richness (%)	Individual abundance (n)	Individual abundance (%)
Adesmia	1	1.2	6	0.4
Alcinoeta	1	1.2	2	0.1
Alphitobius	1	1.2	2	0.1
Bioramix	2	2.4	3	0.2
Blaps	8	9.5	118	7.7
Cabirutus	1	1.2	33	2.2
Calyptopsis	1	1.2	2	0.1
Catomus	2	2.4	6	0.4
Cyphogenia	4	4.8	77	5.0
Dailognatha	1	1.2	81	5.3
Diaperis	1	1.2	5	0.3
Dichillus	1	1.2	4	0.3
Dila	2	2.4	94	6.1
Dissonomus	1	1.2	1	0.1
Eustenomacidius	1	1.2	3	0.2
Gnaptor	1	1.2	2	0.1
Gonocephalum	4	4.8	63	4.1
Lasiostola	2	2.4	16	1.0
Microplatyscelis	1	1.2	18	1.2
Ocnera	1	1.2	2	0.1
Omophlina	2	2.4	7	0.5
Omophlus	1	1.2	3	0.2
Opatroides	1	1.2	63	4.1
Pelorocnemis	1	1.2	86	5.6
Penthicus	3	3.6	236	15.4
Podhomala	2	2.4	30	2.0
Prosodes	15	17.9	139	9.1
Somocoelia	1	1.2	57	3.7
Stalagmoptera	8	9.5	192	12.5
Stenosis	3	3.6	21	1.4
Tagona	2	2.4	2	0.1
Tenebrio	3	3.6	51	3.3
Tentyria	2	2.4	10	0.7
Thriptera	1	1.2	26	1.7
Tribolium	1	1.2	24	1.6
Zophosis	1	1.2	46	3.0

As shown in Table 3, in the regional Tenebrionidae fauna, 20 genera are represented by only a single species. Among them, the genera *Dissonomus*, *Alcinoeta*, *Alphitobius*, *Calyptopsis*, *Gnaptor*, *Ocnera*, and *Tagona* are distinguished by particularly low abundances. Notably, the genus *Gnaptor* is recorded from Central Asia for the first time in the present study, and new distributional records for this genus are provided. All examined specimens of *Gnaptor spinimanus* are deposited in the entomological collection of Samarkand State University with complete locality data. The identification was based on stable diagnostic characters described in the taxonomic revision of the genus and confirmed by an external expert. Given the faunistic nature of the present study, morphological examination and expert validation provide sufficient evidence for this regional record. Overall, the observed taxonomic structure, characterized by dominance of Tenebrioninae and key tribes, provides the foundational pool of species through which diversity patterns and elevational turnover are subsequently expressed.

New records for Uzbekistan and Central Asia

The present survey resulted in the documentation of one genus newly recorded from Central Asia and eleven species newly recorded from Uzbekistan. All new records are based on voucher specimens collected during this study and deposited in the entomological collection of Samarkand State University (SSU). To ensure full specimen-level traceability, detailed voucher information for each newly recorded taxon, including locality, coordinates, elevation, date, collector, and number of individuals, is provided below in a standardized “Material examined” format. All specimens are available for verification upon request.

Gnaptor spinimanus

Material examined: Uzbekistan, Samarkand Region, Zarafshan Ridge, Agalyk Village, 39°27′05″N, 66°51′02″E, 1550 m asl, 3.III.2022, leg. Khamzayev, 2 specimens.

Blaps medvedevi

Material examined: Uzbekistan, Samarkand Region, Narpay District, Durman Village, 40°02′59″N, 65°52′54″E, 407 m asl, 5.IV.2024, leg. Umurzoqova, 1 specimen.

Calyptopsis deplanata

Material examined: Uzbekistan, Samarkand Region, Kushrabad District, Kuralas Village, 40°15′37″N, 66°39′22″E, 745 m asl, 10.IV.2023, leg. Umurzoqova, 2 specimens.

Cyphogenia aurita cratii

Material examined: Uzbekistan, Samarkand Region, Nurabad District, Ingichka, 39°43′01″N, 66°01′01″E, 650 masl, 3.VII.2022, leg. Khamzayev, 4 specimens; Samarkand Region, Zarafshan Ridge, Yetti Uyli River, 39°26′07″N, 66°59′02″E, 1050 m asl, 3.VII.2022, leg. Khamzayev, 2 specimens; Samarkand Region, Urgut District, Chep Village, 39°26′00″N, 67°25′00″E, 1050 m asl, 4.VII.2023, leg. Rakhimov, 1 specimen.

Diaperis boleti

Material examined: Uzbekistan, Samarkand Region, Jambay District, Zarafshan National Park, Sector 1, 39°40′02″N, 67°05′03″E, 750 m asl, 26.IV.2022, leg. Khalimov, 1 specimen; same locality, 10.III.2023 and 9.IV.2023, leg. Rakhimov, 4 specimens.

Prosodes kataevi

Material examined: Uzbekistan, Samarkand Region, Zarafshan Ridge, Takhtakoracha Pass, 39°18′02″N, 66°53′03″E, 1800 m asl, 22.VII.2022, leg. Khamzayev, 1 specimen.

Prosodes sogdiana

Material examined: Uzbekistan, Samarkand Region, Zarafshan Ridge, Saridukan Pass, 39°19′00″N, 67°11′00″E, 2200-2600 m asl, 8.VI.2024, leg. Rakhimov, 1 specimen.

Stalagmoptera pachyscelis alticola

Material examined: Uzbekistan, Zarafshan Ridge, Amankutan Village, Bulbulzorsay River, vicinity of Leva Cave, 39°18′03″N, 66°57′04″E, 1460 m asl, 12.IV.2022, 5 specimens; 20.III.2023, 1 specimen; 14.VI.2023, 2 specimens, leg. Khamzayev; Samarkand Region, Zarafshan Ridge, Takhtakoracha Pass, 39°18′02″N, 66°53′03″E, 1800 m asl, 22.V.2023, leg. Khamzayev, 6 specimens; Samarkand Region, Nurabad District, Ingichka, 39°43′01″N, 66°01′01″E, 650 m asl, 15.VI.2022, leg. Mamanov, 4 specimens; Samarkand Region, Zarafshan Ridge, Yetti Uyli River, 39°26′07″N, 66°59′02″E, 1050 m asl, 25.V.2022, leg. Khamzayev, 5 specimens.

Stalagmoptera staudingeri

Material examined: Uzbekistan, Samarkand Region, Nurabad District, Ingichka, 39°43′01″N, 66°01′01″E, 650 m asl, 10.VII.2022, leg. Mamanov, 2 specimens; Samarkand Region, Zarafshan Ridge, Yetti Uyli River, 39°26′07″N, 66°59′02″E, 1050 m asl, 20.V.2022, leg. Khamzayev, 12 specimens; same locality, 29.V.2024, leg. Umurzoqova, 4 specimens.

Stenosis kuntzeni

Material examined: Uzbekistan, Samarkand Region, Zarafshan Ridge, Agalyk Village, 39°27′05″N, 66°51′02″E, 1550 m asl, 22.III.2022, leg. Khamzayev, 2 specimens. Deposited in SSU.

Tagona acuminata

Material examined: Uzbekistan, Samarkand Region, Nurabad District, Karnabchul Desert, 39°51′00″N, 65°27′00″E, 420 m asl, 11.IV.2022, leg. Rakhimov, 1 specimen. Deposited in SSU.

Species diversity and dominance patterns

Quantitative data on the 84 species of darkling beetles recorded in the biocenoses of the Zarafshan Valley determine the relative importance of species within the community. In this study, species accounting for more than 5% of the total number of individuals were interpreted as dominant species. The dominant species in the community are *Penthicus granulosus* (dominance value 15.35%), *Pelorocnemis punctigera* (5.62%), and *Dailognatha nasuta* (5.29%). Together, these three species account for 26.26% of the total tenebrionid fauna of the Zarafshan Valley (Table 4). Notably, the presence of only a single clearly dominant species (*P. granulosus*), along with the overall low number of dominant species (three species in total), indicates that the contribution of individual species to the community structure is relatively limited.

Species with dominance values ranging from 2% to 5% were interpreted as subdominant species. As shown in Table 4, the subdominant group comprises 11 species. Naturally, the composition of dominant and subdominant species is variable and may differ among years and across regions. Under certain environmental conditions, when the number of dominant species decreases, subdominant species may act as a reserve component, partially compensating for changes in community structure.

Species with dominance values of 1-2% were classified as rare species and include 16 species, accounting for 23% of the tenebrionid fauna. The majority of the recorded species (54 species) contribute less than 1% to the total fauna and were therefore interpreted as very rare species.

The Zarafshan Valley encompasses foothill, upland, and valley ecosystems. This area is characterized by a high level of ecosystem diversity, including the distinctive fauna of dry mountain and semi-desert landscapes (Khalimov et al. 2023; Narzullayev et al. 2024). Assessing the diversity of the darkling beetle fauna in the region allows insights into population structure**,** habitat stability, and the overall ecological condition of ecosystems. For this purpose, the fauna was analyzed using several diversity indices (Table 5).

Thus, the obtained results indicate that the biocenoses of the Middle Zarafshan geographical district are characterized by a high level of biodiversity. High values of the Shannon and Simpson indices reflect a balanced structure of the tenebrionid fauna, while the Margalef and Fisher’s alpha indices confirm a high level of species richness. The low values of the Dominance and Berger-Parker indices indicate a limited number of dominant species.

The Chao-1 estimator suggests the potential presence of additional, undetected species in the fauna, emphasizing the need to increase sampling effort in future studies. Species accumulation curves (Figure 6) approached an asymptote, indicating that sampling effort was sufficient to capture the majority of species present in the studied communities. These diversity indices, indicating high richness and low dominance, suggest a relatively balanced community structure that facilitates gradual species turnover along the elevational gradient rather than abrupt compositional shifts.

Comparative analysis of the tenebrionid fauna of selected parts of the region

The Zarafshan Valley region encompasses biocenoses ranging from desert habitats to high-mountain ecosystems. Consequently, the studied areas differ markedly in elevation above sea level as well as in their hydrothermal characteristics, which results in pronounced differences in the structure and composition of the tenebrionid fauna.

For the purpose of comparative analysis, the study area was conditionally divided into four regions: the lowland areas of the Zarafshan Valley**,** the Chakilkalyan Mountains**,** the Karatepa Mountains, and the Zirabulak Mountains**.** The elevational gradient of these regions increases in the following order: Zarafshan Valley lowlands → Zirabulak Mountains → Karatepa Mountains → Chakilkalyan Mountains.

The highest diversity of the tenebrionid fauna was recorded in the Karatepa Mountains, where 51 species were documented. In the lowland part of the Zarafshan Valley, 43 species were recorded, while 37 species were found in the Zirabulak Mountains. The lowest species richness of the tenebrionid fauna was observed in the Chakilkalyan Mountains, with only 23 species recorded.

Table 4. Species dominance in the tenebrionid fauna of the Zarafshan Valley

Species	Number of individuals	Dominance level (%)	Presence of the species in designated areas			
			Zarafshan Valley Plains	Chakalikalon Mountain	Qaratepa Mountain	Zirabulak Mountains
Adesmia planidorsis	6	0.39	-	-	+	+
Alcinoeta helopioides	2	0.13	+	-	-	-
Alphitobius diaperinus	2	0.13	-	-	+	-
Bioramix faldermanni	2	0.13	-	+	-	-
Bioramix sp.	1	0.07	-	-	+	-
Blaps allardiana alaiensis	10	0.65	-	+	+	-
Blaps deplanata	23	1.50	+	+	+	-
Blaps inflexa	11	0.72	+	-	-	-
Blaps lethifera lethifera	10	0.65	+	-	-	-
*Blaps medvedevi**	1	0.07	+	-	-	-
Blaps mortisaga	26	1.70	+	+	+	+
Blaps scutellata	13	0.85	+	-	-	-
Blaps seriata	24	1.57	+	-	-	+
Cabirutus pusillus	33	2.16	-	-	+	+
*Calyptopsis deplanata**	2	0.13	+	-	-	-
Catomus niger	2	0.13	+	-	-	-
Catomus sulcatus	4	0.26	-	-	+	-
Cyphogenia gibba gibba	40	2.61	+	+	+	+
Cyphogenia lucifuga	2	0.13	+	-	-	-
Cyphogenia aurita aurita	28	1.83	+	-	+	+
*Cyphogenia aurita cratii**	7	0.46	+	+	-	+
Dailognatha nasuta	81	5.29	-	-	+	+
*Diaperis boleti**	5	0.33	+	-	-	-
Dichillus epipleuralis	4	0.26	-	+	-	-
Dila laevicollis	56	3.66	+	+	+	+
Dila seriata	38	2.48	-	-	+	+
Dissonomus latiusculus	1	0.07	-	-	+	-
Eustenomacidius laevicollis	3	0.20	-	+	-	-
*Gnaptor spinimanus**	2	0.13	-	-	+	-
Gonocephalum granulatum pusillum	9	0.59	+	-	+	+
Gonocephalum pubiferum	3	0.20	+	-	+	-
Gonocephalum rusticum	44	2.87	+	-	+	+
Gonocephalum setulosum setulosum	7	0.46	-	-	+	+
Lasiostola pubescens	13	0.85	-	-	+	+
Lasiostola sp.	3	0.20	-	-	+	-
Microplatyscelis seriepunctata	18	1.18	+	-	-	+
Ocnera pilicollis	2	0.13	-	-	-	+
Omophlina corva	3	0.20	-	-	+	-
Omophlina hirtipennis	4	0.26	-	-	+	-
Omophlus pilicollis	3	0.20	+	+	+	-
Opatroides punctulatus	63	4.11	+	+	+	+
Pelorocnemis punctigera	86	5.62	+	+	+	+
Penthicus dilectans	1	0.07	+	-	-	-
Penthicus granulosus	235	15.35	+	+	+	+
Penthicus sp.	1	0.07	-	-	-	+
Podhomala fausti	5	0.33	+	-	-	-
Podhomala heydeni	25	1.63	+	-	-	-
*Prosodes kataevi**	1	0.07	-	-	+	-
Prosodes ballionis	15	0.98	-	+	+	+
Prosodes brevitarsis	9	0.59	-	+	+	-
Prosodes chigrayi	1	0.07	-	-	+	-
Prosodes fleischeri	5	0.33	-	-	+	-
Prosodes heydeni	11	0.72	-	-	+	-
Prosodes nuratensis	21	1.37	-	-	-	+
Prosodes obliquesulcata	15	0.98	-	-	+	-
Prosodes oblonga	30	1.96	-	-	+	+
Prosodes pygmaea pygmaea	1	0.07	+	-	-	-
*Prosodes sogdiana**	1	0.07	-	+	-	-
Prosodes sp.	1	0.07	-	-	-	+
Prosodes staudingeri	18	1.18	-	-	+	-

Prosodes suturidens	6	0.39	-	-	+	+
Prosodes undulata	3	0.20	+	-	-	+
Somocoelia pinguis pinguis	57	3.72	-	+	+	-
Stalagmoptera confusa tuberculosa	6	0.39	-	+	+	-
Stalagmoptera intermedia	45	2.94	+	-	+	+
Stalagmoptera laticollis	47	3.07	-	+	+	+
*Stalagmoptera pachyscelis alticola**	21	1.37	+	-	+	+
Stalagmoptera seriatogemmata	4	0.26	+	-	+	-
Stalagmoptera sp.	2	0.13	-	+	-	-
*Stalagmoptera staudingeri staudingeri**	18	1.18	-	-	+	+
Stalagmoptera tuberculatocostata	49	3.20	+	+	+	-
Stenosis fausti	16	1.05	+	-	+	+
*Stenosis kuntzeni**	2	0.13	-	-	+	-
Stenosis sulcicollis	3	0.20	+	-	-	+
*Tagona acuminata**	1	0.07	+	-	-	-
Tagona macrophthalma macrophthalma	1	0.07	+	-	-	-
Tenebrio angustus	12	0.78	+	-	+	+
Tenebrio molitor	16	1.05	+	-	-	+
Tenebrio obscurus	23	1.50	+	-	-	+
Tentyria gigas	6	0.39	-	-	+	-
Tentyria intermittens	4	0.26	-	+	+	-
Thriptera ballioni	26	1.70	+	-	-	-
Tribolium confusum	24	1.57	+	-	-	+
Zophosis punctata punctata	46	3.00	+	+	+	+
Total	1531	100	43	23	51	37

Note: *Species recorded for the first time in Uzbekistan

Table 5. Results of ecological diversity assessment of the tenebrionid fauna in the Zarafshan Valley

Index name	Index value	Description
Dominance_D	0.04	Reflects the degree of dominance within the community. Low values indicate that no single species overwhelmingly dominates the assemblage
Simpson_1-D	0.96	Indicates a high level of diversity and relatively even distribution of abundances among species
Shannon_H	3.67	A general measure of community diversity. The observed value suggests relatively high diversity, though interpretation depends on sampling design and regional context
Evenness_eH/S	0.47	Reflects the evenness of species abundances. The observed value indicates moderate evenness, with some variation in species dominance
Brillouin	3.56	Measures the ordered distribution of species within the sample
Menhinick	2.15	Estimates species richness relative to the number of individuals
Margalef	11.32	An index of species richness relative to sample size, indicating high species richness in the studied assemblage
Equitability_J	0.83	Degree of even distribution among species
Fisher_alpha	19.11	A diversity parameter reflecting species richness. The observed value indicates relatively high diversity compared to typical temperate assemblages
Berger-Parker	0.15	Reflects the proportional abundance of the most dominant species. The observed value indicates moderate dominance rather than strong dominance by a single species
Chao-1	90	An estimator of true species richness, suggesting the possible presence of additional undetected species beyond the observed taxa

Among the studied areas, the Karatepa Mountains and the Zirabulak Mountains share the highest number of species, with 25 species occurring in both regions. The next most similar pair is the Zarafshan Valley lowlands and the Zirabulak Mountains, which share 22 species. The lowest similarity was observed between the Zarafshan Valley lowlands and the Chakilkalyan Mountains, with only 8 species shared between these two regions.

The results of the analysis of region-specific species are as follows: the number of species unique to the Zarafshan Valley lowlands (i.e., not recorded in other regions) is 15 species, to the Karatepa Mountains 14 species, to the Chakilkalyan Mountains 5 species, and to the Zirabulak Mountains 3 species. The low number of region-specific species in the Zirabulak Mountains is likely due to the similarity of their biotope conditions and elevational position to those of the surrounding lowland habitats on the one hand and the Karatepa Mountains on the other. Similarly, the relatively small number of unique species in the Chakilkalyan Mountains (5 species) can be explained by the limited representation of darkling beetle species adapted exclusively to high-mountain environments. This pattern is presumably related to the sparse vegetation cover characteristic of these regions. Among the studied areas, the Zirabulak and Chakilkalyan Mountains are characterized by the poorest vegetation cover.

The degree of similarity of the tenebrionid beetle fauna among different geographical areas of the Zarafshan Valley was assessed using the Jaccard and Chekanovsky-Sørensen similarity coefficients. The calculated coefficient values ranged from 0.20 to 0.57, indicating a high level of differentiation among the faunas of the studied regions (Table 6).

As shown in Table 6, the similarity coefficient between the Karatepa and Zirabulak Mountains is the highest (Chekanovsky-Sørensen coefficient: 0.57; Jaccard coefficient: 0.40), which corresponds to the geomorphological and climatic similarity of these two regions.

In contrast, similarity coefficients between the Chakilkalyan Mountains and the other regions are relatively low (Chekanovsky-Sørensen coefficient: 0.33-0.46; Jaccard coefficient: 0.20-0.30). This pattern corresponds to the higher elevation of this area and its relatively cooler and more humid climatic conditions. The tenebrionid fauna of the Chakilkalyan Mountains is therefore dominated by species specialized for high-mountain environments.

The dendrograms constructed based on both similarity coefficients show similar clustering patterns and confirm the close affinity between the tenebrionid faunas of the Karatepa and Zirabulak Mountains (Figure 7). Among the compared faunas, the tenebrionid fauna of the Chakilkalyan Mountains appears to be the most isolated. This pattern indicates a high proportion of species adapted to high-mountain environments within the fauna of this region.

Although the tenebrionid fauna of the Zarafshan Valley lowlands is also considerably separated from the other regions, it retains a greater number of faunal elements (species) characteristic of the Karatepa and Zirabulak Mountains. The variation in species richness and similarity among regions reflects spatial differentiation that aligns with elevational positioning, supporting the role of altitude in structuring community composition.

Altitudinal gradient as a factor in the formation of Tenebrionidae communities

To evaluate the influence of elevation on Tenebrionidae assemblages, sampling sites were grouped into three elevational tertiles (low, middle, and high). Multivariate analyses were conducted using both Euclidean-based and dissimilarity-based approaches in order to assess potential linear and non-linear patterns of community differentiation.

Principal component analysis (PCA) based on the Hellinger-transformed abundance matrix revealed a structured arrangement of sampling sites along the altitudinal gradient (Figure 8). The first principal component (PC1) captured the main axis of compositional variation, whereas PC2 reflected secondary gradients.

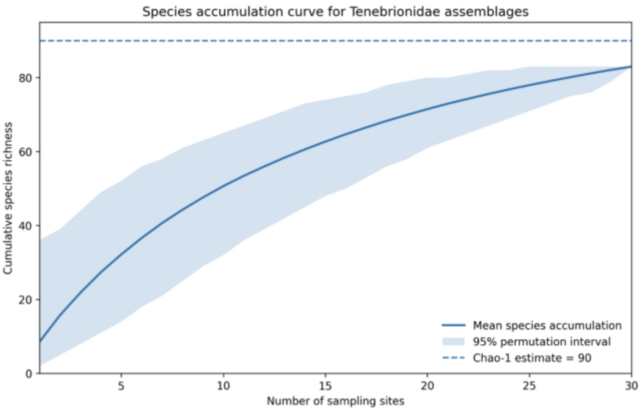

Figure 6. Species accumulation curve for Tenebrionidae assemblages across 30 sampling sites in the Zarafshan Valley. The solid line shows mean cumulative species richness across random site permutations, the shaded area indicates the 95% permutation interval, and the dashed line marks the Chao-1 estimate (90 species)

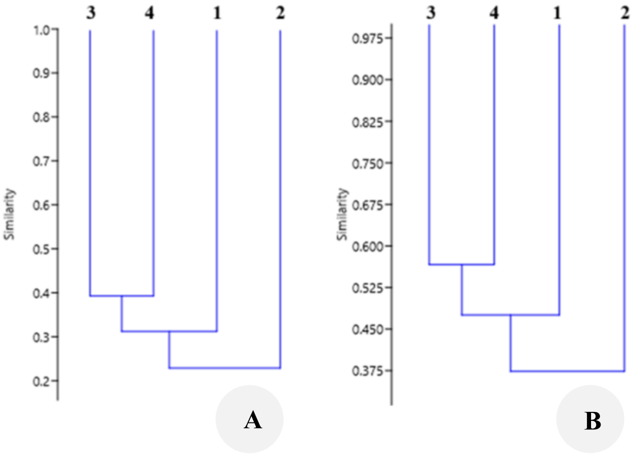

Figure 7. Similarity dendrograms of Tenebrionidae assemblages from four regions of the Zarafshan Valley based on Jaccard (A) and Chekanovsky-Sørensen (B) coefficients. 1: lowlands, 2: Chakilkalyan Mts, 3: Karatepa Mts, 4: Zirabulak Mts

Table 6. Similarity coefficients of the tenebrionid fauna among different areas of the Zarafshan Valley (Jaccard\Chekanovsky-Sørensen coefficients)

Areas	Zarafshan Valley Lowlands	Chakilkalyan Mountains	Karatepa Mountains	Zirabulak Mountains
Zarafshan Valley Lowlands	1.00	0.33	0.40	0.55
Chakilkalyan Mountains	0.20	1.00	0.46	0.33
Karatepa Mountains	0.25	0.30	1.00	0.57
Zirabulak Mountains	0.38	0.20	0.40	1.00

Sites from the lower (≤697 m) and upper (>1050 m) tertiles were positioned at opposite ends of PC1, while sites belonging to the middle tertile were distributed between them. This spatial configuration indicates gradual species turnover along the gradient rather than abrupt transitions between discrete altitudinal zones. The ordination plot demonstrates partial overlap among tertiles, particularly between low and middle elevations, suggesting continuity in species composition across intermediate elevations.

Fitting elevation as a continuous environmental variable using the envfit procedure revealed a strong and statistically significant association with the PCA configuration (R^2: 0.492, p: 0.002; 999 permutations). The direction of the elevation vector corresponds to coordinated changes in species composition with increasing altitude.

Two-dimensional NMDS based on Bray-Curtis dissimilarities yielded a stress value of 0.281, indicating a high level of distortion between ordination distances and observed ecological dissimilarities (Figure 9). Therefore, the 2D configuration should be interpreted with strong caution and considered suitable only for identifying broad tendencies in community structure rather than precise spatial relationships among sampling sites (Figure 2). The ordination shows substantial overlap among elevational tertiles, and no clearly separated clusters are evident in the 2D configuration.

Elevation fitted onto the NMDS space using envfit was not statistically significant (R^2: 0.099, p: 0.242; 999 permutations), indicating that the two-dimensional Bray-Curtis solution does not provide strong support for elevation-related structuring. Because the 2D solution provided a poor representation of ecological distances, a three-dimensional NMDS solution was computed using identical parameters (k: 3). The 3D solution reduced stress to 0.220, indicating a modest improvement in fit (Figure 10). However, this value still exceeds commonly accepted thresholds for reliable ordination (<0.2) and therefore should also be interpreted with caution (Figure 3). Partial overlap among elevational tertiles persisted, supporting the interpretation of gradual compositional turnover rather than sharply delimited assemblages. In three-dimensional space, separation between low- and high-elevation sites became more apparent, although complete segregation of tertiles was still not observed. Taken together, the NMDS results suggest that community structure is highly multidimensional and cannot be adequately captured in low-dimensional ordination space.

Given these limitations, the NMDS results are interpreted here as supplementary and exploratory, whereas the primary inference regarding altitudinal structuring is based on the PCA and PERMANOVA results. PERMANOVA based on Bray-Curtis dissimilarities detected significant differences in Tenebrionidae assemblage composition among elevational tertiles (pseudo-F: 2.886, df: 2, R^2: 0.176, p: 0.009; 999 permutations). Thus, elevation explained approximately 17.6% of the total variation in community composition. However, the test for homogeneity of multivariate dispersions (PERMDISP) indicated significant differences in within-group dispersion (p: 0.035). This suggests that part of the PERMANOVA signal may reflect differences in beta-diversity (within-group heterogeneity) in addition to centroid separation among elevational tertiles. Therefore, the observed compositional differentiation should be interpreted cautiously as reflecting both shifts in group centroids and variation in internal dispersion. In this context, an R^2 value of 0.176 represents a modest but statistically significant effect size, indicating that elevation is one of several factors contributing to community structuring, while a substantial proportion of variation remains unexplained by elevation alone.

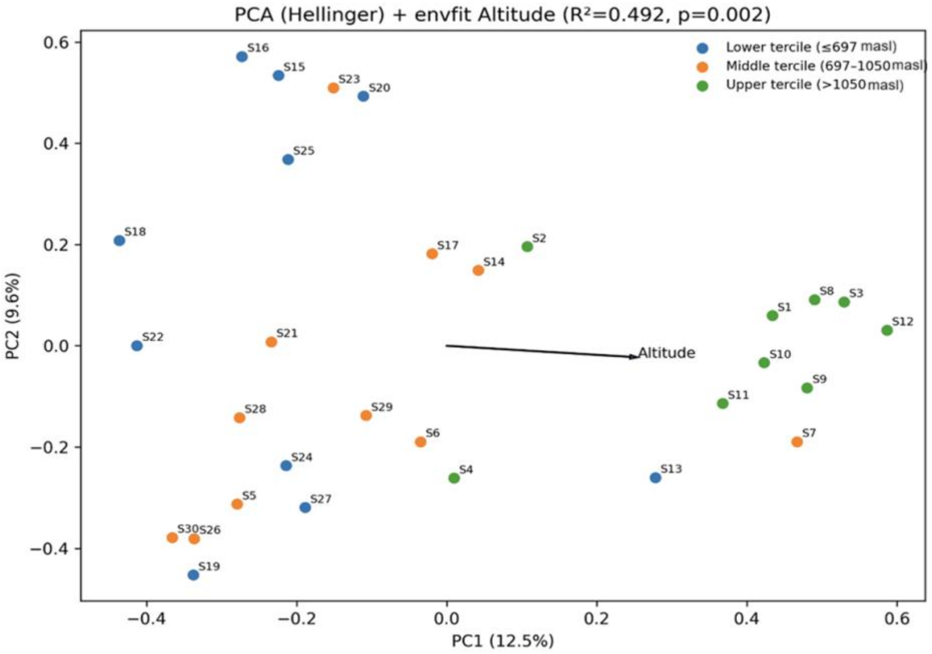

Figure 8. PCA ordination (Hellinger-transformed data) of sampling sites grouped by elevational tertiles. Colors indicate low, middle, and high elevation groups

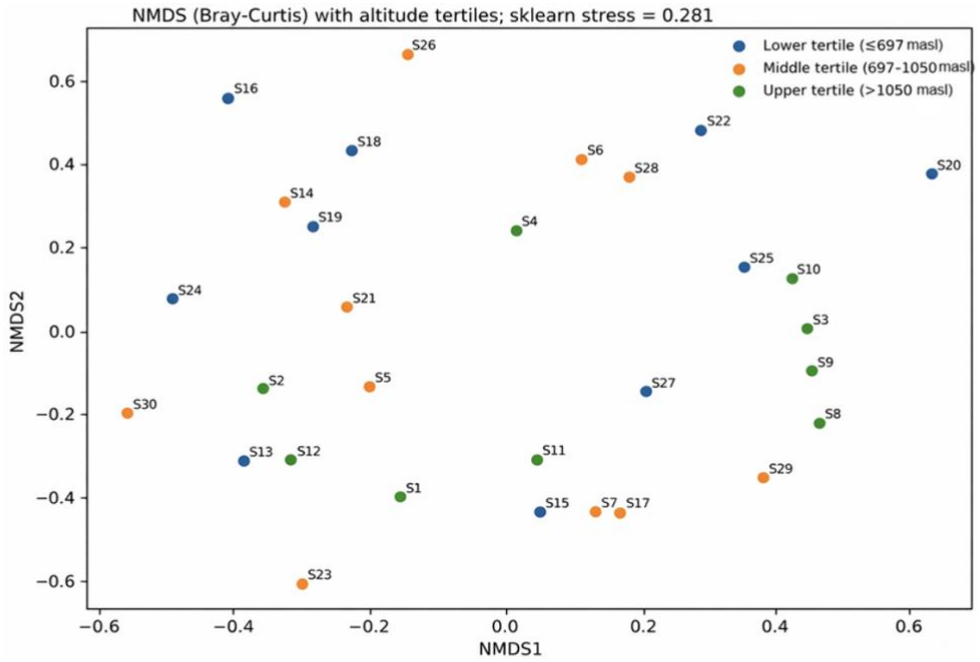

Figure 9. Two-dimensional NMDS ordination (Bray-Curtis dissimilarity) of sampling sites grouped by elevational tertiles. Stress value is indicated on the plot

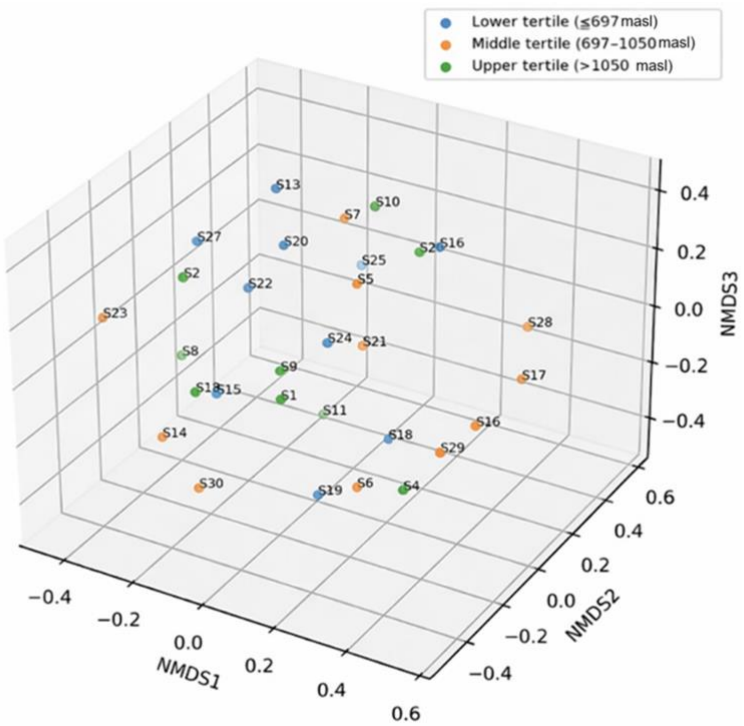

Figure 10. Three-dimensional NMDS (Bray-Curtis) of communities grouped by altitudinal tertiles. Note: The three-dimensional NMDS ordination improves the goodness of fit compared with the two-dimensional solution (stress: 0.281 → 0.220)

Pairwise PERMANOVA comparisons revealed that assemblages at high elevations differed significantly from both low and middle elevations (High-Low: pseudo-F: 4.665, R^2: 0.215, p: 0.002, p_adj(FDR): 0.006; High-Middle: pseudo-F: 3.654, R^2: 0.169, p: 0.009, p_adj(FDR): 0.0135). In contrast, low and middle elevational tertiles did not differ significantly (pseudo-F: 0.817, R^2: 0.041, p: 0.553).

Indicator species analysis (IndVal with 999 permutations and FDR correction) identified two taxa significantly associated with the high-elevation tertile: *P. granulosus* (IndVal: 0.624, p_adj: 0.0425) and *Cabirutus pusillus* (IndVal: 0.624, p_adj: 0.0425). The analysis was conducted using presence-absence data. Analysis of multivariate dispersion (betadisper) revealed significant differences in within-group variability among elevational tertiles (F: 4.09, p: 0.035; 999 permutations) (Figure 11).

Distances of sites to their respective group centroids in Bray-Curtis-based PCoA space differed significantly, indicating unequal levels of β-diversity along the altitudinal gradient. These results indicate that elevation is associated with measurable compositional differentiation among tertiles, particularly through contrasts involving high-elevation sites, while also contributing to within-tertile variability.

No taxa showed significant associations with low or middle elevations after correction for multiple testing. These species-level associations support the interpretation that elevational structuring is driven primarily by differentiation at the upper segment of the gradient, reinforcing the pattern of gradient-dependent turnover detected by multivariate analyses.

UPGMA hierarchical clustering based on Bray-Curtis dissimilarities revealed a mosaic pattern of similarity among sampling sites (Figure 12). Sites did not cluster strictly according to elevational tertiles; however, partial grouping by elevation was observed.

The dendrogram demonstrates that some sites from different elevational ranges exhibit high compositional similarity, while others within the same tertile are relatively distinct, reflecting heterogeneous community organization along the gradient. The identification of high-elevation indicator species further confirms that environmental filtering intensifies along the gradient, reinforcing the connection between species-level responses and broader community structuring.

Discussion

The present study represents the first comprehensive assessment of the taxonomic structure, dominance patterns, ecological diversity, and spatial differentiation of the darkling beetle fauna of the Zarafshan Valley. The recorded species richness-84 species belonging to 36 genera, 17 tribes, and 4 subfamilies-confirms that the Zarafshan Valley is one of the important centers of Tenebrionidae diversity in Central Asia. These results are consistent with current views on the high biogeographical importance of arid and mountain ecosystems in the region, which form a complex mosaic of habitats and faunal assemblages (Ragionieri et al. 2023; Medetov et al. 2025).

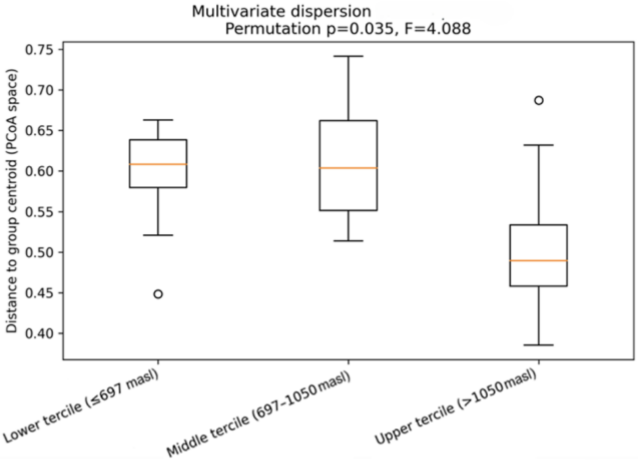

Figure 11. Homogeneity of multivariate dispersions (betadisper) across elevation tertiles. Note: Distances of plots to the centroid of the corresponding group in PCoA space (Bray-Curtis) are shown. The permutation test revealed significant differences in dispersion among tertiles (F: 4.09, p: 0.035)

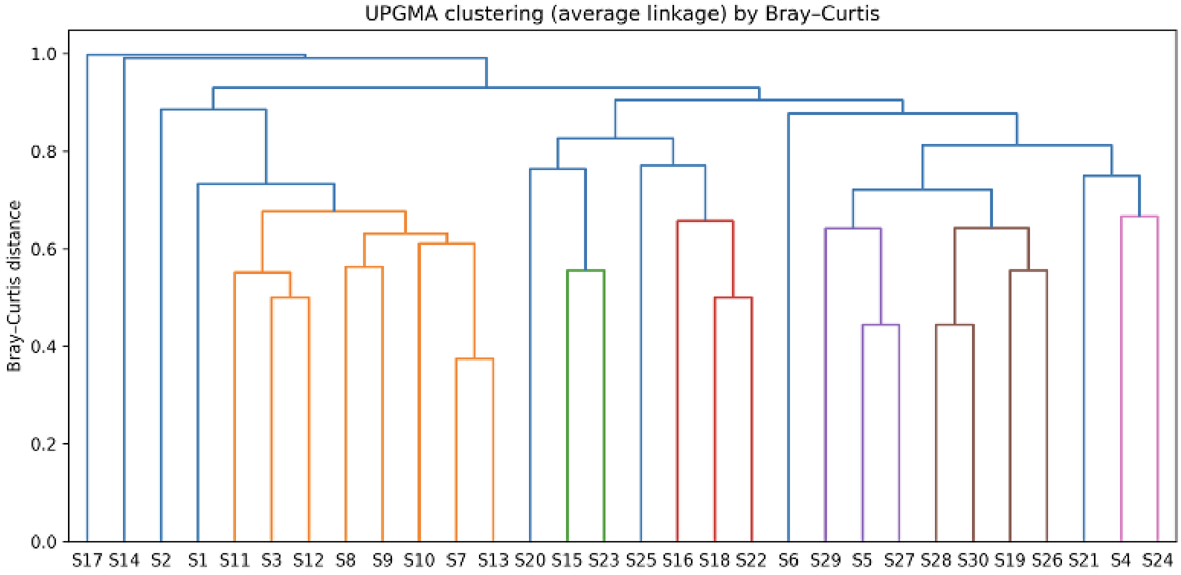

Figure 12. UPGMA clustering of sampling sites based on Bray-Curtis dissimilarity. The dendrogram (average linkage) is constructed from the Bray-Curtis dissimilarity matrix. The convergence of branches reflects similarity in community species composition

Taxonomic structure and dominance patterns

The predominance of the subfamilies Tenebrioninae and Pimeliinae corresponds to patterns typical of arid and semi-arid areas of the Palaearctic, where representatives of these groups dominate due to high ecological plasticity and morphological and physiological adaptations to xerothermic conditions (Flores et al. 2021; Chigray et al. 2022). At the tribal level, the dominance of Blaptini, Pimeliini, and Opatrini reflects the prevalence of taxa associated with open dry habitats characterized by sparse vegetation cover and pronounced daily temperature fluctuations, a pattern widely reported for desert ecosystems of Eurasia (Medvedev 2007; Chigray 2019).

Differences between the contributions of individual tribes and genera in terms of species richness and individual abundance indicate that taxonomic dominance does not necessarily coincide with numerical dominance. Thus, representatives of Blaptini, despite high species richness, are characterized by relatively low abundance, which is likely related to larger body size and lower population densities. In contrast, representatives of Opatrini are generally smaller but form denser populations, resulting in a higher contribution to total abundance. This pattern observed in our data is consistent with previously reported relationships between body size and population density in insect communities (Gjoni et al. 2020; Khalimov 2023).

Ecological diversity and community structure

High values of the Shannon, Simpson, Margalef, and Fisher's alpha indices indicate that tenebrionid communities of the Zarafshan Valley are characterized by both high species richness and relatively balanced community structure. Comparable diversity patterns have previously been reported for other arid and semi-arid regions of Central Asia (Bekchanov et al. 2023; Nabozhenko et al. 2024). Low values of the Dominance and Berger-Parker indices indicate the absence of strong numerical dominance by single species, which is typical of stable ecosystems with high spatial and ecological heterogeneity (Khalimov 2020).

A substantial proportion of rare and very rare species corresponds to the general structure of desert insect communities, which are often composed of a small number of abundant species and a large number of low-abundance taxa (Alimova et al. 2024). The Chao-1 estimator, suggesting the presence of additional undetected species, emphasizes the need for continued and expanded surveys that account for seasonal and spatial environmental variability (Nabozhenko et al. 2024).

Altitudinal gradient and environmental filtering in semi-arid mountain systems

Altitudinal gradients represent integrated environmental gradients along which temperature, moisture availability, soil structure, vegetation complexity, and productivity change in a coordinated manner. These gradients act as composite ecological filters that structure biological communities through species sorting mechanisms (Lomolino 2001; Körner 2007). Recent advances in gradient ecology emphasize that mountain systems should be interpreted within a metacommunity framework, where dispersal limitation, environmental filtering, and local habitat heterogeneity interact across spatial scales (Leibold and Chase 2018).

In the Zarafshan Valley, Tenebrionidae assemblages exhibit a structured yet non-discrete response to elevation. Rather than forming sharply separated altitudinal belts, communities demonstrate gradual compositional turnover along the gradient, accompanied by variation in β-diversity among elevational ranges. Such patterns are consistent with those reported in semi-arid mountain systems, where environmental transitions are continuous and modulated by microtopographic heterogeneity, leading to both species turnover and variability in community composition (Uhey et al. 2022; Jiang et al. 2024).

Our results suggest that altitude functions primarily as a continuous filtering gradient rather than as a threshold-generating factor. These patterns are further supported by β-diversity analyses (PERMDISP p: 0.035), which indicate increased variability in community composition along the elevational gradient. This interpretation is consistent with contemporary ecological theory emphasizing that many elevational systems exhibit clinal variation rather than abrupt community shifts (Zhao et al. 2025).

A key limitation of this study is the absence of explicitly measured environmental covariates such as temperature, precipitation, soil properties, and vegetation structure. Although elevation integrates many of these factors, it cannot disentangle their individual contributions to community composition. Therefore, the observed patterns should be interpreted as reflecting a composite environmental gradient rather than direct causal relationships. Future studies incorporating direct environmental measurements will be necessary to clarify the mechanisms underlying the observed patterns.

Ordination structure and multidimensional gradient expression

The strong association between elevation and PCA (Hellinger-based) ordination structure provides robust evidence of coordinated species replacement along a linear environmental gradient. The Hellinger transformation reduces the influence of rare taxa and renders Euclidean distances ecologically meaningful, allowing reliable detection of structured turnover patterns (Legendre and Gallagher 2001).

However, Bray-Curtis PERMANOVA detected significant compositional differentiation among elevational tertiles, whereas NMDS ordination revealed substantial overlap among groups in multivariate space. This pattern reflects a distinction between statistically detectable centroid displacement and the persistence of continuous gradient-driven turnover, in which compositional changes occur gradually rather than as sharply discrete assemblage boundaries.

Recent methodological syntheses (e.g., Warton 2022) emphasize that multivariate centroid tests and ordination-based approaches capture different aspects of community structure. While PERMANOVA detects overall differences in multivariate centroids, ordination and gradient-fitting procedures can reveal directional alignment along continuous environmental gradients, even when group boundaries are imposed on inherently clinal systems.

Thus, the Zarafshan Tenebrionidae communities exemplify a multidimensional gradient system in which elevation is associated with measurable compositional structuring, particularly at higher elevations, without producing sharply delimited categorical assemblages. The relatively high NMDS stress values indicate that the ordination provides only a limited representation of ecological distances and should be interpreted with caution. Although the three-dimensional solution slightly improves the fit, it remains above commonly accepted thresholds, reinforcing the interpretation that community differentiation is multidimensional and not fully captured by NMDS. At the same time, the absence of complete segregation among tertiles supports a clinal rather than discrete altitudinal organization of assemblages.

β-diversity modulation along elevation

The significant PERMANOVA result indicates that elevation is associated with measurable compositional differentiation in Tenebrionidae assemblages. Because multivariate dispersion differed significantly among tertiles, the PERMANOVA result likely reflects both centroid displacement and heterogeneity in β-diversity. Therefore, detected differences should be interpreted as reflecting a combination of centroid displacement and heterogeneity in β-diversity, rather than strictly discrete group separation. However, the observed pattern is not uniform across the gradient. Pairwise comparisons demonstrate that the primary differentiation occurs between the high-elevation tertile and both lower elevational levels, whereas low and middle elevations remain compositionally similar. This distinction suggests that compositional differentiation along the elevational gradient is partly driven by increased within-group variability, particularly at higher elevations. Importantly, these group-based results provide evidence of compositional differences among elevational ranges but do not by themselves demonstrate a continuous gradient.

This pattern suggests that elevational structuring is driven mainly by the distinct ecological conditions of the upper part of the gradient rather than by evenly spaced altitudinal zonation. The presence of two significant indicator species associated with high elevations (*P. granulosus* and *C. pusillus*) further supports the interpretation that the upper elevational segment represents a functionally differentiated assemblage subset.

At the same time, the relatively low effect size (R^2: 0.176) indicates that elevational differentiation explains only a limited portion of the overall community variability, with a substantial proportion driven by other environmental and spatial factors. Habitat mosaicity, microtopographic heterogeneity, and local environmental filtering may contribute to within-tertile β-diversity and can be considered as potential explanatory hypotheses. Thus, elevational differentiation in the Zarafshan Valley appears to be expressed primarily as gradient-associated turnover, with the strongest restructuring occurring at higher elevations rather than as discrete, evenly separated altitudinal belts. These findings further suggest that multiple environmental drivers, acting simultaneously across spatial scales, contribute to the observed community structure.

Species-level responses and ecological specialization

Indicator species analysis suggests that some taxa exhibit altitudinal preferences, particularly at higher elevations, providing limited species-level support for compositional differentiation detected by multivariate analyses. The detection of only two significant indicator species at high elevation, and none at lower levels, indicates that species-level specialization is unevenly distributed along the gradient. Although overall community overlap persists, these results imply that differentiation is more strongly expressed at the upper segment of the gradient rather than across all elevational zones. This pattern is consistent with niche-based community assembly models, in which environmental gradients filter taxa according to their ecological tolerances (Leibold and Chase 2018).

Darkling beetles are particularly well suited for detecting such patterns due to their physiological adaptation to aridity, substrate specialization, and sensitivity to microclimatic variation. Recent studies demonstrate that Tenebrionidae communities across Eurasian drylands respond to elevational and climatic gradients through gradual species replacement and trait filtering rather than abrupt turnover (Zhao et al. 2025).

Furthermore, emerging evidence suggests that morphological and functional trait differentiation along elevational gradients may precede detectable shifts in overall community composition (Zokirova and Khalimov 2022; Zokirova et al. 2025). This may partially explain why species-level indicator responses are observed even when multivariate centroid tests are conservative.

Biogeographical and conservation significance

The high proportion of region-specific species, particularly in lowland areas and the Karatepa Mountains, highlights the Zarafshan Valley as a mosaic of locally distinct faunal assemblages. The discovery of taxa newly recorded for the fauna of Central Asia and Uzbekistan, including the genus *Gnaptor*, as well as numerous rare and poorly studied species, indicates that the entomofauna of desert and mountain ecosystems in Central Asia remains insufficiently explored (Romantsov and Rakhimov 2023; Naydenov et al. 2025).

The genus *Gnaptor* currently comprises four species. The most widespread species is *G. spinimanus*, whose distribution lies in Southeastern Europe, with the Don River (southern European Russia) representing the eastern boundary of its range (Martínez et al. 2011; Chigray et al. 2015). *Gnaptor prolixus* is distributed in Iran and Turkey (Medvedev 2001; Merkan et al. 2004). *Gnaptor boryi* is endemic to Greece (Martínez et al. 2011; Chigray et al. 2015). The recently described fourth species, *Gnaptor medvedevi* is known only from Turkey (Chigray et al. 2015). Our study extends the currently documented distribution range of *G. spinimanus*.

In the context of ongoing environmental change in Central Asia, the obtained results highlight the potential importance of incorporating altitudinal gradients into conservation planning. Due to their high sensitivity to environmental change and strong habitat association, darkling beetles can be considered a promising model group for monitoring biodiversity changes in arid and semi-arid ecosystems (Zhang 2012; Zhao et al. 2025).

Thus, the Tenebrionidae assemblages of the Zarafshan Valley exhibit high taxonomic richness (84 species across multiple genera and subfamilies) that is structured along a continuous elevational gradient rather than discrete altitudinal zones. This pattern reflects the action of elevation as a composite environmental filter, integrating changes in temperature, moisture, vegetation, and soil conditions that selectively shape species composition. As a result, community organization is driven by gradual species turnover and increasing β-diversity, particularly at higher elevations where environmental heterogeneity is stronger. The observed linkage between taxonomic richness, gradient-driven structuring, and ecological filtering supports a clinal model of community assembly in semi-arid mountain systems. Collectively, these findings provide a coherent framework in which biodiversity patterns emerge from the interaction between environmental gradients and species-specific ecological tolerances, offering a robust baseline for monitoring climate-driven restructuring of insect communities.

A key limitation of this study is the absence of directly measured environmental variables (e.g., temperature, vegetation structure, soil properties), which restricts the ability to disentangle the specific mechanisms underlying elevational patterns. In addition, relatively high NMDS stress values indicate that low-dimensional ordination only partially captures community variation, suggesting a complex, multidimensional structure. Future research should integrate quantitative environmental covariates and apply multivariate modeling approaches (e.g., db-RDA or structural equation modeling) to explicitly test causal relationships between environmental drivers and community composition. Expanding temporal replication and incorporating functional or trait-based analyses would further improve understanding of ecological processes.

In conclusion, this study provides the first standardized, gradient-wide assessment of Tenebrionidae assemblages in the Zarafshan Valley, documenting 84 species across 36 genera, 17 tribes, and 4 subfamilies, including 1 genus newly recorded for Central Asia and 11 species newly recorded for Uzbekistan. Community structure was characterized by high diversity (Shannon H′: 3.67; Simpson 1-D: 0.96) and low dominance (D: 0.04), indicating a relatively balanced assemblage. Multivariate analyses demonstrated that elevation significantly influences community composition, with a strong association detected in PCA (R^2: 0.492, p: 0.002) and moderate but significant differentiation among elevational groups in PERMANOVA (R^2: 0.176, p: 0.009). However, substantial overlap among groups and significant dispersion differences indicate that community structuring is continuous and gradient-driven, with increased β-diversity at higher elevations reflecting stronger environmental filtering and habitat heterogeneity. Overall, these findings establish a robust baseline for monitoring climate-driven restructuring of Tenebrionidae communities and contribute to broader efforts in biodiversity assessment and conservation in arid and semi-arid ecosystems.

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