Community structure of tenebrionid beetles in the Ulan Buh Desert (Inner Mongolia, China) (Coleoptera: Tenebrionidae)

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Abstract
Tenebrionids are a conspicuous faunal component of Central Asian deserts, but little is known about their community ecology. We investigated how tenebrionid community structure varied along a vegetational gradient in the Ulan Buh Desert (Gobi Desert). Sampling was done with pitfall traps in three sites with different vegetation cover. Species abundance distributions were fitted by the geometric series model, which expresses the “niche pre-emption” hypothesis. Community structure was investigated using different measures of diversity (number of species, Margaleff richness and Shannon-Weaver index), dominance (Simpson and Berger-Parker indexes) and evenness (Pielou’s index). The observed tenebrionid species richness was similar to that known from other Gobi Desert sites. The three investigated sites have similar species-abundance patterns, but the most dominant species varied among them. This suggests that the local environment operates a filtering action on the same basic fauna, allowing different species to dominate under different conditions. Overall, the highest total abundance was observed in the true desert site, however this site had a community structure similar to that observed in the site with more vegetation. By contrast, the investigated site with intermediate conditions showed a higher diversity and evenness, and a lower dominance. Thus, intermediate conditions of plant cover favour tenebrionid diversity, whereas a dense cover or a very sparse cover increases the dominance.

Key words: arid ecosystems, Asia, Community ecology, Diversity, Gobi Desert.

Introduction
The family Tenebrionidae is one of the largest of Coleoptera, comprising about 20,000 known species (Ślipiński et al. 2011). Adult tenebrionids exhibit a superficial diversity of form possibly exceeding that of any other family of beetles and some are often wrongly identified as they closely resemble members of other families (e.g., Carabidae, Passalidae, Scarabaeidae, Chrysomelidae, Curculionidae, Zopheridae).

The tenebrionid beetles inhabiting desert ecosystems are well known for their morphological, physiological and behavioural adaptations to cope with pervading aridity and extremely high temperatures, including the presence of a subelytral cavity, legs adapted to sand-walking, a body shape that facilitates sand-swimming, a wax bloom covering the integument to minimize water loss, the ability of drinking fog water, an active uptake of atmospheric water, the use of metabolic water, and the presence of highly specialized osmoregulation processes (e.g., Nicolson 1990; Colombini et al. 1994; de los Santos 1994; de los Santos et al. 2000, 2002a, 2002b; Fallaci et al. 1997). Thanks to these adaptations, tenebrionid beetles are a conspicuous faunal component of arid and semi-arid environments (Dajoz 2002), where they play an extremely important role as macrodetritivores to nutrient and energy cycling, being the decomposition of detritus by bacteria and fungi strongly limited by the scarcity of water (Hanrahan & Seely 1990).

Owing to the extremely scarce and discontinuous vegetation cover, desert ecosystems present tenebrionid communities characterized by a relatively simple structure that facilitates their study (Thomas 1983). It is known that, in general, habitat distribution of tenebrionid beetles is strongly influenced by species’ preferences for different substrates, plant architecture, topography and microclimatic conditions (Faragalla 1998, 1999; de los Santos et al. 2002b; Aldryhim et al. 1992; Ayal & Merkl 1994; Chikatunov et al. 1997; Thomas 1979, 1983; Krasnov & Shenbrot 1996; Fattorini 2009; Fattorini et al. 2012). In most contexts, disentangling the effects of different biot-
ic and abiotic factors is however difficult because of their multiple interactions. From this point of view, the simplified environmental structure and species diversity of desert ecosystems would make it easier to relate tenebrionid diversity with habitat characteristics. For example, tenebrionid beetles of desert ecosystems may represent ideal organisms to investigate resource partitioning models and patterns of diversity. High values of tenebrionid diversity and abundance have been reported for various deserts all over the world, including the Namib desert (Koch 1962; Holm & Scholtz 1980), NW Libya (Fiori & Crovetti 1972), Mojave desert (Thomas 1983), Negev desert (Ayal & Merkl 1994; Krasnov & Ayal 1995; Krasnov & Shenbrot 1997) and Saudi Arabia (Faragalla 1998, 1999). However, information on tenebrionid community structure in desert ecosystems is still limited. In particular, tenebrionid beetles are very diversified and abundant in the arid ecosystems of Central Asia (e.g. Pfeiffer & Bayanmasen 2012; Khurelpurev & Pfeiffer 2017), yet little is known about their community ecology (e.g. Pfeiffer & Bayanmasen 2012; Liu et al. 2012, 2015; Liu et al. 2013).

In this paper we investigated how tenebrionid community structure varied along a vegetational gradient in the Gobi Desert in Inner Mongolia. For this, we selected sites with the same climatic, topographic and soil characteristics. Selected sites also showed the same vegetation type, but with decreasing vegetation cover. This allowed us to relate changes in community structure to different vegetation setting.

**Methods**

**Study area and data collection**

The Ulan Buh Desert (about 9,900 km²) is located in the southernmost part of the Gobi Desert (Inner Mongolia, north-central China). The Ulan Buh Desert is surrounded by the Yellow river (east), the Jilantai salt lake (west), the Langshan Mountains (north) and the Helan Mountains (south). The climate is dominated in winter by the dry, cold north-westerly winter monsoon and in summer by the warm, moist south-easterly summer monsoon (Chun et al. 2008).

Both landscape and climatic features vary in different parts of the desert. Our study was conducted in the eastern part of the Ulan Buh Desert, where the landscape is mainly represented by low linear dunes near the mountains and by relatively high pyramid dunes further away from the mountains (Chen et al. 2013). Here the mean annual precipitation is 152.7 mm, the mean potential evaporation is 2351 mm, and the mean annual air temperature is 7.5 °C (maximum: 38.7 °C in July; minimum: −32.8 °C in January) (Yang et al. 2014). Vegetation is mainly represented by shrubs of *Artemisia ordosica*, *Artemisia sphaerocephala*, *Haloxylon ammodendron*, *Nitraria tangutorum* and *Psammochloa villosa* in the lower part of the sand dunes and in the interdunes (Yang et al. 2014).

Sampling was done between 19 and 20 June 2018 in three sites that reflected a gradient of vegetation cover:

- **Site A** (40.25.01N and 106.39.84E, 1042 m elevation) was characterized by sandy soil with dense vegetation;
- **Site B** (40.26.51N and 106.34.72E, 1039 m elevation) had also sandy soil but with only sparse vegetation;
- **Site C** (40.26.50N and 106.34.71E, 1035 m elevation) was represented by a true desert dune with very sparse vegetation.

In all three sites, vegetation was mainly represented by tufts of *Artemisia sphaerocephala* and *Psammochloa villosa*. Tenebrionid beetles were sampled with pitfall traps. In each site, beneath tufts of each dominant plant species, three pitfall traps filled with 50 ml of three fluids (propylene glycol, beer and a mixture of beer and propylene glycol in the proportion of 3:1) were placed. Each trap consisted of a cup made of PVC pipe (90 × 100 cm) buried flush with the soil surface. Pitfall traps were put down in the afternoon (at 6 P.M.) and emptied after 16 hours (at 9 A.M.). This sampling strategy was used to assure that local beetle populations were not over-captured due to unnecessary sampling effort (Liu et al. 2011). Previous researches indicated that the use of few traps operating for a short period is adequate to sample tenebrionid communities in this type of habitat (Liu et al. 2012, 2015; Pfeiffer & Bayanmasen 2012; Khurelpurev & Pfeiffer 2017).

The collected specimens were preserved in jars filled with 95% ethanol, identified to species and counted. The species abundance distributions obtained from traps filled with three fluids were strongly correlated (Spearman rank correlation: 0.9 < r < 1; 0.001 = P < 0.0001), thus we pooled the data and conducted the analysis at site level. All material is preserved in the Museum of Hebei University (MHBU).

**Data analysis**

Communities living in harsh environments and early successional stages are known to follow the so-called “niche pre-emption” model, in which the sizes of the niche hypervolumes (measured by species relative abundances) are sequentially pre-empted by the most abundant to the least abundant species (Giller 1984; Fattorini 2005; McGill et al. 2007). This model is mathematically expressed by the geometric series. If in rank-abundance plot, species are ranked from the most to the least abundant, and abundances are logarithmically transformed, a geometric series exactly follows a strength line (May 1975; Magurran 1988; Hayek & Buzas 2010). Thus, Ordinary Least Squares (OLS) regressions can be used to model the rank-abundance representation of the geometric series (Fattorini 2005). With this approach, the coefficient of determination $R^2$ can be used as a goodness-of-fit measure and differences between slopes can be assessed by analysis of covariance (ANCOVA). In the niche pre-emption model, the fixed proportion of used resource is given by the niche pre-emption param-
eter $k$, because the first (most abundant) species in the sequence occupies a fraction $k$ of resource hypervolume, the second species a fraction $k$ of hypervolume not occupied by the first, and so on. The niche pre-emption parameter $k$ was calculated following He & Tang (2008).

Community structure was investigated using different measures of diversity, dominance and evenness (Krebs 1999; Magurran 2004; Hayek & Buzas 2010). To express richness, we used both the number of recorded species ($S$) and Margalef richness index. The Margalef richness index is:

$$Mg = (S - 1)/ln(n)$$

where $n$ is the number of collected individuals. This index seems to have a good discriminant ability (Yeom & Kim 2011), but is strongly influenced by the sampling size and effort (Magurran 2004). However, because our comparative analyses are based on the same sampling procedure, this is not a problem.

To reflect the relative contribution of different species to the total abundance, we used the Shannon-Wiener index

$$H' = -\sum \frac{n_i}{n} \ln \left( \frac{n_i}{n} \right)$$

where $n_i$ is abundance of species $i$ and $n$ is the overall abundance. $H'$ ranges from 0 (when one species dominates the community completely) to high values for communities with many species, each with similar number of individuals. $H'$ represents the uncertainty about the identity of an unknown individual and has its foundations in information theory (Morris et al. 2014). This index is considered particularly effective in encapsulating two aspects of diversity (richness and evenness) into a single value (Hayek & Buzas 2010).

As measures of dominance we used Simpson ($D$) and Berger-Parker ($d$) indexes. Simpson index is calculated as:

$$D = \sum \left( \frac{n_i}{n} \right)^2$$

and represents the probability that two individuals taken at random belong to the same species (see Morris et al. 2014 for details). The Berger-Parker index measures the numerical importance of the most abundant species as:

$$d = \frac{n_{\text{max}}}{n}$$

where $n_{\text{max}}$ is the number of individuals belonging to the most abundant species, and $n$ is the total number of collected individuals. Berger-Parker index does not have restrictions on the sample size (Magurran 2004) and is considered by May (1975) to be one of the best. Both $d$ and $D$ increase when diversity in the community decreases.

Finally, as a measure of evenness we used Pielou’s index ($J$) of equitability:

$$J = H'/\ln(S)$$

where $S$ is the number of species. If all species are represented by the same number of individuals (maximum equitability), $H' = \ln(S)$. Thus, $J$ varies between 0 (one species dominates the community completely) and 1 (all species are equally abundant) (Magurran 1988).

To compare abundances and the aforementioned indexes of diversity, dominance and equitability between the three communities a bootstrapping procedure was applied. For each index, the two samples in a pairwise comparison were initially pooled. Then, 1000 random pairs of samples were extracted from this pool, and the index was calculated for each replicate pair with the same numbers of individuals as in the original two samples. The probability of obtaining the observed difference by random sampling from a unique parental population was calculated as the number of times that the absolute difference of the indexes of a replicate pair exceeded or equalled that of the original samples. A $P$ (equal) < 0.05 was assumed to indicate a significant difference in the index between the two samples. Calculations were done using PAST (Hammer et al. 2001).

**Results**

In total, we collected 1,406 individuals belonging to 10 species (Table 1, Figure 1). The goodness-of-fit statistics of the OLS regression lines (Table 2) indicated that the geometric series fitted adequately all three species assemblages (Figure 2). The slopes of the three regression lines were not significantly different (ANCOVA for the homogeneity of slopes: $F = 1.560$, $P = 0.241$), which indicates that the three communities followed the same pattern. The pre-emption parameter $k$ showed similar values in the three communities ($k=0.580$ in Site A, $k=0.598$ in Site B and $k=0.588$ in Site C).

The three communities differed for the number of sampled individuals (lowest in Site A, highest in Site C and intermediate in Site B), but not for species richness (number of collected species and Margalef index). Diversity (Shannon) and evenness (Pielou) were highest in Site B than in Sites A and C, whereas Site A and C did not show significant differences. Dominance (Simpson and Berger-Parker) showed a reverse pattern being higher in Sites A and C than in Site B (Table 3).

**Discussion**

Tenebrionid species richness values observed in the three sampled sites in the Ulan Buh Desert (7 species in Site A and B, and 8 species in Site C, respectively) perfectly match those recorded in other Gobi Desert sites, including those that were subject to a much higher sampling effort (Table 4). Thus, these results suggest that our short-term sampling approach was adequate to collect virtually all species present in the study sites.
Our results indicate that the tenebrionid communities inhabiting different biotopes in the Ulan Buh Desert not only are composed of few species, but also show a simple structure characterized by high dominance, as clearly illustrated by the high dominance of *Anatolica potanini* (Reitter, 1889) in Sites A and B, where it accounted for 68% and 52% of collected tenebrionids, respectively, and *A. mucronata* (Reitter, 1889) in Site C, where it represented about 72% of the total number of tenebrionid beetles. In all three sites, the two locally most abundant species, taken together, represented about 80% of total individuals.

This pattern of species dominance is also clearly shown by the fact that the species abundance distribution followed a geometric series, and it is indicative of a community dominated by *r*-selected species, as observed for the tenebrionid communities inhabiting other arid environments, such as the Mediterranean sand dunes (see Fattorini 2008; Fattorini et al. 2016, 2017). The geometric series has

### Table 1 – Number of tenebrionid individuals collected in three sites in the Ulan Buh Desert (Gobi Desert, Inner Mongolia, China). Site A was occupied by a relative dense vegetation; Site B by sparse vegetation; Site C is a strict desert site with very scattered vegetation.

| Species                                              | Site A | Site B | Site C |
|------------------------------------------------------|--------|--------|--------|
| *Anatolica mucronata* Reitter, 1889                   | 29     | 57     | 498    |
| *Anatolica potanini* Reitter, 1889                    | 183    | 232    | 31     |
| *Anatolica immarginata* Reitter, 1889                | 0      | 1      | 61     |
| *Anatolica suturalis* Reitter, 1889                   | 0      | 0      | 9      |
| *Microdera (Dordanae) kraatzi alashanica* Skopin, 1964| 6      | 15     | 3      |
| *Epitrichia semenowi* Bogachev, 1949                  | 3      | 1      | 61     |
| *Sternotrigon zichyi* (Csiki, 1901)                   | 45     | 122    | 0      |
| *Mantichorula semenowi* Reitter, 1889                 | 1      | 18     | 28     |
| *Melanesthes (Melanesthes) jenseni meridionalis* Kaszab, 1968| 1 | 0 | 0 |
| *Blaps (Blaps) kiritshenkoi* Semenov & Bogatshev, 1936 | 0      | 0      | 1      |

### Table 2 – Results of regression analyses for the geometric series model for the tenebrionid communities sampled in three sites in the Ulan Buh Desert.

|                | Intercept ± SE | Slope ± SE | R²   | t     | P    |
|----------------|----------------|------------|------|-------|------|
| Site A         | 2.530 ± 0.148  | −0.396 ± 0.033 | 0.966 | −11.933 | <0.0001 |
| Site B         | 2.927 ± 0.212  | −0.423 ± 0.047 | 0.941 | −8.932 | <0.001 |
| Site C         | 2.828 ± 0.177  | −0.333 ± 0.035 | 0.938 | −9.518 | <0.001 |

### Table 3 – Abundance, richness, diversity, dominance and evenness of tenebrionid beetles in the three sampled sites in the Ulan Buh Desert. Differences between sites were tested using a bootstrapping procedure. *P* (equal) < 0.05 indicates a significant difference between the two compared sites.

|                                | Site A | Site B | Site C | P (A = B) | P (A = C) | P (B = C) |
|--------------------------------|--------|--------|--------|-----------|-----------|-----------|
| Number of individuals          | 268    | 446    | 692    | <0.0001   | <0.0001   | <0.0001   |
| Number of species              | 7      | 7      | 8      | 1.000     | 0.631     | 0.996     |
| Margalef richness              | 1.073  | 0.984  | 1.070  | 0.920     | 1.000     | 0.391     |
| Simpson dominance              | 0.507  | 0.365  | 0.537  | 0.0001    | 0.321     | 0.0001    |
| Berger-Parker dominance        | 0.683  | 0.520  | 0.720  | 0.0001    | 0.311     | 0.0001    |
| Shannon diversity              | 0.978  | 1.228  | 1.023  | 0.001     | 0.555     | 0.0007    |
| Pielou evenness                | 0.503  | 0.631  | 0.492  | 0.05      | 0.865     | 0.0001    |
Tenebrionid beetle community structure in the Gobi Desert

Fig. 1 – Proportion of tenebrionid species in three sites with different vegetation cover in the Ulan Buh Desert (Gobi Desert, Inner Mongolia, China). Site A was occupied by a relative dense vegetation; Site B by sparse vegetation; Site C was a strict desert site with very scattered vegetation.

Fig. 2 – Rank-abundance plot of the tenebrionid beetles collected from three sampled sites: Site A (black dots, continuous line), Site B (red triangles, dotted line) and Site C (blue squares, broken line). Species are ranked from the most to the least abundant (x-axis). Species abundances are log-transformed (y-axis). Data were fitted using linear regressions.

been typically used to model communities of early successions (Whittaker 1972; Bazzaz 1975), which are subject to disturbances (Gray 1981; Nummelin 1998) or which occupy poor habitats (Whittaker 1965; Keeley & Fotheringham 2003). Both desert and beach-dune systems are ecosystems characterized by harsh climatic and edaphic factors and very limited food resources (mostly represented by vegetable detritus). Thus, these environments can be best colonized only by a few, sand-specialized and r-selected species which can use decaying organic matter. Slopes of regression lines for the three communities investigated in this study varied between -0.42 and -0.33, being therefore slightly higher than those reported from Mediterranean dune systems (-0.29 to -0.25; Fattorini 2008; Fattorini et al. 2017), which suggests a higher dominance effect. This is supported by k-values. In the three communities investigated in this study, k was about 0.6. This indicates that the most common species would represent about 60% of
individuals in the community, the second most common species would represent half of the remaining half (20%), the third, half of the remaining quarter (10%), and so on. This shows sharper declines in the species niche hypervolumes than found in Mediterranean dune ecosystems (with $k$ about 0.4-0.5; Fattorini et al. 2016, 2017). Also, our $k$-values are consistent with the highest values that can be calculated from other sites with similar environmental characteristics (Table 4).

Tenebrionid communities can have similar species composition but very different community structure in biotopes spatially close but with striking environmental differences (Fattorini 2009). The three sites investigated here have similar species-abundance patterns, but the most dominant species varied among them. In particular, while A. potanini was the most favoured species in semidesert conditions, A. mucronata was the most dominant species in the true desert community. This suggests that the local environment operates a filtering action on the same basic fauna, allowing different species to dominate under different conditions.

Overall, the highest total abundance was observed in the true desert site (Site C), however this site had a community structure similar to that observed in the site with more vegetation (Site A). By contrast, the investigated site with intermediate conditions (Site B) showed a higher diversity and evenness, and a lower dominance. This is unexpected because Site B is separated from Site A by about 100 m, whereas it is about 10 km from Site C.

These results suggest that (1) community structure is strongly influenced by local environmental characteristics, more than spatial proximity; and (2) that intermediate conditions of plant cover favour tenebrionid diversity, allowing a more balanced species-abundance distribution, whereas a dense cover or the very sparse cover increases the dominance, albeit of different species. This may be explained by assuming that the habitat with intermediate plant cover density can be exploited by both species that tend to prefer denser vegetation and those that are more associated with less dense vegetation. From this regard, the habitat of Site B can be considered a sort of an ecotone, where species associated with different habitats overlap. An intermediate vegetation cover can be also particularly favourable because it may allow individuals to benefit from the inherent environmental heterogeneity, for example by moving from open spaces to shaded places according to variation in insolation and temperature. Finally, an intermediate vegetation density may represent a trade-off between the pros and cons of habitats with higher and lower plant density: a denser vegetation may offer more detritus, and hence more food, but a high amount of detritus, as well as the density of plant roots, may hamper beetle movements.

We are aware that our results are based on only three sites and on a snapshot sampling. Thus, it would be interesting, in the future, to extend this type of study by including more sites and investigating seasonal changes in community structure.

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