Fragmenta entomologica, 51 (2): 193-200 (2019)

Research article

Submitted: June 8th, 2019 - Accepted: November 2nd, 2019 - Published: November 15th, 2019

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

Yiping NIU^{1,2}, Guodong REN^{1,2}, Giulia LIN³, Letizia DI BIASE⁴, Simone FATTORINI^{4,*}

¹ College of Life Sciences, Hebei University - Baoding, Hebei, 071002, P. R. China - niu 20040118@126.com

² Museum of Hebei University - Baoding, Hebei, 071002, P. R. China - gdren@hbu.edu.cn

³ Via Principe Amedeo 175, 00185 Rome, Italy - giulia.lin997@gmail.com

⁴ Department of Life, Health & Environmental Sciences, University of L'Aquila - Via Vetoio, Coppito, 67100 L'Aquila, Italy

simone.fattorini@univaq.it

* Corresponding author

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-Weaner 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 biotic 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 surround-ed 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 (40.25.010N and 106.39.841E, 1042 m elevation) was characterized by sandy soil with dense vegetation;
- Site B (40.26.511N and 106.34.722E, 1039 m elevation) had also sandy soil but with only sparse vegetation;
- Site C (40.26.501N and 106.34.718E, 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 gylcol, beer and a mixture of beer and propylene gylcol 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: $0.9 < r_s < 1$; 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 (ANCO-VA). In the niche pre-emption model, the fixed proportion of used resource is given by the niche pre-emption parameter 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:

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

where n_{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 shortterm sampling approach was adequate to collect virtually all species present in the study sites.

	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 (Dordanea) kraatzi alashanica Skopin, 1964	6	15	3
Epitrichia semenovi 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
Total	268	446	692

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.

Table 2 – R	Results of regression	analyses for the g	geometric series m	odel for the ter	nebrionid commun	ities sampled in th	ree sites in the
Ulan Buh D	esert.						

	Intercept ± SE	Slope ± SE	R ²	t	Р
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	$P(\mathbf{A}=\mathbf{B})$	$P(\mathbf{A}=\mathbf{C})$	$P(\mathbf{B}=\mathbf{C})$
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

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



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

Site	Region	Coordinates	Species Richness	k	Source
Hongoryn Els	Gobi-Altai	43.46.478N 102.15.482E	7	0.450	Pfeiffer & Bayannasan (2012)
Tsogt testii	East-Gobi	43.43.087N 105.48.913E	3	0.423	Pfeiffer & Bayannasan (2012)
Nemegt	Gobi-Altai	43.27.782N 101.23.577E	8	0.393	Pfeiffer & Bayannasan (2012)
Ekhin-gol	Transaltai Gobi	43.13.890N 099.00.450E	7	0.348	Pfeiffer & Bayannasan (2012)
Tohom	Gobi-Altai	46.08.398N 094.31.362E	7	0.206	Khurelpurev & Pfeiffer (2017)
Heihe River	Gobi (Inner Mongolia)	39.24.00N, 100.07.00E	7	0.601	Liu et al. (2012)
Heihe River	Gobi (Inner Mongolia)	39.21.00N, 100.09.00E	7	0.639	Liu et al. (2015)

Table 4 – Species richness and values of the k parameter of the geometric series model for tenebrionid communities from various sites in the Gobi Desert

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 hyper-volumes 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.

Acknowledgments – We are grateful to Xiaoying Wei for her help in the fieldwork. Part of the research described in this paper was supported by Fondo per il finanziamento delle attività base di ricerca 2017 (FFABR 2017) to S. Fattorini, and supported by key project of Science-technology basic condition platform from The Ministry of Science and Technology of the People's Republic of China (Grant No. 2005DKA21402).

References

- Aldryhim Y.N., Mills III C.W., Aldawood A.S. 1992. Ecological distribution and seasonality of darkling beetles (Coleoptera: Tenebrionidae) in the central region of Saudi Arabia. Journal of Arid Environments, 23: 415–422.
- Ayal Y., Merkl O. 1994. Spatial and temporal distribution of tenebrionid species (Coleoptera) in the Negev Highlands, Israel. Journal of Arid Environments, 27: 347–361.
- Bazzaz F.A. 1975. Plant species diversity in old-field successional ecosystems in southern Illinois. Ecology, 56: 485–488.
- Chen F., Li G., Zhao H., Jin M., Chen X., Fan Y., Liu X., Wu D., Madsen D. 2013. Landscape evolution of the Ulan Buh Desert in northern China during the late Quaternary. Quaternary Research, 81: 476–487.
- Chikatunov V., Lillig M., Pavlíček T., Blaustein L., Nevo E. 1997. Biodiversity of insects at a microsite, "Evolution Can-

yon", Nahal Oren, Mt. Carmel, Israel. Coleoptera: Tenebrionidae. Journal of Arid Environments, 37: 367–377.

- Chun X., Chen F.H., Fan Y.X. 2008. Formation of Ulan Buh Desert and its environmental changes during the Holocene. Frontiers of Earth Science in China, 2: 327–332.
- Colombini I., Chelazzi M., Fallaci I., Palesse L. 1994. Zonation and surface activity in some tenebrionid beetles living on a Mediterranean sandy beach. Journal of Arid Environments, 28: 215–230.
- Dajoz R. 2002. Les Coléoptères Carabides et Ténébrionidés. Ecologie et Biologie. Lavoisier, Paris, xii + 524 pp.
- de los Santos A., 1994. Generic diversity patterns in the tenebrionid beetle communities (Col. Tenebrionidae). Ecologia Mediterranea, 20: 125–136.
- de los Santos A., Gómez-Gonzáles L.A., Alonso C., Arbelo C.D., De Nicolás J.P. 2000. Adaptive trends of darkling beetles (Col. Tenebrionidae) on environmental gradients on the island of Tenerife (Canary Islands). Journal of Arid Environments, 45: 85–98.
- de los Santos A., Alonso E.J., Hernández E., Pérez A.M. 2002a. Environmental correlates of darkling beetle population size (Col. Tenebrionidae) on the Cañadas of Teide in Tenerife (Canary Islands). Journal of Arid Environments, 50: 287– 308.
- de los Santos A., De Nicolás J.P., Ferrer F. 2002b. Habitat selection and assemblage structure of darkling beetles (Col. Tenebrionidae) along environmental gradients on the island of Tenerife (Canary Islands). Journal of Arid Environments, 52: 63–85.
- Fallaci M., Colombini I., Palesse L., Chelazzi L. 1997. Spatial and temporal strategies in realtion to environmental constraints of four tenebrionids inhabiting a Mediterranean coastal dune system. Journal of Arid Environments, 37: 45–64.
- Faragalla A.A. 1998. Seasonal occurrence and habitat distribution of tenebrionid beetles (Coleoptera: Tenebrionidae) in Khulais Valley, Western Saudi Arabia. Elytron, 12: 105– 112.
- Faragalla A. A. 1999. Habitat preference of tenebrionid beetles (Coleoptera: Tenebrionidae) in Khulais Valley, Western Saudi Arabia. Elytron, 13: 49–55.
- Fattorini S. 2005. A simple method to fit geometric series and broken stick models in community ecology and island biogeography. Acta Oecologica, 28: 199–205.
- Fattorini S. 2008. Ecology and conservation of tenebrionid beetles in Mediterranean coastal areas, pp. 165–298. In: Fattorini S. (ed.), Insect Ecology and Conservation. Research Signpost, Trivandrum.
- Fattorini S. 2009. Darkling beetle communities in two geologically contrasting biotopes: testing biodiversity patterns by microsite comparisons, Biological Journal of the Linnean Society, 98: 787–793.
- Fattorini S., Bergamaschi D., Galassi D.M.P., Biondi M., Acosta A.T.R., Di Giulio A. 2017. Spatial organization of an insect ensemble in a Mediterranean ecosystem: the tenebrionid beetles (Coleoptera Tenebrionidae) inhabiting an Adriatic coastal sand dune area. Acta Zoologica Bulgarica, 69: 201–208.
- Fattorini S., Bergamaschi D., Mantoni C., Acosta A.T.R., Di Giulio A. 2016. Niche partitioning in tenebrionid species (Coleoptera: Tenebrionidae) inhabiting Mediterranean coastal dunes. European Journal of Entomology, 113: 462–468.
- Fattorini S., Santoro R., Maurizi E., Acosta A.T.R., Di Giulio A. 2012. Environmental tuning of an insect ensemble: the tenebrionid beetles inhabiting a Mediterranean coastal dune zonation. Comptes Rendus Biologies, 335: 708–711.
- Fiori G., Crovetti A. 1972. Composizione della entomofauna e in particolare della coleotterofauna della Ghibla (Tripolitania del Sud). Redia, 3: 449–484.

- Giller P. S. 1984. Community structure and the niche. Chapman and Hall, London, 176 pp.
- Gray J.S. 1981. The Ecology of Marine Sediments. Cambridge University Press, Cambridge, 185 pp.
- Hammer Ø., Harper D.A.T., Ryan P.D. 2001. PAST Palaeontological statistics software package for education and data analysis. Version 1.89. Palaeontologia Electronica, 4: 1–9.
- Hanrahan S.A., Seely M.K. 1990. Food and habitat use by three tenebrionid beetles (Coleoptera) in a riparian desert environment, pp. 143–147. In: Seely M.K. (ed.), Namib ecology: 25 years of Namib research. Transvaal Museum Monograph No.7, Transvaal Museum, Pretoria.
- Hayek L.C., Buzas M.A. 2010. Surveying Natural Populations. Quantitative Tools for Assessing Biodiversity. Columbia University Press, New York, 616 pp.
- He F., Tang D.L. 2008. Estimating the niche pre-emption of the geometric series. Acta Oecologica, 33: 105–107.
- Holm E., Scholtz C.H. 1980. Structure and pattern of the Namib Desert dune ecosystem at Gobabeb. Madoqua, 12: 5–39.
- Keeley J.E., Fotheringham C.J. 2003. Species–area relationships in Mediterranean climate plant communities. Journal of Biogeography, 30: 1629–1657.
- Khurelpurev O., Pfeiffer M. 2017. Coleoptera in the Altai Mountains (Mongolia): species richness and community patterns along an ecological gradient. Journal of Asia-Pacific Biodiversity, 10: 362–370.
- Koch C. 1962. The Tenebrionidae of southern Africa. XXXI. Comprehensive notes on the tenebrionid fauna of the Namib Desert. Annals of the Transvaal Museum, 24: 61–106.
- Krasnov B., Ayal Y. 1995. Seasonal changes in darkling beetle communities (Coleoptera: Tenebrionidae) in the Ramon erosion cirque, Negev Highlands, Israel. Journal of Arid Environments, 31: 335–347.
- Krasnov B., Shenbrot G. 1996. Spatial structure of community of darkling beetles (Coleoptera: Tenebrionidae) in the Negev Highlands, Israel. Ecography, 19: 139–152.
- Krasnov B., Shenbrot G. 1997. Seasonal variations in spatial organisation of a darkling beetle (Coleoptera: Tenebrionidae) community. Environmental Entomology, 26: 178–190.
- Krebs C. 1999. Ecological Methodology, 2nd Edition. Benjamin Cummings, Menlo Park, 624 pp.
- Li G.Q., Jin M., Chen X.M., Wen L.J. 2015. Environmental changes in the Ulan Buh Desert, southern Inner Mongolia, China since the middle Pleistocene based on sedimentology, chronology and proxy indexes. Quaternary Science Reviews, 128: 69–80.
- Liu J.L., Li F.R., Liu C., Liu Q.J., Niu R.X. 2012. Influences of shrub vegetation on distribution and diversity of a ground beetle community in a Gobi desert ecosystem. Biodiversity and Conservation, 21: 2601–2619.
- Liu R., Zhu F., Song N., Yang X., Chai Y. 2013. Seasonal distribution and diversity of ground Arthropods in microhabitats following a shrub plantation age sequence in desertified steppe. PLoS ONE, 8: e77962.
- Liu R.T., Zhao H.L., Zhao X.Y., Drake S. 2011. Facilitative effects of shrubs in shifting sand on soil macrofaunal community in Horqin sand land of Inner Mongolia, northern China. European Journal of Soil Biology, 47: 316–321.
- Liu J., Zhao W., Li F. 2015. Effects of shrub presence and shrub species on ground beetle assemblages (Carabidae, Curculionidae and Tenebrionidae) in a sandy desert, northwestern China. Journal of Arid Land, 7: 110–121.
- Magurran A.E. 1988. Ecological diversity and its measurement, Princeton University Press, Princeton, 192 pp.
- Magurran A.E. 2004. Measuring Biological Diversity. Wiley-Blackwell, Oxford, 264 pp.
- May R. M. 1975. Patterns of species abundance and diversity, pp.

81–120. In: Cody M.L., Diamond M.J. (eds), Ecology and Evolution of Communities. Harvard University Press, Cambridge.

- McGill B.J., Etienne R.S., Gray J.S., Alonso D., Anderson M.J., Benecha H.K., Dornelas M., Enquist B.J., Green J.L., He F., Hurlbert A.H., Magurran A.E., Marquet P.A., Maurer B. A., Ostling A., Soykan C.U., Ugland K I., White E.P. 2007. Species abundance distributions: moving beyond single prediction theories to integration within an ecological framework. Ecology Letters, 10: 995–1015.
- Morris E.K., Caruso T., Buscot F., Fischer M., Hancock C., Maier T.S., Meiners T., Müller C., Obermaier E., Prati D., Socher S.A., Sonnemann I., Wäschke N., Wubet T., Wurst S., Rillig M.C. 2014. Choosing and using diversity indices: insights for ecological applications from the German Biodiversity Exploratories. Ecology and Evolution. 4: 3514– 3524.
- Nicolson S.W. 1990. Water relations of the Namib tenebrionid beetles, pp. 173–178. In: Seely M.K. (ed.), Namib ecology: 25 years of Namib research. Transvaal Museum Monograph No.7, Transvaal Museum, Pretoria.
- Nummelin M. 1998. Log-normal distribution of species abundances is not a universal indicator of rain forest disturbance. Journal of Applied Ecology, 35: 454–457.
- Pfeiffer M., Bayannasan E. 2012. Diversity and Community Pat-

tern of Darkling Beetles (Coleoptera: Tenebrionidae) along an Ecological Gradient in Arid Mongolia. Erforschung biologischer Ressourcen der Mongolei / Exploration into the Biological Resources of Mongolia, 12: 251–266.

- Ślipiński S.A., Leschen R.A.B., Lawrence J.F. 2011. Order Coleoptera Linnaeus, 1758. Animal Biodiversity: an Outline of Higher-Level Classification and Survey of Taxonomic Richness. Zootaxa, 3148: 203–208.
- Thomas D.B. 1979. Patterns in the abundance of some tenebrionid beetles in the Mojave Desert. Environmental entomology, 8: 568–574.
- Thomas D.B. 1983. Tenebrionid beetle diversity and habitat complexity in the Eastern Mojave Desert. The Coleopterists Bulletin, 37: 135–147.
- Whittaker R.H. 1965. Dominance and diversity in land plant communities. Science, 147: 250–260.
- Whittaker R H. 1972. Evolution and measurement of species diversity. Taxon, 21: 213–251.
- Yang W.B., Feng W., Jia Z.Q., Zhu Y.J., Guo J.Y. 2014. Soil water threshold for the growth of Haloxylon ammodendron in the Ulan Buh desert in arid northwest China. South African Journal of Botany, 92: 53–58.
- Yeom D.J., Kim J.H. 2011. Comparative evaluation of species diversity indices in the natural deciduous forest of Mt. Jeombong. Forest Science and Technology, 7: 68–74.