



Research article

Influence of grazing and solar panel installation on tenebrionid beetles (Coleoptera Tenebrionidae) of a central Asian steppe

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ABSTRACT

Grazing may represent a major threat to biodiversity in arid grasslands. The increasing use of grasslands for solar parks may represent a new important threat. No study has investigated the effects of solar parks on soil insects. Tenebrionids are a major component of the arthropod fauna of grasslands of central Asia. These ecosystems are threatened by grazing and increasing land use for solar parks. Aim of this work was to investigate the effects of grazing and solar panels on tenebrionids in arid grasslands (desert steppe) in China by comparing their community structure in ungrazed, heavily grazed, and solar park sites. Beetles were sampled by pitfall traps, and sites were compared for abundance and diversity (Hill numbers). All sites were characterized by simple, strongly dominated tenebrionid communities. Species proportions varied among sites. Grazing negatively influenced overall abundance, but did not alter species proportions; by contrast, solar panels had no effect on the average abundance, but reduced the proportion of the most abundant species. Compared with the other two sites, the solar park was characterized by a higher plant biomass and lower temperatures. A major availability of resources and less harsh conditions in the solar park might have a role in reducing the dominance of the most abundant species, allowing other species to attain higher abundances. This led to a more balanced community structure, with higher values of diversity. Although neither grazing nor solar panel installation modified radically tenebrionid species-abundance distribution or diversity, grazing and solar panel installation had different effects in species abundances and their impact might amplify the effect of other disturbance factors such as the ongoing climate change.

1. Introduction

Grasslands account for about 8% of Earth land (Wesche and Treiber, 2012) and therefore constitute one of the most widespread biomes worldwide. Grasslands have long been used for grazing activities, which have profoundly shaped their landscape (Fuhlendorf et al., 2006). Grazing may represent a serious threat to grassland ecosystems, since it causes alterations in water balance and soil erosion, compaction and

degradation, with detrimental effects on biodiversity, especially in areas characterized by low precipitation regimes (Dennis et al., 1998; Fuhlendorf et al. 2006; Zhu et al., 2017, 2020). As regards insect communities, livestock not only reduce resources available for insects, but also alter soil characteristics by trampling, with obvious negative effects on soil dwelling species (Weiss et al., 2013; Ruan et al., 2021). Aridity and low productivity may exacerbate these effects in insect communities of arid grassland (steppe) ecosystems.

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Recently, a new form of threat to grassland ecosystems is emerging: the increasing use of grassland areas for installation of solar panels, especially in steppe ecosystems, which are poorly suitable for other land uses like agriculture. The consequences on insect biodiversity seem to be highly variable: while the new environmental conditions established in the solar plants might even be beneficial to pollinators (Dolezal et al., 2021; Graham et al., 2021), solar plants represent ecological traps for aquatic insects attracted by polarized light (Horváth et al., 2010). To our knowledge, however, no study has investigated the effects of solar power plants on soil insects, which are an obviously important component of grassland biotas, especially in arid steppe ecosystems.

In this study, we investigated the effects of grazing and solar parks in a central Asian arid grassland (Ningxia Province, China) on tenebrionid beetles (Coleoptera, Tenebrionidae).

Tenebrionids are a diverse family of beetles, including more than 30,000 described species worldwide (Bouchard et al., 2021). Tenebrionids exploit the most disparate environments and are one of the most prominent arthropod groups in arid environments, including Mediterranean coastal areas, deserts and steppes (De Los Santos et al., 2000; Dajoz, 2002; Fattorini, 2008; Cheng et al., 2022).

In central Asia, the natural landscape is largely dominated by steppes, which provide many essential ecosystem services to the human population (Lü et al., 2011) and may constitute the last barrier before desert (Kang et al., 2007; Ren et al., 2008). Many studies investigated tenebrionid ecology in these environments (Pfeiffer and Bayannassan, 2012; Liu et al., 2012; Liu et al., 2015; Li et al., 2016; Khurelpurev and Pfeiffer, 2017; Niu et al., 2019, 2020). The influence of human-induced transformations of steppe ecosystems on their communities are, however, largely unknown.

Although grazing in the Ningxia province is legally prohibited since 2003 (Li et al., 2013; Zhou et al., 2018), there are still some farmers that bring their sheep flock for grazing. Along with this form of illegal grazing, the steppes of Ningxia province are experiencing an increasing diffusion of large solar power plants. Thus, this area offers the intriguing opportunity of comparing the effects of grazing and solar park installations on the tenebrionids of arid grasslands. To this end, we compared the tenebrionid community of ungrazed, grazed and solar park areas.

Specifically, we tested the following hypotheses:

- (1) Grazing should reduce abundance and diversity of tenebrionids because of alterations in vegetation and soil characteristics. Because of plant consumption by livestock, vegetation in grazed areas is expected to have a lower biomass, which should turn into less resources available for tenebrionids. Since the larvae of steppe tenebrionids live into the soil, they are expected to be negatively affected by compaction induced by grazing. Also, tenebrionids can be negatively affected by increased temperatures and reduced humidity determined by reduction in plant height/coverage due to grazing, since intolerable temperatures and lack of water are important limiting factors for tenebrionids of arid environments (Dajoz, 2002; Fattorini, 2008). Thus, we expect that both overall abundance (H1.1) and diversity (H1.2) of tenebrionids in the grazed site will be decreased compared to the ungrazed site as a result of the negative influence of grazing. Also, we expect changes in species proportions (H1.3), as some species would be more affected than others. Finally, we expect changes in the species-abundance distribution, with a reduction in species evenness in the grazed site compared to the ungrazed site because of increased dominance of the most resistant species (H1.4).
- (2) Solar panel installation should have a positive impact on the tenebrionid community for various reasons. First, because of shading provided by solar panels, we expect a higher vegetation biomass and hence more resources for tenebrionids, not only in comparison with the grazed site, but also in comparison with the ungrazed one. Second, shading might be beneficial to

tenebrionids by lowering temperatures and increasing humidity. Finally, being more humid and with more roots, soil in the solar panel area should be more penetrable, and hence more favorable to tenebrionid larvae. Thus, we expect that both overall abundance (H2.1) and diversity (H2.2) of tenebrionids will be higher than in the ungrazed and grazed sites. Also, we expect changes in species proportions (H2.3), as some species would be more advantaged than others by these new conditions. Finally, we expect changes in the species-abundance distribution, with a reduction of dominance of the most abundant species, and hence a higher evenness compared to the ungrazed site (H2.4).

2. Materials and methods

2.1. Study area

The present study was carried out in the Yanchi county (Ningxia Hui Autonomous Region), near Gaoshawo and Sidunzi villages (about 1400 m a.s.l.) (Fig. 1). This area is occupied by an arid steppe ecosystem known as “desert steppe” (Sun, 2005), characterized by a cold semi-arid continental monsoonal climate. Monthly average temperatures vary between -8°C in January to 22°C in July (annual average: 8.3°C), whereas monthly precipitation ranges from 2 mm in December to 78 mm in August (annual average: 287 mm) (Kang et al., 2007; Tsafack et al., 2019). Vegetation is dominated by *Stipa* spp., *Agropyron* spp. and *Allium polyrhizum* Turcz. ex Regel (Sun, 2005; Lü et al., 2011; Tsafack et al., 2019).

The study area is characterized by patches still subject to intensive sheep grazing (Nan et al., 2018), areas protected from grazing, and large areas occupied by photovoltaic panel parks.

2.2. Sampling design and insect identification

The study was conducted in a photovoltaic power station (Ningxia Gaoshawo solar park: $37^{\circ}58'24.35''\text{N}$ - $107^{\circ}01'41.99''\text{E}$) and in two grassland sites representative of undisturbed (ungrazed: $37^{\circ}45'51.52''\text{N}$ - $107^{\circ}16'50.22''\text{E}$) and highly grazed ($37^{\circ}44'59.08''\text{N}$ - $107^{\circ}17'52.76''\text{E}$) grasslands. The Ningxia Gaoshawo solar park was opened in September 2016 and occupies an area of about 20 km². In each site, we took five sampling points at least 200 m apart, and in each sampling point we placed four pitfall traps separated by at least 100 m from each other, for a total of 20 traps per site. Pitfall traps were made of plastic cups (diameter: 7.15 cm, depth: nine cm) dug into the ground and filled with 60 ml of a solution of vinegar, sugar, 70% alcohol and water (in the following proportion: 2:1:1:20). Pitfall traps were put down once a month in mid-month, from April to August 2019, and collected five days later. In total, we obtained 300 pitfall trap samples (60 traps \times 5 sampling dates: 100 samples per site). The location of the traps remained constant over the entire sampling period and no trap was damaged or lost during the study. Trap content was sorted in the laboratory and tenebrionids identified to species level using Guodong and Youzhi (1999), specialized literature and museum voucher specimens with the assistance of expert taxonomists (see Acknowledgments). All material is preserved in the insect collections of the School of Agriculture of Ningxia University.

For an environmental characterization of the study sites, we collected the following data in a 1 m² quadrat frame: plant dry biomass (g/m²), plant height (average height of plants in the quadrat frame), plant cover (proportion of soil covered by plants), soil temperature (using a portable multiparametric probe TRS-II, Zhejiang Tuopu Instrument Co. Ltd., Hangzhou City, China; accuracy of $\pm 0.5^{\circ}\text{C}$) and soil bulk density (as described in Tsafack et al., 2019) (Table S1, Fig. S1).

2.3. Data analysis

Differences among sites in plant biomass, plant height, plant cover,

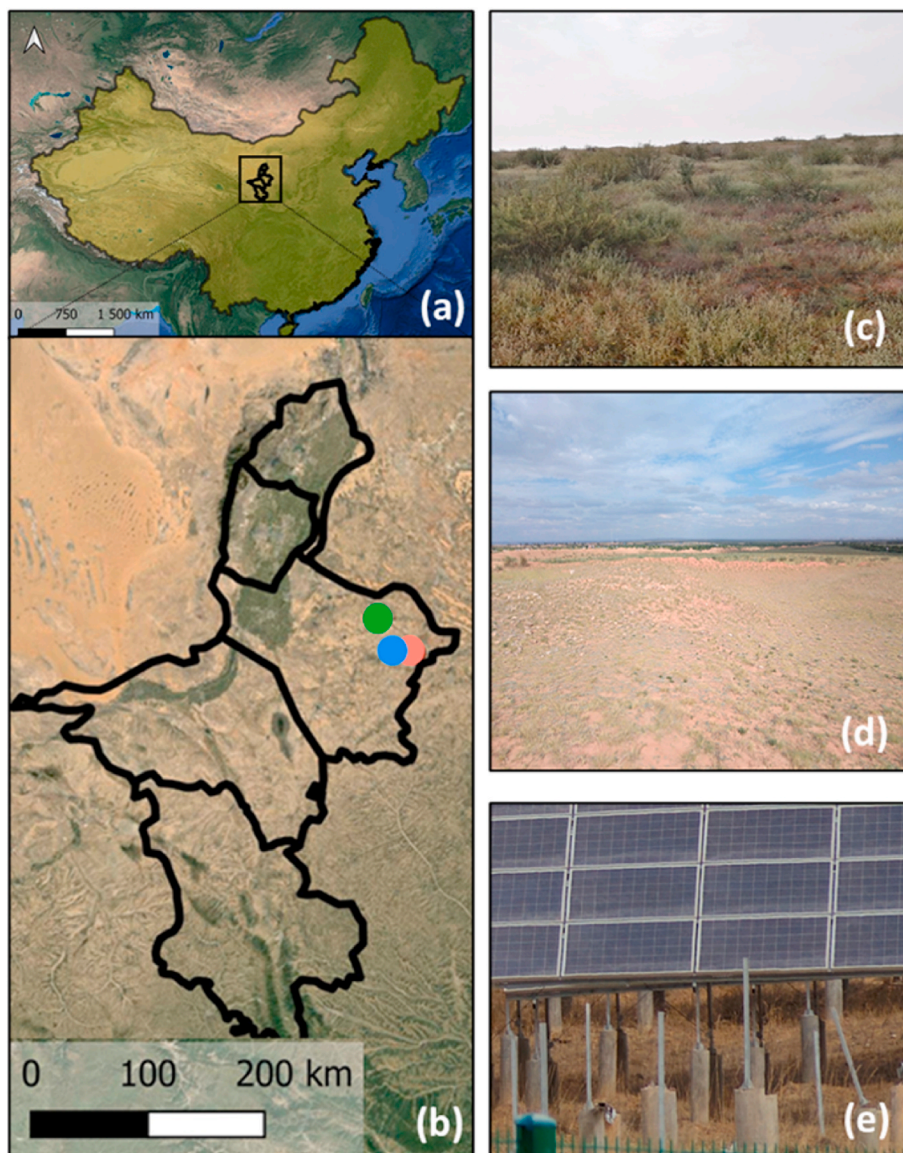


Fig. 1. Study area and sampling sites selected to investigate the effects of grazing and solar panel installation on tenebrionid beetles in a central Asian steppe. Panel (a) indicates the location of the Ningxia Province within China. Panel (b) shows the position of the sampling sites within the Ningxia Province (with administrative subdivisions). Panel (c) shows the landscape of the undisturbed (ungrazed) site used as a reference. Panel (d) shows the heavily grazed steppe. Panel (e) shows the investigated solar park. Colours of dots in panel (b) indicate the ungrazed site (blue), the grazed site (red) and the solar park (green). Satellite images of panels (a) and (b) from Google Earth. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

soil temperature and soil bulk density were tested using linear mixed-effects models with site as a fixed effect and sampling point as a random effect, using the `lme` function of the `nlme` package in R 4.0.3 (R Core Team, 2021) according to the model: `site characteristics ~ site`, `random = ~1|sampling point`. Linear mixed-effects models were followed by Analysis of Variance (ANOVA, with the `anova` function) and Tukey tests using the R package `multcomp`. For plant cover, which is expressed as proportions, we used the logit transformation as suggested by Warton and Hui (2011).

We modelled tenebrionid species abundance distribution patterns at the three sites using the geometric series model (Fattorini, 2005) as tenebrionids of arid ecosystems conform to this model (Fattorini and Carpaneto, 2001; Fattorini, 2008; Fattorini et al., 2012, 2016, 2017; Niu et al., 2019, 2020). The geometric series expresses the so-called “niche pre-emption” hypothesis, in which the sizes of niche hypervolumes (measured as species abundances) are determined by certain species that pre-empt part of the niche space, leaving the remaining species to occupy the rest. Thus, the niche hypervolume is sequentially pre-empted by the most abundant to the least abundant species. The first, most dominant species in the sequence occupies a fraction k of the resource hypervolume, the second species a fraction k of hypervolume not occupied by the first, and so on (Giller, 1984; Fattorini, 2005; McGill et al., 2007). In

the rank-abundance plot, if the abundances are logarithmically transformed and the species are ranked from the most to the least abundance, a geometric series exactly follows a strength line, which can be fitted using an Ordinary Least Squares regression (Fattorini, 2005). Higher slopes indicate more unbalanced communities, with slopes decreasing at increasing evenness. We used the coefficient of determination r^2 as a measure of goodness-of-fit of the regressions modelling the rank-abundance plots and the Analysis of Covariance (ANCOVA, with the R function `aov`) to test for homogeneity of their slopes.

We investigated species similarity among sites and level of nestedness, i.e. the degree to which tenebrionid assemblages of sites with fewer species are subsets of successively larger assemblages. Species similarity between sites was evaluated by using the Dice-Sørensen coefficient of similarity, which ranges from 0 (no shared species between two sites) to 1 (the two sites have the same species), putting more weight on joint occurrences than on mismatches. Nestedness was tested using the software `NeD` (Strona et al., 2014) with spectral radius as a metric (Staniczenko et al., 2013) and the proportional-proportional algorithm (which is preferred when the scale of analysis is small; Ulrich and Gotelli, 2012) to generate 100 random matrices.

To determine if there is an association between species and habitat (i.e., if species abundances varied among sites) we applied a χ^2 test to a

species × site contingency table.

We compared sites for differences in tenebrionid diversity using Hill numbers. Hill numbers qD are a mathematically unified family of indices which are all expressed in the same units (i.e., effective number of species), being therefore comparable between each other (Schalk, 1987; Liu et al., 2015). We compared diversity of the three sites for the following three orders of taxonomic diversity: $q = 0$ (which returns species richness), $q = 1$ (which produces the exponential of Shannon entropy and expresses the effective number of frequent species in the assemblage), and $q = 2$ (which corresponds to the inverse of the Simpson index of concentration and hence expresses the effective number of highly frequent species in the assemblage) (Chao et al., 2014, 2020). In the following, we use the expression “Shannon diversity” to indicate this exponential version of the index. Since diversity estimates are influenced by the number of sampled individuals, in addition to the observed values we calculated for each sample asymptotic estimates using the functions ChaoRichness for $q = 0$, ChaoShannon for $q = 1$, and Chao-Simpson for $q = 2$ (Chao et al., 2014). We omitted trap samples with zero individuals from the calculation of Shannon diversity and those with fewer than two individuals from Simpson diversity, as these indices are undefined under such circumstances.

Observed and asymptotic values of richness, Shannon diversity and Simpson diversity were then used as response variables in generalized linear mixed models (GLMMs). In GLMMs, the independent variables were sites (with ungrazed as reference) and month (with April as reference), with traps nested into sites as a random factor. Calculations were done using the *glmmTMB* R package with the model: diversity measure ~ site*month+(1|site/trap). The *r.squaredGLMM* function of the *MuMIn* R package was used to calculate the r^2 explained by fixed and random factors. For observed richness, we used a Poisson link, whereas a Gaussian one was assumed for the other measures of diversity. The same GLMM approach was applied to test for differences in tenebrionid abundance; in this case, a Poisson distribution was adopted. The R library *ggplot2* was used for graphs.

3. Results

The three investigated sites showed significant differences in plant biomass and soil temperature, whereas they did not differ in plant cover (Table 1, Fig. S1). The solar park had a higher biomass than the ungrazed and grazed sites, which did not differ from each other (Table 1, Fig. S1). Average temperature was highest in the grazed site, lowest in the solar park, and intermediate in the ungrazed site. Significant differences were found for plant height, which was higher in the solar park than in the grazed site, and for soil bulk density, which was lower in the solar park than in the grazed site (Table 1, Fig. S1).

Ten species of tenebrionids were collected (Fig. 2, Table S1). Three species (*Blaps femoralis* [Fischer von Waldheim, 1844], *Microdera kraatzii* [Reitter, 1889] and *Anatolica amoenula* [Reitter, 1889]) represented together 94% of the collected individuals (Fig. 2); separately, they represented 45%, 37% and 12% of the overall abundance, respectively (Table S1). *M. kraatzii* was the most abundant species in the solar park site, representing 55% of the total abundance (Fig. 2). *B. femoralis* was the most abundant species in both the ungrazed and the grazed sites, representing respectively 70% and 58% of the total abundance (Fig. 2). Overall, species composition between sites (Table S1) was very similar (Dice-Sørensen coefficient of similarity, DSC, between grazed and ungrazed: 0.933; DSC between ungrazed and solar park: 0.823; DSC between grazed and solar park: 0.875) and clearly nested (spectral radius: 4.694, Z-score = 2.387, $P < 0.01$). However, a significant association between species abundance and sites ($\chi^2 = 279.849$, $df = 18$, $P < 0.001$) indicates that species have different habitat preferences, with solar park showing an increased abundance of *M. kraatzii* and a reduction of *B. femoralis* in comparison with grazed and ungrazed sites, which supports our hypothesis (H2.3) of a reduction in the proportion of the most dominant species in the solar park. By contrast, there was no

Table 1

ANOVA tables of mixed effect models with plant biomass, plant height, plant cover, soil temperature and soil bulk density as dependent variables in three biotopes in a central Asian steppe: an ungrazed (undisturbed) site, a heavily grazed site, and a solar park. Plant cover was logit-transformed. According to Tukey tests, average plant biomass in solar park was significantly higher than in the ungrazed ($P < 0.0001$) and grazed ($P < 0.0001$) sites, whereas temperatures differed significantly in the order grazed > ungrazed > solar park (difference between grazed and ungrazed $P = 0.033$; difference between ungrazed and solar park $P < 0.001$; difference between grazed and solar park $P < 0.001$). Higher plant height in solar park than in grazed site was marginally significant ($P = 0.064$). Lower soil bulk density in the solar park than in the grazed site was marginally significant ($P = 0.060$).

	numDEF	denDF	F-value	P
Plant biomass				
Intercept	1	45	105.830	<0.0001
Biotope	2	12	26.943	<0.0001
Plant height				
Intercept	1	45	113.990	<0.0001
Biotope	2	12	2.564	0.118
Plant cover				
Intercept	1	45	0.820	0.370
Biotope	2	12	0.186	0.832
Soil temperature				
Intercept	1	45	5896.791	<0.0001
Biotope	2	12	42.255	<0.0001
Soil bulk density				
Intercept	1	45	8556.572	<0.0001
Biotope	2	12	2.736	0.105

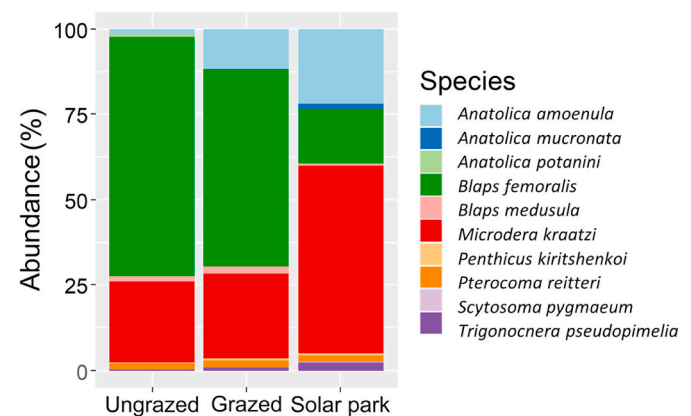


Fig. 2. Proportional abundance of tenebrionid beetle species collected in three biotopes in a central Asian steppe: an ungrazed site, a heavily grazed site and a solar park.

support for the hypothesis of a substantial change in species proportions under grazing disturbance (H1.3).

The goodness-of-fit statistics of the OLS regression lines indicated that the geometric series fitted adequately all three species communities (Table 2, Fig. 3). The slopes of the three regression lines were not significantly different (ANCOVA for homogeneity of slopes: $F_{(2,18)} = 0.772$, $P = 0.477$). This means that, contrary to our expectation, neither grazing (H1.4) nor solar panel installation (H2.4) changed the overall species-abundance distribution model.

Tenebrionid abundance in the grazed site and in the solar park was lower than that observed in the ungrazed site, although the difference

Table 2

Regression parameters (slope and intercept), goodness of fit (R^2), t -value (t) and probability (P) of geometric series models for the tenebrionid communities sampled in three biotopes in a central Asian steppe: an ungrazed (undisturbed) site, a heavily grazed site, and a solar park. For each model, the niche pre-emption parameter k is also reported. Errors refer to standard errors.

	Slope	Intercept	T	P	R^2	k
Ungrazed	-0.322 ± 0.053	2.316 ± 0.269	-6.046	<0.001	0.856	0.524
Grazed	-0.361 ± 0.029	2.450 ± 0.128	-12.643	<0.0001	0.970	0.565
Solar Park	-0.291 ± 0.026	2.482 ± 0.147	-11.105	<0.0001	0.946	0.488

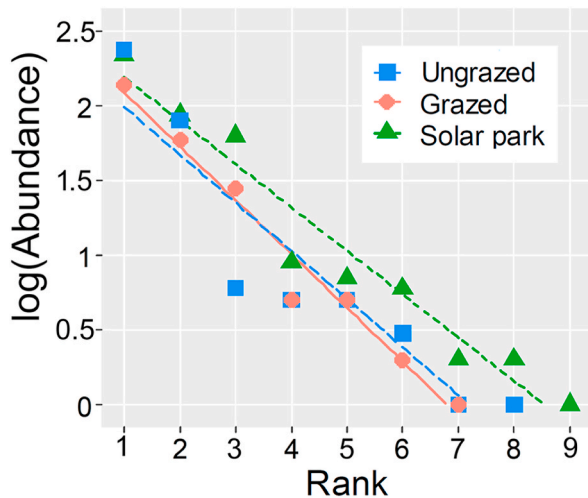


Fig. 3. Rank-abundance plot of the tenebrionid beetles inhabiting three biotopes in a central Asian steppe: an ungrazed (undisturbed) site, a heavily grazed site, and a solar park. Species are ranked from the most to the least abundant (x-axis). Species abundances are log-transformed (y-axis). Data were fitted using OLS regressions.

between the ungrazed site and the solar park was negligible ($P = 0.05$, Table 3, Fig. 4 a). This is in agreement with our hypothesis that grazing reduces abundance (H1.1), but does not support our claim of a positive

Table 3

Results of generalized linear mixed models for species abundance of tenebrionids sampled from April to August in three biotopes in a central Asian steppe: an ungrazed (undisturbed) site (used as reference), a heavily grazed site and a solar park. Variance explained by fixed effects: Marginal $R^2 = 0.76$. Variance explained by the entire model: Conditional $R^2 = 0.80$.

	Estimate	Std. Error	Z-value	P
Habitat				
Intercept	2.01	0.137	14.691	<0.0001
Grazed	-1.07	0.223	-4.794	<0.0001
Solar Park	-0.39	0.201	-1.959	0.050
Month				
May	-0.44	0.129	-3.430	<0.001
June	-1.35	0.177	-7.596	<0.0001
July	-1.30	0.174	-7.464	<0.0001
August	-3.09	0.386	-7.998	<0.0001
Interaction				
Grazed \times May	1.10	0.214	5.119	<0.0001
Grazed \times June	1.39	0.263	5.266	<0.0001
Grazed \times July	0.78	0.286	2.734	<0.001
Grazed \times August	0.53	0.647	0.813	0.420
Solar Park \times May	1.04	0.177	5.887	<0.0001
Solar Park \times June	0.91	0.237	3.837	<0.001
Solar Park \times July	0.12	0.267	0.452	0.650
Solar Park \times August	0.06	0.599	0.094	0.930

effect of solar panels on overall abundance (H2.1). The observed number of species was lower in the grazed site than in the ungrazed site (as expected by our hypothesis H1.2), whereas the difference between ungrazed site and solar park was not significant (which does not support our hypothesis of a positive effect H2.2) (Table 4, Fig. 4 b). However, estimated species richness (asymptotic values of Chao1 estimator) was higher in the solar park than in the ungrazed site, as expected under our hypothesis of a positive effect (H2.2), whereas there was no difference between the ungrazed site and the grazed site, which contrasts with our hypothesis (H1.2) (Table S2, Fig. S2 a). Thus, Chao1 varied among sites in the order: solar park $>$ grazed site \approx ungrazed site, which is in partial agreement with our expectations. Observed values of Shannon and Simpson diversity were marginally significantly higher in the solar park than in the ungrazed site as expected under our hypothesis (H2.2) (Tables 5 and 6, Fig. 4 c, d), whereas this difference disappeared when using estimated values (Tables S3 and S4, Fig. S2 b and c).

Tenebrionid abundance varied across months, decreasing from spring to summer (Fig. 5). However, we found a significant interaction between sites and months in all cases except August, which had the lowest abundances (Table 3, Fig. 5 a). In the ungrazed site, April had a higher abundance than May and the other months, whereas in the grazed site and in the solar park the pattern was reversed (Fig. S3 a). Thus, both grazing and solar panel installation reduced the activity of tenebrionids in April. Also, it appears that differences in tenebrionid abundances between May and June were strongly reduced by grazing, which supports our hypothesis (H1.1). Tenebrionid richness also varied across months, decreasing from spring to summer (Fig. 5 b). Interaction between sites and months was significant only for the grazed site in June (Table 4, Fig. S3 b). Grazing strongly reduced richness in April, whereas panel installation had a strong effect in July, which contrasts with our hypothesis (H2.2). Shannon or Simpson diversity varied across months without any obvious trend. Diversity was high between April and May, then decreased in June, increased again in July, and finally dropped in August (Fig. 5 c, d). Grazing reduced both Shannon and Simpson diversity (as expected under our hypothesis H1.2), while solar park increased these indices (as expected under our hypothesis H2.2), although not significantly (Tables 5 and 6). We found that interaction between sites and month was significant only for Simpson diversity in June (Tables S3 and S5, Fig. S3 b, c). Results with estimated values were similar (Tables S3 and S4, Fig. S4 b, c, Fig. S5 b, c).

4. Discussion

The number of tenebrionid species found in our sampling sites (7–9) is consistent with values of species richness reported from other central Asian areas with similar environmental conditions: 1–12 species in 16 sites in the Gobi desert (Mongolia) (Pfeiffer and Bayannassan, 2012); 3–10 species in seven sites in the Altai Mountains (Mongolia) (Khurulpurev and Pfeiffer, 2017); seven species in an artificial oasis in the western Gansu Province (north-western China) (Li et al., 2016); seven species in a near desert area (Liu et al., 2012); seven species in a sandy desert ecosystem in the middle reaches of the Heibe River (north-western China) (Liu et al., 2015); 6–8 species in two sites in the Gobi Desert (Inner Mongolia) (Niu et al., 2019). Thus, we are confident that our sampling was virtually complete and provided a clear representation of the tenebrionid diversity of the study sites.

Tenebrionid communities of arid ecosystems are characterized by a high dominance of a few species attaining large abundance values (Thomas, 1983; Aldryhim et al., 1992; Ayal and Merkl, 1994; Niu et al., 2019, 2020), and this situation can be also found in our study system, as shown by the high values of the goodness of fit provided by the geometric series model.

The observed values of the slopes of the regression lines obtained in this study (from -0.36 to -0.29) are consistent with those recorded for the tenebrionid communities of two sites in the Gobi Desert (-0.36 and -0.24 , Niu et al., 2019) and similar to those calculated for

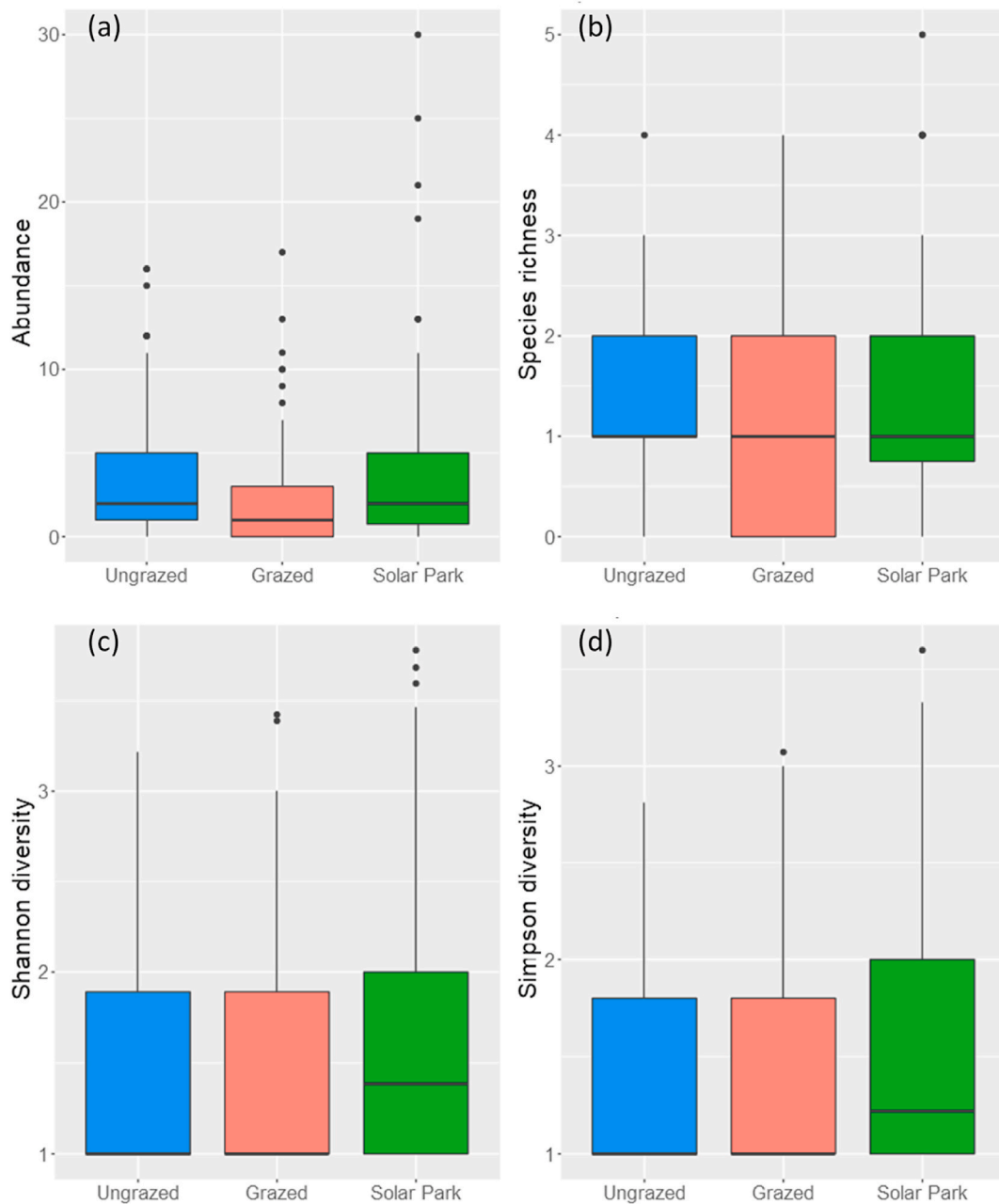


Fig. 4. Boxplots (median, interquartile range, range [$1.5 \times$ interquartile range from the hinges] and outliers) of tenebrionid abundance (number of individuals, a), richness (number of species, b), Shannon diversity (c), and Simpson diversity (d) in three biotopes in a central Asian steppe: an ungrazed (undisturbed) site, a heavily grazed site, and a solar park.

Mediterranean beach-dune systems (-0.29 to -0.25 ; Fattorini, 2008; Fattorini et al., 2017). The lack of differences in the slopes of the regression lines of the three compared sites indicates that the investigated communities have an analogous pattern of species abundance distribution and that the resource hyperspace is divided in a similar way in the three communities. Thus, contrary to our expectations (H2.4), the impact of grazing and solar panel installation did not alter the main mechanism (pre-emption) that shapes species abundance distribution in more natural conditions (ungrazed site). The parameter k , which expresses the sequential, constant fraction of the total number of individuals in a community, ranged between 0.5 and 0.6. This indicates a rather sharp decline in the species niche hypervolumes, as expected for communities where resources are divided according to the pre-emption model. Overall, the observed k values are consistent with those recorded for tenebrionid communities from the Gobi Desert ($k = 0.6$; Niu et al.,

2019, 2020) and Mediterranean dune ecosystems ($k = 0.4$ – 0.5 ; Fattorini et al., 2016, 2017). Thus, the communities of the three study sites are characterized by low richness and high dominance, as already observed for tenebrionid communities of other arid ecosystems (Fattorini and Carpaneto, 2001; Fattorini, 2008; Fattorini et al., 2012, 2016, 2017; Niu et al., 2019, 2020), which suggests a similar response to harsh conditions, with no substantial effect of grazing or solar park installation on the basic mechanisms that regulate the species abundance distributions.

Although species composition between sites was very similar, proportional species abundances varied between sites, as we expected (hypotheses H1.3 and H2.3). It has been found that even close sites with similar tenebrionid species composition can show strong differences in proportional abundances if they are environmentally different (Fattorini, 2009). Also, even in sites with similar environmental conditions, species composition and ensemble organization, the most dominant

Table 4

Results of generalized linear mixed models for species richness of tenebrionids sampled from April to August in three biotopes in a central Asian steppe: an ungrazed (undisturbed) site (used as reference), a heavily grazed site and a solar park. Variance explained by fixed effects: Marginal $R^2 = 0.30$. Variance explained by the entire model: Conditional $R^2 = 0.30$.

	Estimate	Std. Error	z value	P
Habitat				
Intercept	0.62	0.164	3.742	<0.0001
Grazed	-0.57	0.273	-2.073	0.040
Solar Park	0.22	0.221	0.986	0.320
Month				
May	-0.11	0.239	-0.478	0.630
June	-0.67	0.282	-2.361	0.020
July	-0.62	0.278	-2.217	0.030
August	-1.82	0.440	-4.133	<0.0001
Interaction				
Grazed × May	0.60	0.367	1.627	0.100
Grazed × June	0.92	0.405	2.264	0.020
Grazed × July	0.57	0.418	1.355	0.180
Grazed × August	0.16	0.701	0.230	0.820
Solar Park × May	-0.00	0.322	-0.002	0.990
Solar Park × June	0.10	0.374	0.257	0.800
Solar Park × July	-0.32	0.393	-0.822	0.410
Solar Park × August	-0.40	0.645	-0.621	0.530

Table 5

Results of generalized linear mixed models for Shannon diversity of tenebrionids sampled from April to August in three biotopes in a central Asian steppe: an ungrazed (undisturbed) site (used as reference), a heavily grazed site and a solar park. Variance explained by fixed effects: Marginal $R^2 = 0.18$. Variance explained by the entire model: Conditional $R^2 = 0.20$.

	Estimate	Std. Error	z value	P
Habitat				
Intercept	1.66	0.149	11.145	<0.0001
Grazed	-0.21	0.231	-0.925	0.355
Solar Park	0.41	0.210	1.955	0.051
Month				
May	0.02	0.205	0.106	0.916
June	-0.61	0.205	-2.962	0.003
July	-0.36	0.216	-1.651	0.099
August	-0.68	0.295	-2.289	0.022
Habitat × Month				
Grazed × May	0.25	0.305	0.825	0.409
Grazed × June	0.60	0.305	1.953	0.051
Grazed × July	0.23	0.320	0.704	0.481
Grazed × August	0.20	0.467	0.434	0.665
Solar Park × May	-0.25	0.286	-0.867	0.386
Solar Park × June	-0.19	0.288	-0.649	0.516
Solar Park × July	-0.34	0.312	-1.082	0.279
Solar Park × August	0.29	0.492	0.588	0.557

species can be not the same (Niu et al., 2019). This is the case of the solar park site, where *M. kraatzii* was two times more abundant, and *B. femoralis* four times less abundant, than in the grazed and ungrazed sites. We can hypothesize that habitat alterations induced by solar panels might have had a negative impact on *B. femoralis* but favoured *M. kraatzii*. It is interesting to note that *B. femoralis* is 16–22 mm long, whereas *M. kraatzii* is 8.5–11 mm long (Guodong and Youzhi, 1999). Thus, a reduction in the abundance of a large consumer might have favoured that of a smaller one. Since competition is not considered a major driver of tenebrionid community organization (Fattorini et al., 2016), further research is needed to test this hypothesis.

Tenebrionid abundance was depressed by both grazing (as expected according to our hypothesis H1.1) and solar panel installation (contrary to expectation H2.1), although the effect of solar panels was subtle, which indicates that grazing has a much higher detrimental effect on tenebrionid abundance than solar panel installation. Results for species richness, Shannon diversity and Simpson diversity are partially in agreement with our hypotheses of negative effects.

Table 6

Results of generalized linear mixed models for Simpson diversity of tenebrionids sampled from April to August in three biotopes in a central Asian steppe: an ungrazed (undisturbed) site (used as reference), a heavily grazed site and a solar park. Variance explained by fixed effects: Marginal $R^2 = 0.17$. Variance explained by the entire model: Conditional $R^2 = 0.19$.

	Estimate	Std. Error	z value	P
Habitat				
Intercept	1.57	0.137	11.522	<0.0001
Grazed	-0.16	0.211	-0.737	0.460
Solar Park	0.37	0.193	1.908	0.060
Month				
May	0.02	0.186	0.117	0.910
June	-0.52	0.186	-2.807	0.010
July	-0.29	0.196	-1.498	0.130
August	-0.59	0.268	-2.201	0.030
Habitat × Month				
Grazed × May	0.19	0.277	0.669	0.500
Grazed × June	0.50	0.277	1.803	0.070
Grazed × July	0.17	0.290	0.579	0.560
Grazed × August	0.14	0.424	0.335	0.740
Solar Park × May	-0.22	0.260	-0.854	0.390
Solar Park × June	-0.19	0.261	-0.736	0.460
Solar Park × July	-0.28	0.283	-0.979	0.330
Solar Park × August	0.34	0.446	0.757	0.450

Grazing had a significant negative effect on the observed value of richness, but this effect disappeared using estimated values, whereas solar panel installation did not affect observed richness, but had a marginally significant positive effect on estimated richness. These contrasting results between observed and estimated values of diversity suggest a potential influence of abundance. It is possible that, by reducing abundance, grazing increases species rarity, and hence the probability of a species to be collected in a trap, which leads to a depression of species richness. As asymptotic values express the potential number of sampled species in a scenario of maximized sampling intensity (Colwell et al., 2012), they virtually remove the influence of the lower probability of catching rare species due to depressed abundances. This might have led to the lack of a negative effect of grazing on estimated values of richness. Solar panel installation had only a slight negative impact on abundance, and hence no effect on the average richness. In this case, the use of estimated values might have disclosed subtle differences in species richness that do not appear in the observed values.

Grazing did not affect Shannon and Simpson diversity, both using the observed values and the estimated ones. Solar panel installation had a marginal significant positive effect on observed values of Shannon and Simpson diversity, whereas these effects disappeared using estimated values. By reducing the abundances, the solar panel installation reduced the difference in species abundance values per sample, which led to increased values of observed Shannon and Simpson diversity. Use of estimated values removes the consequences of this reduction in species abundances, leading to the disappearance of the effect found on observed values. We are not aware of other studies that highlighted these possible problems in the use of estimated values, a subject that needs further investigation.

An overall trend of decreasing abundance and richness from spring to summer reflects the increasing harsher conditions due to higher temperatures in summer months, since the activity of tenebrionids of arid environments is negatively influenced by increased temperatures (Dajoz, 2002; Fattorini, 2008). However, we detected differences among sites, with environmental alterations (grazing and solar panels) having a strong negative impact on abundance in April. It is not clear why these forms of environmental alterations reduce abundance and richness at the beginning of the activity period of the species, and it is possible that different causes are involved, including tenebrionid reactions to too low temperature. Activity rhythms of tenebrionid of arid environments is inhibited by too low temperatures (Dajoz, 2002; Fattorini, 2008). In

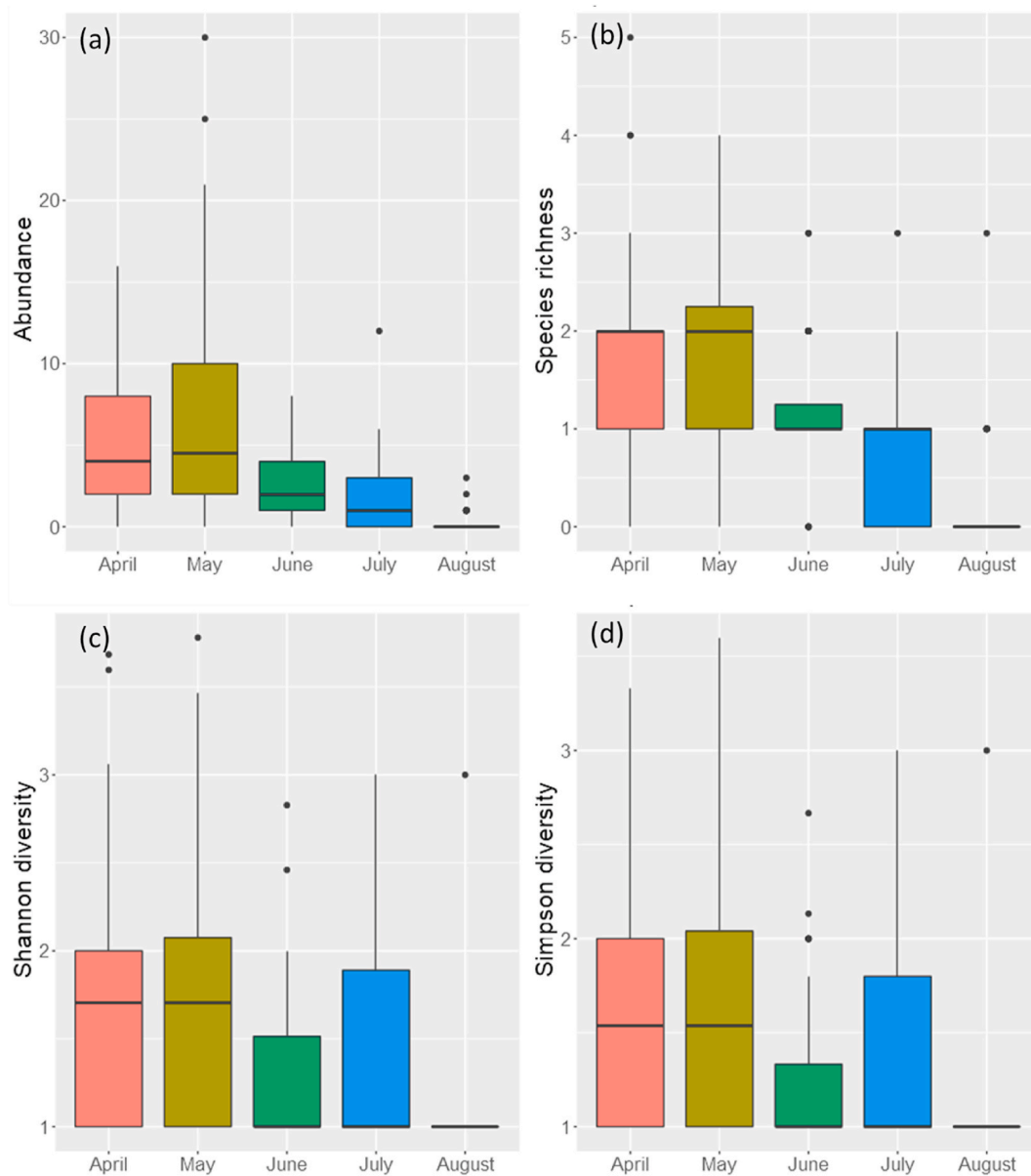


Fig. 5. Boxplots (median, interquartile range, range [$1.5 \times$ interquartile range from the hinges] and outliers) of tenebrionid abundance (number of individuals, a), richness (number of species, b), Shannon diversity (c), and Simpson diversity (d) in different sampling periods in a central Asian steppe.

April, temperatures in spoiled areas subject to intense grazing might be too low during the night, whereas in the solar park they might be low even in daytime because of shading. A more detailed investigation on tenebrionid response to daily variation in temperatures would be helpful.

5. Conclusions

Neither grazing nor solar park installation modified radically the community structure of tenebrionid beetles of the study ecosystem, which was characterized by a simple structure with strong dominance of few species, also in undisturbed contexts. This is consistent with previous findings in other central Asian arid steppes, and more in general in arid environments, where tenebrionids form simple, highly dominated communities. However, grazing and solar panel installation had different effects in species abundances. Grazing negatively influenced the overall abundance, but did not alter profoundly species proportions; by contrast, solar panels had a negligible effect on the average abundance, but a more important impact on species proportions, by reducing

the proportion of the species that was the most dominant in the other two sites. Compared with the other two sites, the solar park was characterized by a higher plant biomass and lower temperatures. A major availability of resources and less harsh conditions might have a role in reducing the dominance of the most abundant species, allowing other species to attain higher abundances. This led to a more balanced community structure, with higher values of diversity. Paradoxically, this change seems to be obscured when asymptotic estimators are used, because asymptotic estimators virtually remove the influence of species abundance differences in the probability of detecting species that became rarer due to habitat alteration. This potential bias in the use of estimators needs, however, further investigation. Our study suggests that neither grazing (at least if it is not too intensive) nor solar panel installations represent an immediate threat to tenebrionid conservation in arid steppes. However, our study was conducted three years after the installation of the solar panels and was based on a single year sampling period. In order to fully understand the impact of solar power plants, further studies should be done to investigate their influence on insect communities at different time laps after their installation and adopt

long-term monitoring to test the robustness of our findings. This is particularly important because the impact of grazing and solar panel installation might amplify the effect of other factors such as those associated with the climate change. This is the first study that investigated the impact of solar panels on a group of ground dwelling insects, the tenebrionid beetles, in a type of ecosystem (arid steppes) where this form of human exploitation is rapidly increasing. Given the simplicity of collecting tenebrionid beetles by pitfall trapping, our study might be easily replicated, adapted to other contexts or modified to test particular hypotheses (for example, changes in the liquid used to attract/preserve beetles). It would be important in the future to develop similar analyses for other groups of ground dwelling insects to corroborate the observed patterns. It would be also important to extend similar analyses in other types of ecosystems worldwide where solar panel installations are common.

Author contribution

Project design: NT, YX, Xinpu W and SF; methodology: NT and SF; data collection: NT, WF, Xingyu W, YX, Xinpu W; data analysis: NT and SF; paper writing - original draft preparation: NT and SF; writing - review and editing: NT, SF, WF, Xingyu W, YX, Xinpu W; supervision: SF; funding acquisition: NT and SF.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.jenvman.2022.115791>.

References

Aldryhim, Y.N., Mills, C.W., Aldawood, A.S., 1992. Ecological distribution and seasonality of darkling beetles (Coleoptera: Tenebrionidae) in the central region of Saudi Arabia. *J. Arid Environ.* 23, 415–422.

Ayal, Y., Merkl, O., 1994. Spatial and temporal distribution of tenebrionid species (Coleoptera) in the Negev Highlands, Israel. *J. Arid Environ.* 27, 347–361.

Bouchard, P., Bousquet, Y., Aalbu, R.L., Alonso-Zarazaga, M.A., Merkl, O., Davies, A.E., 2021. Of genus-group names in the family Tenebrionidae (Insecta, Coleoptera). *ZooKeys* 1050, 1–633.

Chao, A., Gotelli, N.J., Hsieh, T.C., Sander, E.L., Ma, K.H., Colwell, R.K., et al., 2014. Rarefaction and extrapolation with Hill numbers: a framework for sampling and estimation in species diversity studies. *Ecol. Monogr.* 84, 45–67.

Chao, A., Kubota, Y., Zelený, D., Chiu, C.-H., Li, C.-F., Kusumoto, B., et al., 2020. Quantifying sample completeness and comparing diversities a 498 mong assemblages. *Ecol. Res.* 35, 292–314.

Cheng, L., Tong, Y., Zhao, Y., Sun, Z., Wang, X., Fangzhou, M., et al., 2022. Study on the relationship between richness and morphological diversity of higher taxa in the darkling beetles (Coleoptera:Tenebrionidae). *Diversity* 14, 60.

Colwell, R.K., Chao, A., Gotelli, N.J., Lin, S.-Y., Mao, C.X., Chazdon, R.L., et al., 2012. Models and estimators linking individual-based and sample-based rarefaction, extrapolation and comparison of assemblages. *J. Plant Ecol.* 5, 3–21.

Dajoz, R., 2002. Les Coléoptères Carabides et Ténébrionidés. Lavoisier, Paris.

De Los Santos, A., Gómez-González, 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). *J. Arid Environ.* 45, 85–98.

Dennis, P., Young, M.R., Gordon, I.J., 1998. Distribution and abundance of small insects and arachnids in relation to structural heterogeneity of grazed, indigenous grasslands. *Ecol. Entomol.* 23, 253–264.

Dolezal, A.G., Torres, J., O'Neal, M.E., 2021. Can solar energy fuel pollinator conservation? *Environ. Entomol.* 50, 757–761.

Fattorini, S., 2005. A simple method to fit geometric series and broken stick models in community ecology and island biogeography. *Acta Oecol.* 28, 199–205.

Fattorini, S., 2008. Ecology and conservation of tenebrionid beetles in Mediterranean coastal areas. In: *Insect Ecology and Conservation*. Kerala, India, pp. 165–297.

Fattorini, S., 2009. Darkling beetle communities in two geologically contrasting biotopes: testing biodiversity patterns by microsite comparisons. *Biol. J. Linn. Soc.* 98, 787–793.

Fattorini, S., Carpaneto, G.M., 2001. Tenebrionid density in Mediotyrrhenian coastal dunes: habitat and temporal variations (Coleoptera, Tenebrionidae). *Fragm. Entomol.* 33 (1), 97–118.

Fattorini, S., Santoro, R., Maurizi, E., Acosta 532, A.T.R., Di Giulio, A., 2012. Environmental tuning of an insect ensemble: the tenebrionid beetles inhabiting a Mediterranean coastal dune zonation. *Comptes Rendus Biol.* 335, 708–711.

Fattorini, S., Bergamaschi, D., Mantoni, C., Acosta, T.R.A., Di Giulio, A., 2016. Niche partitioning in tenebrionid species (Coleoptera: Tenebrionidae) inhabiting Mediterranean coastal dunes. *Eur. J. Entomol.* 113, 462–468.

Fattorini, S., Bergamaschi, D., Galassi, D., Biondi, M., Acosta, A., Giulio, A.D., 2017. Spatial organisation of an insect ensemble in a Mediterranean ecosystem: the Tenebrionid beetles (Coleoptera: Tenebrionidae) inhabiting an Adriatic Coastal sand dune area. *Acta Zool. Bulg.* 201–208.

Fuhlendorf, S.D., Harrell Wade, C., Engle David, M., Hamilton Robert, G., Davis Craig, A., Leslie David, M., 2006. Should heterogeneity be the basis for conservation? Grassland bird response to fire and grazing. *Ecol. Appl.* 16, 1706–1716.

Giller, P.S., 1984. Community Structure and the Niche. Chapman and Hall.

Graham, M., Ates, S., Melathopoulos, A.P., Moldenke, A.R., DeBano, S.J., Best, L.R., et al., 2021. Lateral shading by solar panels delays bloom, increases floral abundance during the late-season for pollinators in a dryland, agrivoltaic ecosystem. *Sci. Rep.* 11, 7452.

Guodong, R., Youzhi, Y., 1999. Tenebrionidae from the Arid and Semi-arid Region of China. HebeiUniversity Press, Baoding, China.

Horváth, G., Blahó, M., Egri, Á., Kriska, G., Seres, I., Robertson, B., 2010. Reducing the maladaptive attractiveness of solar panels to polarotactic insects. *Conserv. Biol.* 24, 1644–1653.

Kang, L., Han, X., Zhang, Z., Sun, O.J., 2007. Grassland ecosystems in China: review of current knowledge and research advancement. *Phil. Trans. R. Soc. B Biol. Sci.* 362, 997–1008.

Khurelpurev, O., Pfeiffer, M., 2017. Coleoptera in the Altai Mountains (Mongolia): species richness and community patterns along an ecological gradient. *J. Asia Pac. Biodivers.* 10, 362–370.

Li, J., Yang, X., Jin, Y., Yang, Z., Huang, W., Zhao, L., et al., 2013. Monitoring and analysis of grassland desertification dynamics using Landsat images in Ningxia, China. *Rem. Sens. Environ.* 138, 19–26.

Li, F.-R., Liu, J.-L., Sun, T.-S., Ma, L.-F., Liu, L.-L., Yang, K., 2016. Impact of established shrub shelterbelts around oases on the diversity of ground beetles in arid ecosystems of Northwestern China. *Insect Conserv. Divers.* 9, 135–148.

Liu, J.-L., Li, F.-R., Liu, C.-A., Liu, Q.-J., 2012. Influences of shrub vegetation on distribution and diversity of a ground beetle community in a Gobi desert ecosystem. *Biodivers. Conserv.* 21, 2601–2619.

Liu, J.-L., Zhao, W., Li, F.-R., 2015. Effects of shrub presence and shrub species on ground beetle assemblages (Carabidae, Curculionidae and Tenebrionidae) in a sandy desert, northwestern China. *J. Arid Land* 7, 110–121.

Lü, Y., Fu, B., Wei, W., Yu, X., Sun, R., 2011. Major ecosystems in China: dynamics and challenges for sustainable management. *Environ. Manag.* 48, 13–27.

McGill, B.J., Etienne, R.S., Gray, J.S., Alonso, D., Anderson, M.J., Benecha, H.K., et al., 2007. Species abundance distributions: moving beyond single prediction theories to integration within an ecological framework. *Ecol. Lett.* 10, 995–1015.

Nan, L., Dong, Z., Xiao, W., Li, C., Xiao, N., Song, S., et al., 2018. A field investigation of wind erosion in the farming–pastoral ecotone of northern China using a portable wind tunnel: a case study in Yanchi County. *J. Arid Land* 10, 27–38.

Niu, Y., Ren, G., Lin, G., Di Biase, L., Fattorini, S., 2019. Community structure of tenebrionidbeetles in the Ulan Buh Desert (Inner Mongolia, China) (Coleoptera: Tenebrionidae). *Fragm. Entomol.* 51, 193–200.

Niu, Y., Ren, G., Lin, G., Di Biase, L., Fattorini, S., 2020. Fine-scale vegetation characteristics drive insect ensemble structures in a desert ecosystem: the

- tenebrionid beetles (Coleoptera: Tenebrionidae) inhabiting the Ulan Buh Desert (Inner Mongolia, China). *Insects* 11, 410.
- Pfeiffer, M., Bayannassan, E., 2012. Diversity and community pattern of darkling beetles (Coleoptera: Tenebrionidae) along an ecological gradient in arid Mongolia. In: *Erforschung Biologischer Ressourcen der Mongolei/Exploration into the Biological Resources of Mongolia*. Halle & Wittenberg, Germany, pp. 251–266.
- R Core Team, 2021. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.
- Ren, J.Z., Hu, Z.Z., Zhao, J., Zhang, D.G., Hou, F.J., Lin, H.L., et al., 2008. A grassland classification system and its application in China. *Rangel. J.* 30, 199–209.
- Ruan, H., Wu, X., Wang, S., Yang, J., Zhu, H., Guo, Q., et al., 2021. The responses of different insect guilds to grassland degradation in northeastern China. *Ecol. Indic.* 133, 108369.
- Schalk, Louw, 1987. Species Composition and Seasonality of Pitfall Trapped Coleoptera at a Site in the Central Orange Free State, South 566 Africa, vol. 5. Navorsing van die Nasionale Museum : Researches of the National Museum.
- Staniczenko, P., Kopp, J., Allesina, S., 2013. The ghost of nestedness in ecological networks. *Nat. Commun.* 4, 1391.
- Strona, G., Galli, P., Seveso, D., Montano, S., Fattorini, S., 2014. Nestedness for Dummies (NeD): a user friendly web interface for exploratory nestedness analysis. *J. Stat. Software* 59. Code Snippet 3.
- Sun, H.-L., 2005. *Ecosystems of China*. Science Press, Beijing, China.
- Thomas Jr., D.B., 1983. Tenebrionid beetle diversity and habitat complexity in the Eastern Mojave desert. *Coleopt. Bull.* 37, 135–147.
- Tsafack, N., Rebaudo, F., Wang, H., Nagy, D.D., Xie, Y., Wang, 600, X., et al., 2019. Carabid community structure in northern China grassland ecosystems: effects of local habitat on species richness, species composition and functional diversity. *PeerJ* 6, e6197.
- Ulrich, W., Gotelli, N.J., 2012. A null model algorithm for presence–absence matrices based on proportional resampling. *Ecol. Model.* 244, 20–27.
- Warton, D.I., Hui, F.K.C., 2011. The arcsine is asinine: the analysis of proportions in ecology. *Ecology* 92, 3–10.
- Weiss, N., Zucchi, H., Hochkirch, A., 2013. The effects of grassland management and aspect on Orthoptera diversity and abundance: site conditions are as important as management. *Biodivers. Conserv.* 22, 2167–2178.
- Wesche, K., Treiber, J., 2012. Abiotic and biotic determinants of steppe productivity and performance – a view from central Asia. In: Werger M.J.A., Staalduinen M.A van (Eds.), *Eurasian Steppes. Ecological Problems and Livelihoods in a Changing World*. Springer Netherlands, Dordrecht, pp. 3–43.
- Zhou, L., Wang, Y., Yang, G., 2018. Study on the timely adjustment of the grazing prohibition policy: ban or lift? Empirical research from local government managers. *Sustainability* 10, 616–4852.
- Zhu, H., Qu, Y., Zhang, D., Li, J., Wen, M., Wang, D., et al., 2017. Impacts of grazing intensity and precipitation on a grasshopper assemblage (Orthoptera: Acrididae) in a meadow steppe. *Ecol. Entomol.* 42, 458–468.
- Zhu, H., Nkurunziza, V., Wang, J., Guo, Q., Ruan, H., Wang, D., 2020. Effects of large herbivore grazing on grasshopper behaviour and abundance in a meadow steppe. *Ecol. Entomol.* 619 45, 1357–1366.