Spatiotemporal variations of tenebrionid beetles (Coleoptera: Tenebrionidae) in the Gobi desert, Northwest China postprint

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Date: 2025-01-14T00:00:00+00:00

Abstract

Tenebrionid beetles represent a crucial arthropod taxon in the Gobi desert ecosystems owing to their species richness and high biomass, both of which are essential for maintaining ecosystem health and stability. However, the spatiotemporal variations of tenebrionid beetle assemblages in the Gobi desert remain poorly understood. In this study, the monthly dynamics of tenebrionid beetles in the central part of the Hexi Corridor, Northwest China, a representative area of the Gobi desert ecosystems, were monitored using pitfall trapping during 2015-2020. The following results were showed: (1) monthly activity of tenebrionid beetles was observed from March to October, with monthly activity peaking in spring and summer, and monthly activity periods and peak of tenebrionid beetle species exhibited interspecific differences that varied from year to year; (2) spatial distribution of tenebrionid beetle community was influenced by structural factors. Specifically, at a spatial scale of 24.00 m, tenebrionid beetle community was strongly and positively correlated with the dominant species, with distinct spatial distribution patterns observed for Blaps gobiensis and Microdera kraatzi alashanica; (3) abundance of tenebrionid beetles was positively correlated with monthly mean precipitation and monthly mean temperature, whereas monthly abundance of B. gobiensis and M. kraatzi alashanica was positively correlated with monthly mean precipitation; and (4) the cover of Reaumuria soongarica (Pall.) Maxim. and Nitraria sphaerocarpa Maxim. had a positive influence on the number of tenebrionid beetles captured. In conclusion, monthly variation in precipitation significantly influences the community dynamic of tenebrionid beetles, with precipitation and shrub cover jointly determining the spatial distribution pattern of these beetles in the Gobi desert ecosystems.

Full Text

Preamble

Spatiotemporal Variations of Tenebrionid Beetles (Coleoptera: Tenebrionidae) in the Gobi Desert, Northwest China

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Abstract: Tenebrionid beetles represent a crucial arthropod taxon in Gobi desert ecosystems owing to their species richness and high biomass, both of which are essential for maintaining ecosystem health and stability. However, the spatiotemporal variations of tenebrionid beetle assemblages in the Gobi desert remain poorly understood. In this study, we monitored the monthly dynamics of tenebrionid beetles in the central Hexi Corridor, Northwest China—a representative area of Gobi desert ecosystems—using pitfall trapping during 2015-2020. Our results showed: (1) Monthly activity of tenebrionid beetles occurred from March to October, peaking in spring and summer, with both activity periods and peaks exhibiting interspecific differences that varied from year to year; (2) Spatial distribution of the tenebrionid beetle community was influenced by structural factors. Specifically, at a spatial scale of 24.00 m, the community was strongly and positively correlated with dominant species, with distinct spatial distribution patterns observed for *Blaps gobiensis* and *Microdera kraatzi alashanica*; (3) Abundance of tenebrionid beetles was positively correlated with monthly mean precipitation and monthly mean temperature, whereas the monthly abundance of *B. gobiensis* and *M. kraatzi alashanica* was positively correlated with monthly mean precipitation; and (4) The cover of *Reaumuria soongarica* (Pall.) Maxim. and *Nitraria sphaerocarpa* Maxim. had a positive influence on the number of tenebrionid beetles captured. In conclusion, monthly variation in precipitation significantly influences community dynamics of tenebrionid beetles, with precipitation and shrub cover jointly determining the spatial distribution pattern of these beetles in Gobi desert ecosystems.

Keywords: Gobi desert; precipitation change; tenebrionid beetles; temporal dynamics; spatial pattern

Citation: REN Jialong, ZHAO Wenzhi, HE Zhibin, WANG Yongzhen, FENG Yilin, NIU Yiping, XIN Weidong, PAN Chengchen, LIU Jiliang. 2025. Spatiotemporal variations of tenebrionid beetles (Coleoptera: Tenebrionidae) in the Gobi desert, Northwest China. *Journal of Arid Land*, 17(1): 112–129. https://doi.org/10.1007/s40333-025-0001-2; https://cstr.cn/32276.14.JAL.02500012

1 Introduction

Beetles are among the most diverse animal groups in desert ecosystems, with tenebrionid beetles being a prominent ground-dwelling group characterized by wide distribution, high species richness, complex morphological differentiation, and diverse life forms (Twardowski et al., 2017). Tenebrionid beetles are primarily found in desert and semi-desert areas, where they function as key consumers and primary decomposers. Along with ants, they are omnivorous arthropods whose abundance and biomass are the highest among desert arthropods, playing a pivotal role in desert ecosystem food webs (Polis, 1991; Whitford, 1993; Feng et al., 2022; Ren et al., 2024a). Additionally, tenebrionid beetles are vital for the survival and reproduction of vertebrates such as reptiles, birds, and mammals, as they provide essential food and water resources in desert ecosystems (Groner and Ayal, 2001; Valdez, 2020).

The assemblage of tenebrionid beetles across various spatial scales is influenced by changes in shrub species, shrub coverage, and soil texture. Furthermore, variations in precipitation affect soil moisture and temperature, which in turn influence how tenebrionid beetles respond to vegetation and soil conditions (Liu et al., 2012, 2015; Ren et al., 2024b). Tenebrionid beetles represent the most important arthropod groups in the Gobi desert of Northwest China, and their activities and populations depend on seasonal dynamics and shrub presence and species (Liu et al., 2010). Arid and hyper-arid shrubs, which are the dominant plant species in the Gobi desert, are typically distributed in strips or patches with less than 10.00% vegetation cover. Notably, the impacts and regulatory roles of interactions among precipitation, shrubs, and soil conditions on tenebrionid beetle assemblages at different spatial and temporal scales remain poorly understood.

Therefore, long-term data on the mutual feedback relationships between tenebrionid beetle assemblages and climate, vegetation, and soil factors in the Gobi desert are crucial for understanding the roles of these beetles in maintaining the stability and biodiversity of desert ecosystems. Habitat heterogeneity provides diverse ecological niches that facilitate the coexistence of multiple arthropod species in desert ecosystems, and pattern-process analyses can help reveal the mechanisms underpinning biodiversity maintenance (Decaëns, 2010; Gao et al., 2018). In recent years, various researchers have investigated the population dynamics of arthropods such as ground beetles and soil-dwelling beetles and their influencing factors in forest, grassland, and farmland ecosystems. However, knowledge regarding population changes of ground beetles in desert ecosystems remains limited (Zhu et al., 2017; Hu et al., 2018).

Deserts represent one of the most heterogeneous habitats, experiencing resource variations due to precipitation fluctuations and interactions with shrubs and animal nests. These variations considerably affect the population dynamics of desert arthropods, especially tenebrionid beetles. Shrubs provide food resources along with shelter from predators and thermal stress, thereby positively influencing tenebrionid beetle activity in arid and semi-arid areas. Annual and seasonal variations in precipitation and temperature can alter the extent of tenebrionid beetles' dependence on shrubs (Mazía et al., 2006; Bartholomew and El Moghrabi, 2018). At a regional scale, desert vegetation cover, community structure, and soil texture are the main factors influencing the aggregation and changes in tenebrionid beetle assemblages (Stapp, 1997). Variations in the intensity of bird predation and landscape destruction may also influence the sensitivity of tenebrionid beetles with different body sizes to changes in vegetation cover (Groner and Ayal, 2001; Sackmann and Flores, 2009; Shelef and Groner, 2011; Lescano et al., 2017). Significant regional and interspecific variations exist in the responses of desert arthropods such as tenebrionid beetles and ants to precipitation changes. Moreover, omnivorous arthropods like beetles and ants may exhibit delayed responses to annual precipitation fluctuations (Barrows, 2012; Kwok et al., 2016; Gibb et al., 2019; Lin et al., 2022). The bottom-up effect (via carrying capacity) of desert precipitation increases resource availability, which, in combination with resource enhancement by shrubs and improved habitat conditions, influences tenebrionid beetle assemblages. Concurrently, the top-down effect (via biological rate) of predators such as birds and mammals is intensified, facilitating the coexistence of multiple desert animal species (Gibb et al., 2022).

Considering these aspects, this study focuses on typical desert tenebrionid beetles in the central Hexi Corridor, China, evaluating the monthly dynamic changes and main factors affecting tenebrionid beetle assemblages in the Gobi desert. Our goal is to provide scientific basis and data support for biodiversity conservation in desert ecosystems. Therefore, the aims of the study are: (1) to explore the seasonal variations in desert tenebrionid beetle community that affect the spatial aggregation patterns of these beetles; (2) to examine the influence of climate and shrub coverage on the aggregation of desert tenebrionid beetles; and (3) to study the interactions among precipitation, temperature, and shrubs and their influence on the aggregation patterns of desert tenebrionid beetles.

2.1 Study Area

The study was conducted in the National Sandy Land Closure Protection Area, located in the northern arid desert of Linze County, Gansu Province, Northwest China (39°24 52 N, 100°07 04 E). The reserve was established in 2005 with the objective of preventing desertification and protecting rare flora and fauna resources endemic to the desert. The study area lies at 1350 m a.s.l. and experiences a temperate continental arid desert climate. Annual precipitation varies significantly, with sparse snowfall in winter and rainfall predominantly concentrated in summer and autumn. Mean annual precipitation was 117.0 mm, with 79.70% of the total rainfall occurring between June and September during 2011–2020 [Figure 1: see original paper]. In 2016 and 2018, mean annual precipitation amounts were 65.4 and 81.0 mm, respectively, while in 2019 it was 130.8 mm. Annual mean temperature is 7.6°C, with values from 2011 to 2020 ranging from 8.1°C to 9.5°C. Annual mean temperature during 2015–2017 was significantly higher than the overall annual mean. Annual evaporation is 2390.0 mm, approximately 20.4 times the annual precipitation (Lin et al., 2022; Chen et al., 2024). Groundwater depth ranges from 10 to 12 m. Soil type is grey-brown desert soil, with coarse sand, fine sand, and silt and clay contents of 38.40%, 55.30%, and 6.30%, respectively.

Vegetation in the study area consists mostly of arid and hyper-arid shrubs such as *Reaumuria soongarica* (Pall.) Maxim. and *Nitraria sphaerocarpa* Maxim., with a distinct patchy or striped distribution pattern. The most important vertebrates in the Gobi desert include *Isabellina*, *Oenanthe desert*, *Lanius*, *Phrynocephalus przewalskii*, *Pica pica*, *Oenanthe sphenocercus*, *Podoces hendersoni*, *Hemiechinus auratus*, and *Vulpes corsac*. In terms of abundance, biomass, and species richness, tenebrionid beetles are among the dominant arthropod taxa in the Gobi desert (Liu et al., 2010) and play a crucial role as consumers and food resources for desert reptiles, birds, and mammals (Lin et al., 2022; Ren et al., 2024b).

Fig. 1 Monthly mean precipitation (MAP) and monthly mean temperature (MAT) changes in the Gobi desert from January to December during 2011–2020.

2.2 Tenebrionid Beetle Collection and Monitoring of Environmental Elements

In 2012, a long-term monitoring site was established in the study area to monitor the distribution and diversity of ground arthropods in the Gobi desert (Ren et al., 2024a). First, a 60 m × 120 m area was selected for ground arthropod sampling. Subsequently, 72 sampling plots of 8 m × 8 m were established, with a pitfall trap placed at the centre of each plot. From January 2015 to December 2020, tenebrionid beetles were collected monthly for seven consecutive days per sampling period using pitfall traps. The trap preservative was replenished every three days using a 75.00% alcohol solution (Liu et al., 2010). Collected beetles were preserved in polyethylene terephthalate vials containing 75.00% alcohol solution and identified to the species level in the laboratory using relevant taxonomic references (Zheng and Gui, 1999; Ren and Ba, 2010; Ren, 2016). The body length of each beetle was measured using a vernier calliper.

Meteorological data, including annual and monthly mean temperature and precipitation during 2015–2020, were obtained from the Linze Inland River Basin Research Station, part of the Chinese Ecosystem Research Network. Vegetation composition and coverage for each of the 72 sampling plots were determined.

Due to annual and seasonal precipitation variations, the herbaceous layer is predominantly composed of annual species, resulting in considerable variation in herbaceous diversity and cover. In this study, we focused on shrub species, cover, and density. For each 8 m × 8 m plot, we measured the length, width, and height of the crown. Five soil samples from the 0–10 cm depth were extracted near the trap in each plot using a soil auger, combined into a single sample, and returned to the laboratory for air drying to determine soil texture and mechanical composition.

2.3 Data Analysis

The numbers of tenebrionid beetles captured in the 72 traps from January 2015 to December 2020 were recorded. We classified tenebrionid beetle species as dominant (>10.00%), common (1.00%-10.00%), or rare (<1.00%) based on their proportion of the total number of individuals in the community. Annual and monthly catches, as well as species richness of tenebrionid beetles, were determined per trap, and the number of catches for each species was also determined per trap. Differences in community composition and contribution of dominant species during 2015–2020 were analyzed using permutational multivariate analysis of variance (PERMANOVA) and similarity percentage (SIMPER) multivariate statistical analyses, performed using the Paleontological Statistics (PAST) v.4.13 software package. Correlations of annual and monthly abundance with precipitation and temperature were determined through correlation and regression analyses using SPSS v.21.0 software.

Changes in tenebrionid beetle assemblages during 2015–2020 were analyzed using a semi-variance function and Moran's I value. The semi-variance function indicates the degree of spatial variation within the community. Main coefficients of the variogram model include nugget, sill, range, and spatial heterogeneity (SH). Nugget represents measurement error or spatial variation at distances smaller than the sampling interval. Sill is the maximum semi-variance, indicating the spatial autocorrelation structure. Range is the distance at which the model reaches the sill, indicating the spatial autocorrelation distance. SH reflects the proportion of variation in spatial autocorrelation, with values <25.00%, 25.00%–75.00%, and >75.00% indicating weak, moderate, and strong spatial autocorrelation, respectively (Gao et al., 2018; Hu et al., 2018; Ren et al., 2024a). At SH <25.00%, spatial variance attributable to stochastic factors (such as dispersal and disturbance) is considerably higher than that associated with structural factors (such as topography, climate, and soil). In contrast, at SH >75.00%, spatial variance associated with structural factors is considerably higher than that caused by stochastic factors. SH values between 25.00% and 75.00% indicate that spatial variance is attributable to both structural and stochastic factors (Wang et al., 2016). Ordinary Kriging interpolation was used to map spatial distribution patterns across different years, comparing patch shapes, sizes, and spatial patterns. Calculations based on semi-variance function, semi-variance function maps, and spatial Kriging interpolation maps were performed using geostatistics (GS+) v.9.0 software. Spatial autocorrelation analysis was performed using Moran' s I value to quantitatively describe spatial dependence and identify clustering within sample plots. Moran' s I values range from -1 to 1, where 0 represents a uniform distribution with no spatial autocorrelation. Values greater or smaller than 0 indicate positive or negative spatial autocorrelation, representing clustered or discrete spatial patterns, respectively. A higher absolute value corresponds to a greater degree of spatial autocorrelation (Sun et al., 2022). In this work, Moran' s I value was computed and plotted using the spdep, vegan, ade4, and sp packages in R v.4.2.2 software.

3.1 Tenebrionid Beetle Assemblage

A total of 11,941 tenebrionid beetles representing eight species were captured in 72 traps between January 2015 and December 2020 . The dominant species were *Blaps gobiensis* and *Microdera kraatzi alashanica*, accounting for 38.24% and 39.72% of total captures, respectively. Common species included *Anatolica sternalis* (9.28%), *Cyphogenia chinensis* (1.62%), *Pterocoma loczyi* (7.33%), and *Sternotrigon kraatzi* (3.12%). Rare species, namely *Anatolica potanini* and *Platyope victori*, constituted only 0.69% and 0.02% of total individuals. *B. gobiensis* and *M. kraatzi alashanica* were the main large and small beetle species in the Gobi desert, together comprising 65.30%-88.20% of total catches during 2015-2020. These two species exhibited high abundance during 2017-2019 but lower abundance in 2016 and 2020 (Table S1).

Table 1 Number of individuals and species composition of tenebrionid beetles captured during 2015-2020 in the Gobi desert, Northwest China.

3.2 Dynamic Changes in Tenebrionid Beetle Community

Activity periods of tenebrionid beetles during 2015-2020 spanned from March to October, with significant annual variations and interspecific differences observed ($F = 35.04$, $P < 0.001$), which were related to their biological characteristics. All eight beetle species were omnivorous; however, variations in their daily, monthly, and annual activity rhythms were observed ($F = 12.28$, $P < 0.001$). Large and small beetle species including *B. gobiensis*, *C. chinensis*, *S. kraatzi*, and *M. kraatzi alashanica* were active at night, dawn, or dusk, whereas medium-sized species including *A. sternalis*, *A. potanini*, *P. victori*, and *P. loczyi* were active during the day. These tenebrionid beetle species use shrubs and rodent burrows to escape temperature stress and avoid predators. At the annual scale, activity periods of *B. gobiensis* extended from April to October, whereas *A. sternalis* and *M. kraatzi alashanica* were active from March to September [Figure 2: see original paper]. Activity periods of *P. loczyi* were from April to July, with minimal annual variation [Figure 2: see original paper].

Monthly captures of *B. gobiensis* during 2015-2020 showed bimodal or multimodal patterns, with peaks observed between April and August [Figure 2: see original paper]. Monthly capture counts of medium-sized beetles *A. sternalis* and *P. loczyi* showed a single peak, occurring in April–May and May, respectively [Figure 2: see original paper]. Monthly captures of the small beetle *M. kraatzi alashanica* also exhibited single, double, or multiple peaks, with peak periods between April and August [Figure 2: see original paper]. *B. gobiensis* and *M. kraatzi alashanica* exhibited life cycles of 1–2 and 1–3 generations per year, respectively.

Community composition changed significantly during 2015–2020 ($F = 28.53$, $P < 0.001$), with notable differences observed between years ($P < 0.050$). According to SIMPER analysis, the average dissimilarity of tenebrionid beetle community ranged from 38.30% to 63.10% during 2015–2020. Furthermore, *B. gobiensis*, *M. kraatzi alashanica*, *A. sternalis*, and *P. loczyi* were the main species contributing to differences between years, accounting for 57.50%–83.50% of observed differences in community composition. The abundance of tenebrionid beetles was significantly higher in 2017, 2019, and 2020 than in 2015, 2016, and 2018 ($F = 35.65$, $P < 0.001$). Variations in species richness and diversity index were similar to those in abundance, with significant increases in 2016, 2018, 2019, and 2020 compared with 2015 and 2017 (Fig. S1). Significant differences were observed in the abundance of eight tenebrionid beetle species, except for *A. potanini* and *P. victori*. The abundance of *C. chinensis*, *P. loczyi*, and *S. kraatzi* followed a similar trend, being significantly more abundant in 2020 than in previous years (Fig. S2).

Fig. 2 Abundance of eight tenebrionid beetle species captured from March 2015 to October 2020 in the Gobi desert, Northwest China. (a) *Anatolica sternalis*; (b) *Anatolica potanini*; (c) *Blaps gobiensis*; (d) *Cyphogenia chinensis*; (e) *Platyope victori*; (f) *Pterocoma loczyi*; (g) *Microdera kraatzi alashanica*; (h) *Sternotrigon kraatzi*. Bars are standard errors.

3.3 Spatial Patterns of Tenebrionid Beetles

Nugget values in semivariogram analysis of dominant tenebrionid beetle species during 2015–2020 were small, indicating that the spatial scale and plot settings were appropriate . Spatial distribution was predominantly influenced by structural factors . The variation range of the optimal model for semivariogram analysis was between 9.54 and 21.27 m. Semivariogram models for the number of tenebrionid beetles captured in 2018 and 2019 exhibited the narrowest and broadest variation ranges, respectively . In years with reduced precipitation, the range increased, while increased precipitation resulted in a narrower and more stable range. In 2016, the SH value for *B. gobiensis* was 71.50%, whereas in 2015 and during 2017–2020, SH values ranged from 87.60% to 100.00%. Spatial distribution of *B. gobiensis* was predominantly influenced by structural factors , with the optimal semivariogram model ranging from 12.18 to 22.26 m and the lowest range observed in 2016 . SH values for *M. kraatzi alashanica* ranged from 88.20% to 100.00%, indicating that its spatial distribution was also predominantly influenced by structural factors . The range of the optimal semivariogram model was between 8.76 and 25.50 m, with the lowest and highest ranges observed in

2019 and 2018, respectively . Except for *B. gobiensis* in 2016 and *A. sternalis* in 2017, for which SH values ranged from 25.00% to 75.00%, SH values for *C. chinensis* were generally above 75.00% across different years, indicating that structural factors controlled its spatial distribution .

In 2019, a significant negative correlation was observed between *B. gobiensis* and *M. kraatzi alashanica*, indicating opposing spatial aggregation patterns. Decreased annual precipitation led to a more dispersed spatial distribution of these species, while increased precipitation resulted in a more concentrated distribution with opposite aggregation areas. Ordinary Kriging interpolation maps showed that in 2015 and 2018, the spatial distribution was not significantly clustered, whereas a clustered distribution was observed in 2016, 2017, 2019, and 2020 [Figure 3: see original paper]. Tenebrionid beetles exhibited positive spatial autocorrelation at a scale of 24.00 m, with almost no spatial autocorrelation observed between 40.00 and 96.00 m [Figure 4: see original paper]. Variation in spatial patterns in 2016, 2017, 2019, and 2020 was similar, with spatial correlation initially decreasing and then increasing with sample distance.

Table 2 Results of semi-variance analysis on community abundance and dominant species of tenebrionid beetles during 2015-2020 in the Gobi desert, Northwest China.

Fig. 3 Kriging map of annual abundance of tenebrionid beetles during 2015-2020 in the Gobi desert, Northwest China. (a) 2015; (b) 2016; (c) 2017; (d) 2018; (e) 2019; (f) 2020.

Fig. 4 Moran' s I value of annual abundance of tenebrionid beetles during 2015-2020 in the Gobi desert, Northwest China. (a) 2015; (b) 2016; (c) 2017; (d) 2018; (e) 2019; (f) 2020. *, $P < 0.05$ level; **, $P < 0.01$ level. Bars are standard errors.

3.4 Factors Influencing Spatial and Temporal Distributions of Tenebrionid Beetles

Correlations between the tenebrionid beetle community and dominant species with annual mean temperature and precipitation were weak . However, both abundance and species richness were strongly and positively correlated with monthly mean precipitation and temperature . Similarly, abundance of *B. gobiensis* was strongly and positively correlated with both monthly mean precipitation and temperature, while abundance of *M. kraatzi alashanica* was strongly and positively correlated with monthly mean temperature . The two dominant shrub species in the Gobi desert are *R. soongarica* and *N. sphaerocarpa*. Our results indicated that shrub presence influenced inter-annual variation in beetle activity. A significant positive correlation between species richness and *R. soongarica* cover was observed in 2016, while both abundance and species richness were significantly and positively correlated with *R. soongarica* cover in 2018 . In other years, correlations with *R. soongarica* cover were relatively weak. In

2019, abundance of *M. kraatzi alashanica* showed a significant positive correlation with *R. soongarica* cover, whereas abundance of *B. gobiensis* was weakly correlated.

Distribution of tenebrionid beetles was positively correlated with *N. sphaerocarpa* cover in 2016, 2017, and 2018 . Both abundance and species richness were significantly and positively correlated with *N. sphaerocarpa* cover in 2016. Additionally, abundance in 2017 and species richness in 2018 exhibited positive correlations with *N. sphaerocarpa* cover . Abundance of *B. gobiensis* was significantly and positively correlated with *N. sphaerocarpa* cover in 2016, 2017, and 2019. Abundance of *M. kraatzi alashanica* also demonstrated a significantly positive correlation with *N. sphaerocarpa* cover, exhibiting variations with shrub species and sampling year .

Table 3 Correlations of activity density, species richness, and tenebrionid beetles with mean precipitation and mean temperature at annual and monthly levels during 2015-2020.

Table 4 Correlations of activity density, species richness, and tenebrionid beetles with covers of *Reaumuria soongarica* (Pall.) Maxim. and *Nitraria sphaerocarpa* Maxim. during 2015-2020.

4.1 Rhythmic Changes of Tenebrionid Beetles

Arthropods, including tenebrionid beetles, are the main invertebrate groups in desert ecosystems. They serve as key decomposers and provide essential food and water resources for vertebrates, thus contributing to the health and stability of desert ecosystems (Vonshak et al., 2009; Valdez, 2020; Sagi and Hawlena, 2021). Numerous studies have confirmed that tenebrionid beetles are the dominant arthropod group in arid and semi-arid desert areas globally, although significant regional differences exist in their composition and community structure (Polis, 1991; Whitford, 1993; Ragionieri et al., 2023). In the central Hexi Corridor, 75.00% of tenebrionid beetle species are endemic to the Palaearctic region. The tenebrionid beetle community in the Gobi desert is primarily composed of *B. gobiensis*, *A. sternalis*, *P. loczyi*, and *M. kraatzi alashanica*. This composition slightly differs from that in adjacent desert habitats (Liu et al., 2015) but resembles findings from Yanchi, Ningxia Hui Autonomous Region (Yang et al., 2012). Tenebrionid beetles are a key beetle group in desert ecosystems, as demonstrated in areas like Ningxia Hui and Xinjiang Uygur autonomous regions and other deserts (Polis, 1991; Lou et al., 2011; Yang et al., 2012). However, notable differences exist in species composition and abundance changes (Cloudsley-Thompson, 2021). In the central Hexi Corridor, tenebrionid beetles accounted for 19.50% of total arthropod numbers and 77.00% of biomass (Liu et al., 2010). Lin et al. (2022) found that birds in the Gobi desert were mainly active during the plant growing season, and their monthly relative multiplicity index was closely related to the number of tenebrionid beetles. Beetle remnants have been found in bird and mammalian faeces, highlighting their role in food web structure and functional dynamics of desert ecosystems. Although the number of tenebrionid beetle species showed little annual variation, capture rates fluctuated significantly, attributable to reproductive changes in main species driven by precipitation and temperature. We also found that *P. victori* was only captured in 2020, suggesting that precipitation changes may affect activity of rare species. In summary, although species composition exhibited little annual variation, significant seasonal variations in capture quantity and monthly activity patterns among species affected community dynamics.

Interspecific differences in daily activity rhythms among main beetle species in the Gobi desert are associated with distinct survival strategies for coping with high temperature and drought stress (Parker and Lawrence, 2001). Tenebrionid beetle species have long adapted to extreme desert environments, and their unique physiological and ecological characteristics result in variations in activity rhythms that influence dynamic changes in the community (Ren et al., 2024a). Most tenebrionid species are nocturnal, and we found that *B. gobiensis*, *C. chinensis*, and *M. kraatzi alashanica* are mainly active at night but also during daytime on rainy days, suggesting that daily temperature changes govern their activity rhythms (Cloudsley-Thompson, 2021). Medium-sized species like *A. sternalis* and *P. loczyi* are primarily active during daytime in spring and summer, using shrubs or animal nests to avoid temperature stress during intense midday heat. This is related to their sheath wing structure and physiology, which can adapt to high temperatures (Cloudsley-Thompson, 2021). Their coleopteran structure and metabolic activities allow them to withstand temperature and solar radiation stress. Day-active beetle species also use microhabitats such as shrubs and vertebrate nests to avoid high midday temperatures, and some burrow into the ground to avoid heat stress. Beetles active at dawn not only avoid heat stress but also use their coleopteran features to condense water vapour from the air to resist drought stress (Zotov, 2017). *B. gobiensis* and *M. kraatzi alashanica* are mainly active at night and on cloudy and rainy days, indicating that daily temperature changes govern their activity rhythms, and environmental changes can affect these rhythms (Krasnov and Ayal, 1995).

Monthly activity periods in the Gobi desert span from March to October, with some annual variations. Changes in temperature during spring and autumn likely serve as the main environmental factors limiting adult beetle activity. The activity period in the central Hexi Corridor can last up to eight months. Dominant species such as *B. gobiensis*, *A. sternalis*, and *M. kraatzi alashanica* exhibit longer activity periods than other species, consistent with findings from the Negev Highlands in Israel (Aldryhim et al., 1992). Sackmann and Flores (2009) observed significant monthly variations in capture numbers in Patagonian shrubland and grassland, although species richness was less varied, which slightly differs from our findings. Our results indicated that although activity periods exhibited little annual variation, there were significant annual and monthly changes in abundance and species richness, attributable to different monthly and annual activity patterns among species. Peaks in abundance of different species occur in spring and summer, with notable annual variations.

This result differs from observations in Saudi Arabian and Argentine deserts (Thomas, 1979) but aligns with seasonal variations of armoured beetles in the central USA, Israel, and coastal sand dunes in Italy (Mazía et al., 2006). Additionally, a study in Australia' s Simpson Desert found significant seasonal variation in energy density of beetles, with higher values in autumn than spring (Gibb et al., 2019). *M. kraatzi alashanica* and *B. gobiensis* are two main species differing in size and exhibiting unimodal or multimodal monthly activity periods. The peak period of monthly activity occurred in both spring and summer during 2015–2020. *B. gobiensis* is large with a 2–3-year life cycle, while *M. kraatzi alashanica* has a 1–3-year life cycle, and changes in precipitation and temperature can affect their reproduction, which in turn affects population dynamics (Fallaci et al., 2002; De Los Santos et al., 2006). These two species accounted for 65.20%–88.30% of total tenebrionid beetles, and their abundance significantly influenced monthly and annual community dynamics. Short-term and long-term enrichment changes of litter resources driven by precipitation have important impacts on larval growth and overwintering, which may affect community dynamics (Henschel, 2021). In addition, long-lived species exhibit lagged responses to annual precipitation changes, thereby affecting long-term response patterns of the beetle community (Maeno et al., 2014).

4.2 Spatial Patterns of Tenebrionid Beetles

Vegetation coverage in the Gobi desert is relatively low, and enrichment of food resources in micro-habitats such as shrubs and ant nests strongly influences spatial distribution patterns of tenebrionid beetles. Previous studies have shown that shrubs and ant nests positively impact arthropod activity, including tenebrionid beetles, though this effect varies seasonally and depends on micro-environments (Liu et al., 2012; Feng et al., 2022). Most tenebrionid beetle species are active in spring and summer when rainfall is low, and shrub presence and interspecific differences can affect their distribution, consistent with findings of Mazía et al. (2006). Desert shrubs reduce daytime temperatures and increase nighttime temperatures, providing suitable niches for beetle activity (Ingimarsdóttir et al., 2012). Large-scale hydrothermal conditions are regarded as a key factor shaping geographic distribution patterns of zonal vegetation and animal diversity (Yang et al., 2019). This study demonstrates that variations in precipitation and temperature influence the degree of shrub dependence among tenebrionid beetles, thereby altering their spatial distribution patterns, which is consistent with Liu et al. (2012). Tenebrionid beetles are typical omnivorous insects, and precipitation- and temperature-driven changes in shrub and ant nest micro-environments influence their spatial distribution patterns. Furthermore, interactions among precipitation, temperature, and shrubs determine distribution patterns across various spatial and temporal scales (Liu et al., 2012, 2015; Bartholomew and El Moghrabi, 2018).

Soil in the Gobi desert is relatively hard, and microhabitats shaped by sand dunes near *N. sphaerocarpa* form important habitats for both adult and larval tenebrionid beetles. Leaves and litter of *R. soongarica* and *N. sphaerocarpa* also serve as critical food and water sources. Our results suggested that monthly and annual variations in precipitation and temperature could affect beetle dependence on shrubs, thereby altering spatial distribution patterns (Liu et al., 2012). The spatial distribution patterns of the tenebrionid beetle community during 2015–2020 were primarily regulated by structural factors, while climatic factors such as precipitation and temperature exhibited a consistent response pattern. Moreover, environmental heterogeneity could enhance species diversity and spatial aggregation of beetles. The influence of climatic factors on small-scale spatial distribution patterns should not be overlooked (Yang et al., 2019). Studies conducted at various spatial and temporal scales are essential for elucidating structural characteristics of surface beetles in the Gobi desert (Zajicek et al., 2021). Gao et al. (2023) found spatial heterogeneity in carrion beetle communities regulated by both deterministic and non-deterministic processes, which is not consistent with this study. Spatial variability of ground beetles in the Gobi desert appears entirely regulated by deterministic processes, likely due to the extreme climatic environment. In years with lower annual precipitation, variable range distances are significantly greater for both the tenebrionid beetle community and interspecific interactions. This may be attributed to changes in food resources and predation intensity, as fluctuations in precipitation and temperature can lead to food scarcity, prompting beetles to expand their variable range distances.

4.3 Factors Influencing the Distribution of Tenebrionid Beetles

Changes in precipitation and temperature have both short-term and long-term effects on the tenebrionid beetle community, altering their dependence on shrubs and thereby affecting spatial aggregation patterns (Ilsøe et al., 2017; Lin et al., 2022). Water is a crucial limiting factor for animal distribution in arid and semi-arid areas. Short- and long-term fluctuations in precipitation strongly affect diversity of large invertebrates such as beetles and ants, with different invertebrate groups responding differently and showing significant regional differences (Gibb et al., 2019; Yang et al., 2019; Feng et al., 2022). The unique climatic conditions in the Gobi desert influence tenebrionid beetle diversity in their habitats. Our research showed that increased precipitation significantly enhanced activity density, which peaked in 2019 and 2020, with species richness being higher in 2020 than in other years. Moreover, activity density significantly increased during the rainy season. Community composition exhibited significant seasonal fluctuations, with notable changes in the abundance of major species. Years with increased precipitation can not only increase captures of certain major species but also enhance diversity of rare species.

In addition to precipitation effects, temperature significantly affected activity rhythms of these beetles. As some beetles tend to be thermophilic in desert environments, areas with higher mean temperatures typically exhibit higher species diversity (Lescano et al., 2017; Ren et al., 2024b). Adult beetles are particularly sensitive to small-scale soil temperature fluctuations, and low temperatures in spring and winter may limit their survival (Zotov, 2017). Additionally, persistent high temperatures lead to low soil moisture, while high water demand during larval development means soil moisture cannot satisfy their needs. This aligns with Wang et al. (2020) on environmental effects on ground beetle diversity in Helan Mountain vegetation zones. Reproduction can be maximized under optimal temperature and soil moisture conditions, while both low and high temperatures can diminish activity frequency (Wang et al., 2020; Cloudsley-Thompson, 2021). Given that larvae require significant water during development, insufficient soil moisture may hinder their development. Consequently, reproduction can be maximally promoted at appropriate temperatures. Our results indicate that activity density and species richness of adult tenebrionid beetles are significantly and positively correlated with monthly mean temperature. The activity and diversity of *B. gobiensis*, *C. chinensis*, and *M. kraatzi alashanica* are significantly and positively correlated with monthly mean precipitation and temperature, highlighting the notable influence of these factors.

Shrubs were also an important factor in the spatial distribution of tenebrionid beetles, with large shrubs such as *N. sphaerocarpa* having greater influence on beetle aggregation than *R. soongarica* (Liu et al., 2012). Shrub presence affects beetle aggregation through various factors such as resource availability, predation intensity, and temperature stress, whereas season, soil texture, and landscape structure have no significant effects (Mazía et al., 2006; Shelef and Groner, 2011; Bartholomew and El Moghrabi, 2018). The study also found that effects of precipitation and temperature on beetle aggregation were nonlinear. In summary, changes in precipitation and temperature have both short- and long-term effects on the tenebrionid beetle community, influencing spatial distribution patterns by altering their dependence on shrubs.

5 Conclusions

A total of 11,941 individual tenebrionid beetles from eight species were captured in the Gobi desert, Northwest China during 2015–2020. The dominant species –the large-sized *B. gobiensis* and small-sized *M. kraatzi alashanica*–accounted for 65.30%–88.20% of the total catch. The active period spanned from March to October, with significant seasonal variations and interspecific differences. Spatial differentiation was primarily influenced by structural factors such as temperature and precipitation. Community dynamics were related to annual and monthly variations in precipitation and temperature, with monthly capture numbers and species richness positively correlated with monthly rainfall and mean temperature. Moran' s I value indicated that the tenebrionid beetle community exhibited spatial autocorrelation at a scale of 24.00 m. Spatial distribution was related to the coverage of *R. soongarica* and *N. sphaerocarpa*. In summary, variations in precipitation and temperature drive the activity rhythms of desert tenebrionid beetles, and interactions among precipitation, temperature, and shrubs affect the aggregation of desert tenebrionid beetles at different temporal and spatial scales.

Conflict of interest: ZHAO Wenzhi is an editorial board member of *Journal of Arid Land* and was not involved in the editorial review or decision to publish this article. All authors declare no competing interests.

Acknowledgements: This research was funded by the National Natural Science Foundation of China (U23A2063), the Gansu Province Top-notch Leading Talents Project (E339040101), and the National Natural Science Foundation of China (41771290, 42377043, 41773086). We sincerely thank anonymous reviewers for helpful suggestions on an earlier draft and the editors for guidance throughout the publication process.

Author contributions: Conceptualization: REN Jialong, LIU Jiliang; Methodology: REN Jialong, LIU Jiliang, WANG Yongzhen, FENG Yilin; Formal analysis: WANG Yongzhen, ZHAO Wenzhi, HE Zhibin, FENG Yilin; Writing—original draft: REN Jialong; Writing—review and editing: ZHAO Wenzhi, HE Zhibin, NIU Yiping, XIN Weidong; Supervision: ZHAO Wenzhi, HE Zhibin, NIU Yiping, XIN Weidong, LIU Jiliang. All authors approved the manuscript.

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Appendix

Table S1 Number of individuals and relative abundance of tenebrionid beetles during 2015-2020 in the Gobi desert, Northwest China.

Fig. S1 Comparison of abundance (a) and species richness (b) of tenebrionid beetles during 2015-2020 in the Gobi desert, Northwest China. Different lowercase letters within years indicate significant differences at $P < 0.05$ level. Bars are standard errors.

Fig. S2 Comparison of abundance of eight tenebrionid beetle species during 2015-2020 in the Gobi desert, Northwest China. (a) *Anatolica sternalis*; (b) *Anatolica potanini*; (c) *Blaps gobiensis*; (d) *Cyphogenia chinensis*; (e) *Platyope victori*; (f) *Pterocoma loczyi*; (g) *Microdera kraatzi alashanica*; (h) *Sternotrigon kraatzi*. Different lowercase letters within years indicate significant differences at $P < 0.05$ level. Bars are standard errors.

Note: Figure translations are in progress. See original paper for figures.