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Interactive effects of vegetation and soil determine the composition and diversity of carabid and tenebrionid functional groups in an arid ecosystem

Ji-Liang Liu [a], Feng-Rui Li [a, b, *], Te-Sheng Sun [b], Ling-Fa Ma [b], Lu-Lu Liu [b], Kun Yang [b]

[a] Linze Inland River Basin Research Station, Cold and Arid Regions Environmental and Engineering Research Institute, Chinese Academy of Sciences, Lanzhou 730000, China
[b] Laboratory of Ecology and Agriculture, Cold and Arid Regions Environmental and Engineering Research Institute, Chinese Academy of Sciences, Lanzhou 730000, China

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ABSTRACT

The community dynamics of ground beetles as a dominant group in arid ecosystems are strongly affected by land-use change associated alterations in vegetation and soil conditions. However, little is known about the relative effects of altered vegetation and soil, or their interactions, on the composition and diversity of beetle functional groups. To address this question, we collected data on the species richness and activity abundance of ground carabid and tenebrionid beetle functional groups (predators, herbivores, and detritivores), along a gradient of land-use conversion from natural grassland to pure and mixed plantations of two shrub species (*Haloxylon ammodendron* and *Tamarix ramosissima*) in an arid region of northwestern China. Additionally, we collected key variables related to the vegetation (shrub cover, height, herbaceous plant biomass, and species richness) and soil (soil pH, texture, and salinity). Variation partitioning showed that vegetation changes had stronger effects on the functional group composition than changes in the soil did. However, vegetation–soil interactions explained more of the composition variation in the beetle functional groups than vegetation or soil alone. Shrub cover and herbaceous species richness were the best predictors of species composition of detritivores and herbivores. For predator species composition, shrub height and cover were the best predictors. Structural equation models showed that changes in vegetation and soil influenced beetle abundance and diversity through both direct and indirect effects, and the strength of this influence varied among the functional groups. Overall, we conclude that vegetation and vegetation–soil interactions are important determinants of beetle community assemblies.

1. Introduction

Beetles, especially three groups of ground-dwelling beetles (Carabidae, Scarabaeidae, and Tenebrionidae), comprise one of the most conspicuous and predominant groups of arthropods in the Asian steppes and deserts (Konstantinov et al., 2009). Many ground-dwelling beetle species are restricted to arid ecosystems (Paknia et al., 2013), where they play key functional roles in processes such as pollination (Steffan-Dewenter et al., 2001), pest control (Suenaga and Hamamura, 2001; Zaller et al., 2009), seed dispersal (Andresen and Feer, 2005; Griffiths et al., 2015), and the decomposition of dung and dead organic material (Wu and Sun, 2010). In addition, they serve as food sources for insectivorous birds, mammals, and arthropods (Jennings and Pocock, 2009). The magnitude of these functional roles is critically linked to the beetle abundance, diversity, and community composition.

The temperate arid regions of northwestern China, which occupy approximately 2 million km^2, are experiencing extensive land-use and land-cover changes due to anthropogenic activities. These activities include land reclamation for urban and agricultural development (Chen, 2008; Wang et al., 2010), and land-cover conversion from natural to planted vegetation (Li et al., 2014). Artificial oases, which account for approximately 5% of the arid

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* Corresponding author. Linze Inland River Basin Research Station, Cold and Arid Regions Environmental and Engineering Research Institute, Chinese Academy of Sciences, Lanzhou 730000, China.
E-mail address: lifengrui@lzb.ac.cn (F.-R. Li).

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land, are the main sites of agriculture and human settlement (Wang and Liu, 2013). Conservation of these ecologically fragile oasis habitats generally consists of surrounding the human-inhabited oases with 500–1000 m wide protective shrub shelterbelts (Chang et al., 2014). Over the past few decades, natural grassland at the margins of many arid region oases have been converted into structurally simple shrub shelterbelts through oasis conservation programs (Pan and Chu, 2012). Because this conversion alters the vegetation type, cover, and structure, the subsequent alterations in surface albedo and other biogeophysical parameters can change the microclimate and soil properties as well (Bright, 2015).

Ground beetles are a dominant component of the soil food web in China's temperate arid ecosystems (Liu et al., 2012; Ren and Yu, 1999). Their abundance, diversity, and community composition can be affected by alterations in vegetation and soil conditions caused by land-use and land-cover change. Over the past decades, ecologists have assessed the effects of land-use change associated changes in plants, soils, and other environmental factors on beetle diversity and community composition (Antvogel and Bonn, 2001; Pakeman and Stockan, 2014; Parmenter et al., 1989; Pétillon et al., 2008; Ruggiero et al., 2009; Schweiger et al., 2005; Slobodchikoff, 1983; Stapp, 1997; Woodcock et al., 2010). However, a complete understanding of the direct and indirect effects of different environmental variables on ground beetle diversity and community composition patterns, and how these effects may vary among ground beetle functional groups at different trophic levels, is still lacking. Different ground beetle functional groups are expected to respond differently to land-use change induced alterations in vegetation and soil, largely because of differences in their trophic position (Van Nouhuys, 2005), and different ecological requirements (Homburg et al., 2014). It is therefore important to quantify the relative effects of altered vegetation and soil conditions on beetle community structure, especially in terms of different functional groups. This will enable us to predict the impacts of anthropogenic environmental changes on local ground beetle community assemblages better.

Overall, the bottom-up effects of plant community composition, productivity, and diversity on arthropod communities have been well documented for a broad range of arthropod taxa, including beetles, spiders, ants, mites, and springtails (Andow, 1991; Barton et al., 2016; Botha et al., 2015; Brose, 2003; Haddad et al., 2009; Harvey et al., 2008; Koricheve et al., 2000; Sabais et al., 2011; Schaffers et al., 2008; Scherber et al., 2010; Siemann, 1998; Wenninger and Inouye, 2008; Zou et al., 2013). Nonetheless, such relationships have been hardly investigated for different functional groups of ground beetles, especially in the temperate arid ecosystems of northwestern China.

For this study, we collected data on the species richness and activity abundance of ground carabid and tenebrionid beetle functional groups (predators, herbivores, and detritivores), along an existing gradient of land-use change in an arid region of northwestern China. Simultaneously, we collected key vegetation variables (shrub cover, shrub height, herbaceous plant biomass, and herbaceous species richness) and soil variables (soil pH, soil texture, and salinity). The gradient in this study included four land-use types: planted stands of a long-lived shrub species (*Haloxylon ammodendron* or *Tamarix ramosissima*), a mixed plantation of both species, and the natural, pre-conversion, grassland. The main objectives of this study were (1) to identify how the species composition of three beetle functional groups is affected by land-use change associated changes in plants and soils, using variation partitioning; (2) to investigate the direct and indirect effects of these vegetation and soil variables on the activity abundance and species richness of the beetle functional groups, using structural equation models. More specifically, we expected that (1) the relative effects of vegetation and soil variables on the structure of beetle communities would vary among the functional groups, and that (2) the strength and direction of the direct and indirect effects of vegetation and soil variables on beetle abundance and diversity would vary across the different functional beetle groups as well.

2. Materials and methods

2.1. Study area

The study was conducted in a temperate arid region in the western Gansu Province, northwestern China (39°21′ N, 100°07′ E; 1384 m a.s.l.; Fig. 1). The study area has a continental arid climate, with a mean annual temperature of 7.6 °C (mean monthly temperature ranges from −10.4 °C in January to 23.9 °C in July). Mean annual precipitation is 117.0 mm, with 12.6%, 28.4%, 19.1%, and 16.6% of annual rainfall occurring in June, July, August, and September, respectively (data from the meteorological station of the Linze Inland River Basin Research Station, Chinese Ecosystem Research Network, 1995–2014). Furthermore, the mean annual pan evaporation is approximately 2390 mm, which is 20 times higher than the annual precipitation. Finally, the area's soil is classified as grey-brown desert soil, developed on gravelly diluvial-alluvial materials of denuded monadnock, and the natural vegetation is a shrub-dominated desert steppe (Zhang and Shao, 2014).

2.2. Sampled sites

The overall study site is an artificial oasis zone, called the Linze oasis, which covers approximately 6000 km^2. This zone consists of several small, isolated oases, three of which were chosen for this study (Fig. 1). The three oases ranged in size from 600 to 800 km^2. The four major land-cover types were selected at the margins of each oasis, and consisted of planted *H. ammodendron* stands (HAP; 21 years old), planted *T. ramosissima* stands (TRP; 20 years old), a mixed plantation of both shrub species (MP; 20–21 years old), and the original natural grassland (NG). Distances between the four habitats in each oasis ranged from 500 to 1000 m.

The sampled NG patches were dominated by the shrub species *Calligonum mongolicum*, *Nitraria sphaerocarpa*, and *Nitraria sibirica*, along with herbaceous species such as *Bassia dasyphylla*, *Halogeton glomeratus*, *Agriophyllum squarrosum*, and *Echinops gmelinii*. The sampled HAP, TRP, and MP stands were planted with seedlings from the local nursery; they were irrigated for three years after planting, but not after that. Once established, these deep-rooted shrubs can survive as long as current-year precipitation and the plants' access to groundwater are sufficient (Tian et al., 2014; Zhang et al., 2011). The herbaceous layer in HAP was dominated by *B. dasyphylla*, *Halogeton arachnoideus*, *Salsola ruthenica*, *Chloris virgata*, and *A. squarrosum*. The herbaceous layer in TRP was dominated by *Onopordum acanthium*, *H. arachnoideus*, *B. dasyphylla*, *Peganum harmala*, *Atriplex centralasiatica*, *Mulgedium tataricum*, and *Cynanchum chinense*. Finally, the herbaceous layer in MP was dominated by *H. arachnoideus*, *S. ruthenica*, *B. dasyphylla*, *Eragrostis minor*, *C. virgate*, *Corispermum hyssopifolium*, *E. gmelinii*, *Phragmites australis*, *Chenopodium album*, *A. squarrosum*, *Artemisia desterorum*, and *C. chinense*.

2.3. Sampling of ground-dwelling beetles

We sampled ground-dwelling beetles with pitfall traps. In each oasis, three 30 m × 50 m plots, located at least 100 m apart, were established in each of the four habitats. In each plot, 10 pitfall traps filled with 75% ethanol as a lethal and preservative agent were placed. Five traps per plot were placed beneath the shrubs, and five

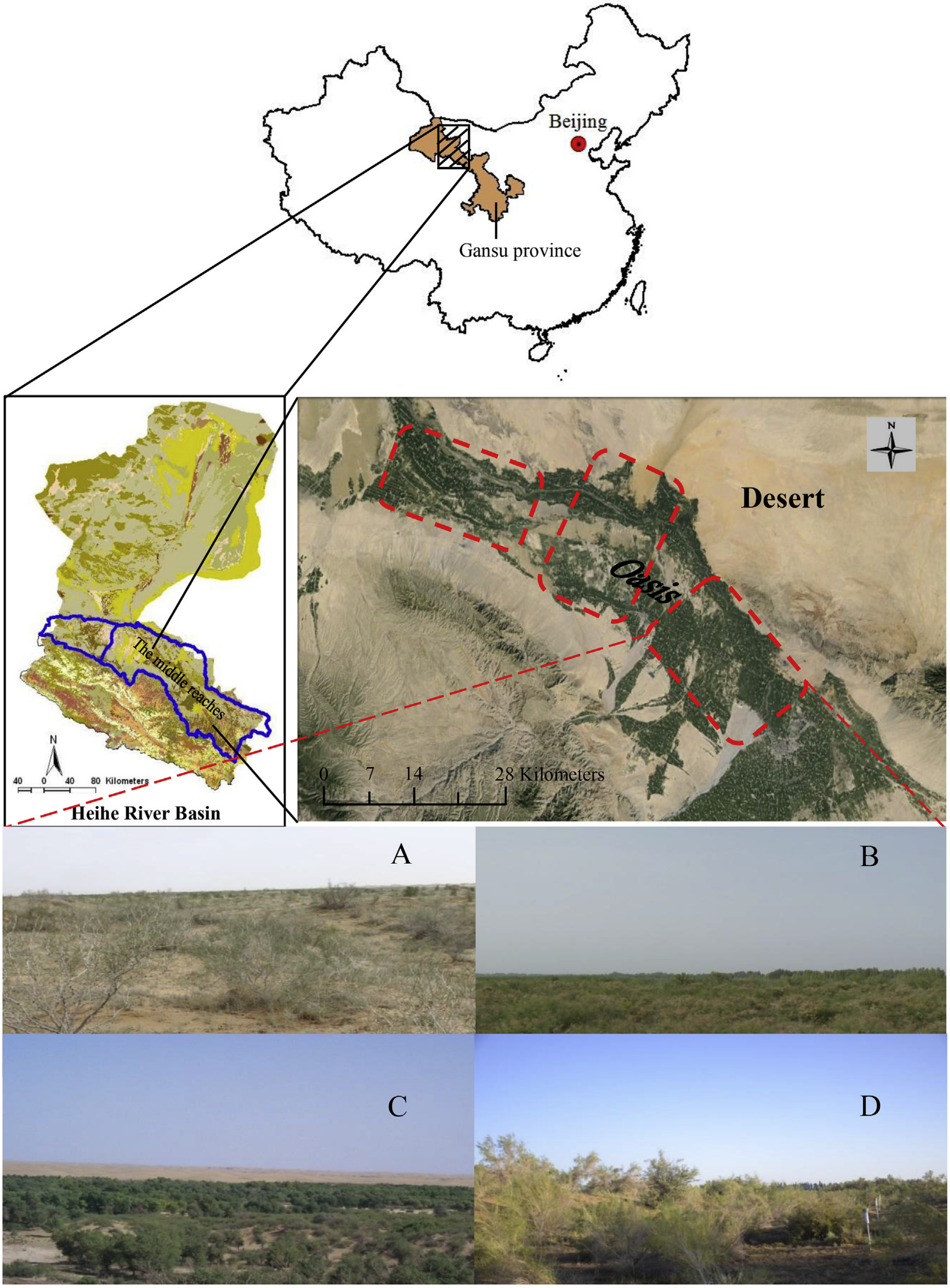


Fig. 1. The study area is located in the middle reaches of the Heihe River Basin, in the western Gansu Province, northwestern China. Pictures show the landscapes of the four studied habitat types: A) natural grassland, B) planted monoculture stand of Tamarix ramosissima, C) planted monoculture stand of Haloxylon ammodendron, and D) planted stand of T. ramosissima and H. ammodendron mixed.

in the open areas between the shrubs. In total, we placed 90 traps in each habitat, and 360 traps in the overall study. Each trap consisted of two cups, an outer permanent cup made of PVC pipe (8.5 cm × 20.0 cm) buried level with the soil surface, and a removable plastic cup inside the PVC pipe. Traps were set in the spring (May 8–15) and summer (August 10–17) of 2012. The traps were emptied at the end of each week-long sampling period, and specimens were preserved in 70% ethanol in a sealed jar.

The captured beetles were counted and identified to the species or genus level (Ren and Yu, 1999; Ren and Ba, 2010; Wang et al., 2008; Zheng and Gui, 1999). Although more than 10 beetle families were recorded, we selected the families Carabidae and Tenebrionidae, which were well represented by pitfall trappings before (Spence and Niemela, 1994). The remaining families were excluded from further analysis. The carabid and tenebrionid species (see Appendix A) were subsequently categorized to one of three functional groups (predators, herbivores, and detritivores/omnivores), based on field observations (Liu et al., 2010) and literature (Lawrence et al., 1999; Liang and Yu, 2000; Ren and Ba, 2010; Wang et al., 2008; Zhang, 2005).

2.4. Measurements of vegetation and soil variables

We measured vegetation and soil variables that are known to affect beetle distribution and activity patterns in all plots in late August 2012, the time of year when plant biomass and diversity are highest (Liu et al., 2010). Plot shrub cover was determined with the line intercept method (Mueller-Dombois and Ellenberg, 1974). Furthermore, shrub height per subplot was determined on five randomly selected shrubs, by measuring their height from the ground surface to the highest point of the plant. Average canopy size of the same shrubs was determined by averaging their long and short canopy diameters (Li et al., 2005). The cover of the herbaceous understory layer was estimated visually, using five 1-m^2 subplots that were located at least 8 m apart. In addition, we identified and counted all herbaceous plant species. Furthermore, the herbaceous plant biomass was determined by clipping all herbaceous plants per subplot at 2–3 cm above the ground. The harvested samples were oven-dried at 80 °C for 24 h and weighed afterwards.

After the aboveground plant harvest from these subplots, we took 10 cm deep soil cores, using a 5-cm diameter soil auger. The five soil cores from each plot were pooled and mixed thoroughly to form one composite sample. Roots and stones were removed by sieving the soils with a 2-mm mesh, and the resulting composite samples were analyzed for soil pH, particle size distribution, and electrical conductivity. Soil pH was determined with a pH meter in a 2:5 soil:water solution (Mettler Toledo 320-S, Mettler-Toledo Instruments Co. Ltd., Shanghai, China), whereas soil electrical conductivity was determined with a conductivity meter in a 1:5 soil:water solution (DDSJ-308A, INESA Scientific Instrument Co. Ltd., Shanghai, China). Furthermore, particle size distribution was determined with a particle size analyzer (Microtrac S3500, Microtrac Inc., USA). The pooled sample's percentage of coarse sand (2.0–0.25 mm), fine sand (0.25–0.05 mm), and silt plus clay (<0.05 mm) was subsequently calculated per air-dried soil weight.

2.5. Statistical analyses

For the three functional groups of beetles, we considered their activity abundance (number of individuals in each plot), and species richness (number of species in each plot) as response variables. The explanatory variables included four plant-related parameters, which were shrub cover (SC), shrub height (SH), herbaceous plant biomass (HPB), and herbaceous species richness (HSR). We additionally included three soil-related parameters as explanatory variables, which were soil pH (pH), soil sand (coarse plus fine sand) content (SSC; as a proxy of soil texture), and soil electrical conductivity (EC; as a proxy of soil salinity). One-way ANOVAs were used to test for the effects of habitat type on the response and explanatory variables. Post-hoc Tukey's tests were used for multiple comparisons, with a significance level of $P < 0.05$. Data were log $(x + 1)$-transformed prior to analysis, in order to meet the ANOVA assumptions of normality and equal variance. All analyses were conducted using SPSS Statistics for Windows, Version 17.0 (Chicago, SPSS Inc.).

Structural equation modeling (SEM) was used to quantify the magnitude and direction (i.e., positive or negative) of the direct and indirect effects of the seven explanatory variables on the response variables of the three beetle functional groups (Grace, 2006). A direct effect indicates how much a response variable changes in response to changes in an explanatory variable, with all other explanatory variables being controlled for. This corresponds to the standardized direct path coefficient in the SEM model (Shipley, 2009). An indirect effect indicates how much an explanatory variable influences a response variable by affecting one or more other explanatory variables. This corresponds to the standardized indirect path coefficients in the SEM model. As a result, the total effect of an explanatory variable is the sum of its indirect and direct effects, which corresponds to the net effect, or trade-off between the direct and indirect effects. With the results of the individual analyses, an SEM diagram was generated, depicting the magnitude and direction of all significant direct and indirect effects on the activity abundance and species richness per functional group. These analyses were performed using the AMOS version 17.0 software package (Arbuckle, 2007).

Furthermore, variance partitioning was used to quantify the relative contribution of the vegetation and soil variables to the variation in the beetle functional group composition, and to identify key drivers of changes in these compositions. First, separate variance partitioning analyses were performed, in order to assess the relative contribution of each of the seven explanatory variables. The relative contribution of each explanatory variable was determined by considering all other explanatory variables as covariates.

Second, to quantify the relative importance of changes in vegetation and soil, the seven explanatory variables were grouped into two groups: one for vegetation (SC, SH, HSR, and HPB), and one for soil (pH, SSC, and EC). Subsequently, separate variance partitioning analyses for these two groups were conducted to determine their relative contribution (i.e., conditional effects) to the variation in beetle functional group assemblage composition. The conditional effects of the vegetation variables were calculated by considering the soil variables as covariates, and *vice versa*. The significance of both the individual explanatory variables and the conditional effects was tested by a permutation test, performed on the relevant pRDA. Data were log $(x + 1)$-transformed before analysis. These analyses were performed using the CANOCO version 5.0 software package (Ter Braak and Šmilauer, 2012).

3. Results

3.1. Variations in vegetation, soil properties, and beetle functional groups

The conversion of NG to HAP, TRP, and MP resulted in significant changes in vegetation and soil properties (Table 1). Shrub cover and height were significantly lower in the NG habitat than in the HAP, TRP, and MP sites, respectively. The number of herbaceous plant species in NG sites was similar to that in HAP sites, but significantly higher than for TRP, and lower than for MP sites. Furthermore, herbaceous plant biomass was consistently significantly higher in

Table 1
Vegetation variables, soil variables, and the performance of three beetle functional groups in natural grassland (NG), and after conversion from natural grassland to planted stands of pure Haloxylon ammodendron plantation (HAP), pure Tamarix ramosissima plantation (TRP), and mixed plantation of both shrub species (MP). F represents the F-values from one-way ANOVAs performed on the variables for the different habitats.

Variables	NG	HAP	TRP	MP	*F*
Vegetation and soil variables					
Shrub cover (%)	15.8 ± 0.6^c	51.0 ± 3.2^a	57.4 ± 3.7^a	30.3 ± 0.9^b	123.59^{***}
Shrub height (m)	0.9 ± 0.1^c	2.2 ± 0.2^b	3.2 ± 0.1^a	2.1 ± 0.1^b	87.94^{***}
Herbaceous species richness (number of species m^{-2})	2.1 ± 0.1^b	1.9 ± 0.1^b	1.4 ± 0.1^c	4.3 ± 0.1^a	110.46^{***}
Herbaceous plant biomass (g m^{-2})	67.3 ± 5.6^a	31.4 ± 2.3^c	1.5 ± 0.3^d	44.1 ± 2.5^b	329.98^{***}
Soil pH_{water}	9.05 ± 0.04^a	8.7 ± 0.1^b	8.4 ± 0.1^c	8.8 ± 0.1^{ab}	16.12^{***}
Soil sand content (2–0.05 mm, %)	98.8 ± 0.1^a	98.7 ± 0.1^a	97.3 ± 0.2^b	96.7 ± 0.2^b	55.33^{***}
Soil electrical conductivity (μs cm^{-1})	108.9 ± 4.7^c	264.5 ± 19.6^b	411.3 ± 33.5^a	244.2 ± 15.6^b	109.57^{***}
Performance of beetle functional groups					
Detritivores					
Number of individuals $plot^{-1}$	52.0 ± 4.7^a	1.8 ± 0.2^b	1.3 ± 0.2^b	50.5 ± 3.1^a	509.95^{***}
Number of species $plot^{-1}$	6.0 ± 0.0^a	4.2 ± 0.2^b	4.3 ± 0.2^b	6.4 ± 0.2^a	30.88^{***}
Herbivores					
Number of individuals $plot^{-1}$	1.8 ± 0.1^b	0.7 ± 0.2^c	1.2 ± 0.2^{bc}	3.8 ± 0.5^a	28.77^{***}
Number of species $plot^{-1}$	2.9 ± 0.1^{ab}	2.6 ± 0.2^b	3.4 ± 0.2^a	2.8 ± 0.1^b	5.49^{**}
Predators					
Number of individuals $plot^{-1}$	0.7 ± 0.1^a	0.1 ± 0.1^b	0.2 ± 0.1^b	0.1 ± 0.1^b	26.14^{***}
Number of species $plot^{-1}$	2.0 ± 0.0^a	1.2 ± 0.3^a	2.0 ± 0.5^a	1.1 ± 0.4^a	$2.31^{n.s.}$

Means (±standard error) with different letters in each variable indicate significant differences among habitats ($^{***}P < 0.001$, $^{**}P < 0.01$, $^{n.s.}P > 0.05$).

Table 2
Results from structural equation models (SEM), quantifying the magnitude and direction (positive or negative) of direct, indirect, and total effects of the seven explanatory variables on the activity abundance and species richness of the sampled carabid and tenebrionid beetle functional groups. Explanatory variables included shrub cover (SC), shrub height (SH), herbaceous plant biomass (HPB), herbaceous species richness (HSR), soil pH (pH), soil sand content (SSC), and soil electrical conductivity (EC). Significant direct effects ($P < 0.05$) are shown in bold.

Explanatory	Effects on activity abundance			Effects on species richness		
Variables	Direct	Indirect	Total	Direct	Indirect	Total
Detritivorous beetles						
SC	−**0.473**	−0.356	−0.829	−0.179	−0.124	−0.303
SH	−0.061	−0.713	−0.774	−**0.422**	−0.167	−0.589
HPB	−0.094	0.840	0.746	−0.272	0.833	0.561
HSR	**0.468**	0.250	0.718	**0.510**	0.105	0.615
SSC	−0.251	0.165	−0.086	−0.294	0.076	−0.218
pH	−0.067	0.733	0.666	−0.210	0.662	0.452
EC	−**0.439**	−0.322	−0.761	−**0.441**	−0.125	−0.566
Herbivorous beetles						
SC	−0.030	−0.356	−0.386	−0.073	0.128	0.055
SH	−**0.367**	0.072	−0.295	−**0.405**	0.527	0.122
HPB	−**0.477**	0.817	0.340	−**1.336**	0.797	−0.539
HSR	**0.584**	0.015	0.599	0.205	−0.353	−0.148
SSC	−0.291	−0.072	−0.363	−0.066	−0.138	−0.204
pH	0.184	0.134	0.318	0.205	−0.323	−0.118
EC	−0.151	−0.130	−0.281	−0.071	0.237	0.166
Predatory beetles						
SC	−**0.819**	0.134	−0.685	0.062	−0.238	−0.176
SH	0.001	−0.645	−0.644	−**0.681**	0.418	−0.263
HPB	−**0.540**	0.782	0.242	−**1.015**	0.887	−0.128
HSR	−**0.282**	0.012	−0.270	0.092	−0.290	−0.198
SSC	0.137	0.264	0.401	0.101	0.036	0.137
pH	0.243	0.239	0.482	**0.349**	−0.125	0.224
EC	−0.088	−0.498	−0.586	0.066	−0.280	−0.214

NG plots than in the other ones. Soil pH was consistently highest in the NG plots, whereas soil sand content in NG was similar to that in the HAP plots, and higher than in the TRP and MP plots. Finally, soil salinity was significantly lowest in the NG habitat (Table 1).

In addition, the conversion of NG to the three shrub plantations influenced the performance of the three beetle functional groups, although the effects varied among the functional groups, and between the performance parameters (activity abundance and species richness). Overall, converting NG to HAP, TRP, and MP had a stronger influence on beetle activity abundance than on the species richness, across the functional groups. Moreover, converting NG to HAP and TRP had a stronger negative effect on the beetle performance variable than a conversion to MP did (Table 1).

3.2. Direct and indirect effects of vegetation and soil variables on beetle functional groups

The SEM model results showed that SC had a significant negative direct effect on activity abundance with a standardized path coefficient of −0.68 (Table 2). HPB had a significant negative direct effect on activity abundance, and it indirectly affected abundance via positive effects on SC and pH (Fig. 2). SH and EC had no significant direct effects on activity abundance, but SH indirectly affected abundance via a positive effect on HPB, and a negative effect on SC. Furthermore, EC indirectly affected beetle abundance via a positive effect on HPB, and negative effects on SC and pH (Fig. 2). Overall, the net effects of SC, SH, EC, and HSR on activity abundance were negative, whereas those of pH, SSC, and HPB on activity abundance were positive (Table 2). Furthermore, the SEM model for predator species richness showed that HPB and SH had a significant negative direct effect on species richness, but HPB indirectly affected species richness via positive effects on SH and pH. SH additionally indirectly affected richness via a positive effect on HPB, and a negative effect on pH (Fig. 2). Except for pH and SSC, all net effects of the soil and plant variables on species richness were negative (Table 2).

For the herbivores, the SEM models showed that HSR had a significant positive direct effect on activity abundance, with a standardized path coefficient of 0.58 (Table 2). HPB had a significant negative direct effect, and a positive indirect effect via its positive effects on SH and HSR, and a negative effect on SC (Fig. 2). This resulted in a net positive effect of HPB on abundance (Table 2). SH had a significant negative direct effect on abundance, but indirectly affected abundance via a negative effect on SC, and a positive effect on HPB (Fig. 2). SC had no significant direct effect on abundance, but indirectly influenced herbivore abundance through a negative effect on SH, and a positive effect on HPB, with net negative effect of SC on abundance as a result (Table 2). Furthermore, the SEM model for herbivore species richness showed a strong negative direct effect on species richness from HPB. Although the latter also indirectly affected richness via a positive effect on SH, there was a net negative effect of HPB on richness (Fig. 2, Table 2). SH had a significant negative direct effect on species richness, but because it indirectly affected richness via a positive effect on HPB, the net effect of SH on richness was positive as a result. The remaining variables had no significant direct effects on species richness, but indirectly affected species richness by influencing other variables (Table 2, Fig. 2).

The SEM model for detritivore activity abundance showed that HSR had a significant positive direct effect, and a positive indirect effect on abundance via a positive effect on SC (Fig. 1). SC and EC had significant negative direct effects on abundance, but SC also indirectly affected abundance via a negative effect on EC. EC itself also indirectly affected abundance via a negative effect on SC (Fig. 2). The other four variables (SH, HPB, SSC, and pH) had no significant direct effects on abundance. However, SH indirectly affected abundance via a negative effect on SC and EC; HPB indirectly affected abundance via positive effects on SC, HSR, and EC; SSC indirectly affected abundance via a positive effect on EC and a negative effect on HSR; and pH indirectly affected abundance via positive effects on SC and EC (Fig. 2). Overall, the net effects of SC, SH, EC, and SCC on detritivore activity abundance were negative, whereas those of HPB, HSR, and pH were positive (Table 2). Furthermore, for detritivore species richness, the SEM model showed that HSR had a significant positive direct effect, and a weak positive indirect effect on species richness, resulting in a positive net effect of HSR on richness (Table 2). Conversely, SH and EC had a significant negative direct effect on richness, but SH also indirectly affected richness via a negative effect on EC. EC indirectly affected richness via a negative effect on SH, resulting in an overall net negative effect of SH and EC on detritivore species richness (Fig. 2; Table 2). SC, HPB, SSC, and pH had no significant direct effects on richness, but they indirectly affected richness by influencing other variables. In sum, the net effects of SH, EC, SC, and SCC on detritivore species richness were negative, whereas those of HSR, HPB, and pH on richness were positive (Table 2).

3.3. Relative effects of vegetation and soil variables on beetle functional groups

Variance partitioning analyses revealed that 91% of the variation in the species composition of detritivorous beetles was explained by the seven variables. More specifically, 66% was explained by SC, 11% by HSR, 6% by the remaining five variables SH, HPB, pH, SSC, and EC, and 8% by interactions between these variables (Table 3). For herbivorous beetles, the seven explanatory variables together accounted for 67% of the variation in species composition. For this group, 28% was explained by SC, 8% by HSR, 5% by SH, 4% by the remaining four variables HPB, pH, SSC, and EC, and 22% by the interactions between the variables (Table 3). Finally, for predatory beetles, the seven variables together accounted for 75% of the variation in species composition. SH explained 35% of the variance, 10% was explained by SC, 8% by HSR, 2% by the remaining four variables HPB, pH, SSC, and EC, and 19% by the interactions between these variables (Table 3). Overall, SC and HSR were the most important predictors of the species composition of detritivores and herbivores, whereas SH, SC, and HSR were the most important predictors of predator species composition.

The variance partitioning analyses furthermore revealed that changes in vegetation explained 34%, 27%, and 21% of the variation in species composition of detritivores, predators, and herbivores, respectively. In contrast, changes in the soil explained only 4%, 2%, and 1%, for these groups respectively (Table 4). Moreover, vegetation–soil interactions accounted for 52% of the variation in detritivore composition, which was 44% for the predator group, and 37% for the herbivores. This indicates that the interactive effect between vegetation and soil variables contributed more to the composition variation in these beetle functional groups than changes in vegetation or soil alone (Table 4).

4. Discussion

In this study, we investigated the effects of land-use induced changes in vegetation and soil conditions on the composition and diversity of three carabid and tenebrionid beetle functional groups, in a temperate arid region in northwestern China. Overall, our results showed that the three beetle functional groups all responded differently to the land-use induced changes in plants and soils. Below, we discuss our findings and their implications for predicting the impacts of future anthropogenic environmental change on beetle communities.

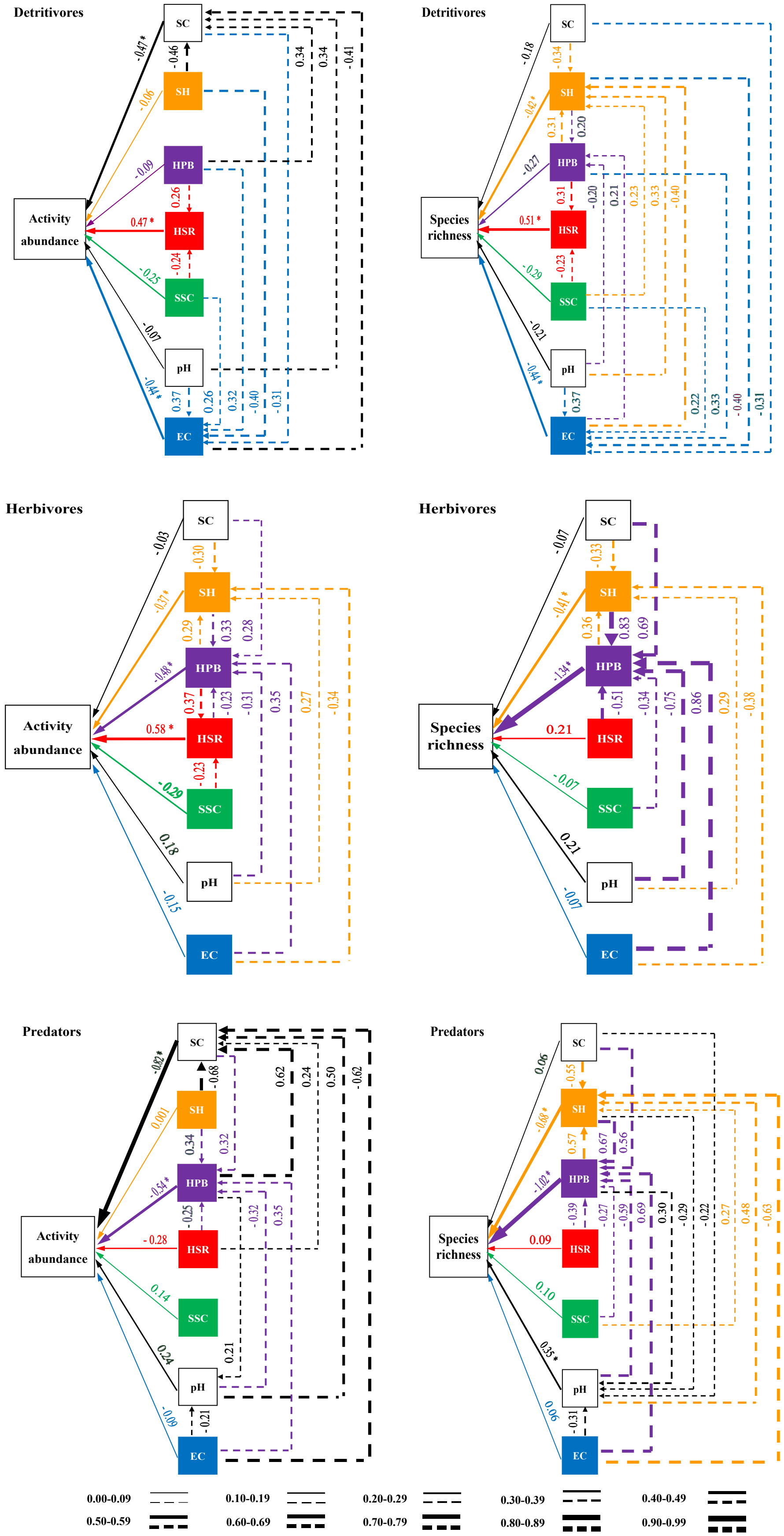
4.1. Effects of vegetation changes on beetle functional groups

The changes in vegetation attributes exerted a greater effect on the beetle functional group species composition than changes in soil attributes, even though the magnitude of the vegetation effects differed among the functional groups. Vegetation variation is therefore a key environmental driver of beetle community structure in our studied region. This finding is consistent with those of previous studies that demonstrated that plant community composition, productivity, and diversity are the primary factors affecting arthropod abundance, diversity, and community composition (Andow, 1991; Axmacher et al., 2009; Barton et al., 2016; Borer et al., 2012; Botha et al., 2015; Brose, 2003; Haddad et al., 2009; Harvey et al., 2008; Schaffers et al., 2008; Siemann, 1998; Wenninger and Inouye, 2008; Woodcock and Pywell, 2009).

One explanation for the significant vegetation-induced bottom-up effects on arthropod diversity and community composition is that sites with a high number of plant species typically have greater plant biomass and litter. Therefore, they can provide more food resources, and consequently support greater assemblages of herbivorous and detritivorous arthropods. Such assemblages support a higher abundance of predatory arthropods as a result (Scherber et al., 2010). Another explanation is that changes in vegetation characteristics affect arthropod diversity and community composition indirectly, through other pathways or mechanisms, such as changing microclimatic conditions and soil properties (Breshears et al., 1998; Hansen, 2000; Schaffers et al., 2008). The relative importance of the four vegetation variables in this study varied considerably in how much they contributed to the species composition variation among the beetle functional groups. Because shrub cover and herbaceous plant diversity explained most of the observed compositional variation in both detritivorous and herbivorous beetles, these vegetation variables are probably the best predictors of species composition for these two functional groups. For predatory beetle species composition variation, a much larger and significant proportion was accounted for by shrub height and cover. This implies that these two vegetation variables are the most important predictors of predatory beetle community composition.

4.2. Effects of vegetation–soil interactions on beetle functional groups

Our variance partitioning analyses for all three functional beetle groups showed that large amounts of the composition variation (44–59%) were accounted for by interactions between the vegetation and soil variables. These amounts were especially large when compared with the amount explained by vegetation (21–34%) or soil (1–4%) alone. Several studies have recognized the importance of interactions among environmental variables in structuring plant and animal populations and communities (Crist, 2008; Farrington


Detritivores
SC
SH
HPB
HSR
SSC
pH
EC
Activity abundance
-0.47*
-0.46
-0.06
-0.09
0.47*
0.26
-0.24
-0.25
-0.07
-0.44*
0.37
0.26
0.32
-0.40
-0.31
0.34
0.34
-0.41
Detritivores
Species richness
-0.18
-0.34
-0.42*
0.31
0.20
-0.27
0.31
0.51*
-0.20
0.21
0.23
0.33
-0.40
-0.23
-0.29
-0.21
-0.44*
0.37
0.22
0.33
-0.40
-0.31
Herbivores
Activity abundance
-0.03
-0.30
-0.37*
0.29
0.33
0.28
-0.48*
0.37
-0.23
-0.31
0.35
0.27
-0.34
0.58*
-0.23
-0.29
0.18
-0.15
Herbivores
Species richness
-0.07
-0.33
-0.41*
0.36
0.83
0.69
-1.34*
-0.51
-0.34
-0.75
0.86
0.29
-0.38
0.21
-0.07
0.21
-0.07
Predators
Activity abundance
-0.82*
-0.68
0.001
0.34
0.32
0.62
0.24
0.50
-0.62
-0.54*
0.25
-0.32
0.35
-0.28
0.14
0.21
0.24
-0.09
-0.21
Predators
Species richness
0.06
-0.55
-0.68*
0.57
0.67
0.56
-1.02*
-0.39
-0.27
-0.59
0.69
0.30
-0.29
-0.22
0.27
0.48
-0.63
0.09
0.10
0.35*
0.06
-0.31
0.00-0.09
0.10-0.19
0.20-0.29
0.30-0.39
0.40-0.49
0.50-0.59
0.60-0.69
0.70-0.79
0.80-0.89
0.90-0.99

et al., 2009; Hegland et al., 2010; Mandle and Ticktin, 2012; Mandle et al., 2015). Our study found weak soil-induced bottom-up effects, but strong vegetation–soil interaction effects on beetle community composition. This suggests that although altered physicochemical soil properties had few direct impacts on the beetle composition, such changes can affect the growth, productivity, and reproductive success of individual plants. Through this influence, these soil changes can consequently affect plant community composition and diversity, with cascading effects on beetle community composition (Janssens et al., 1998; Van der Putten et al., 2013). In terrestrial ecosystems, the interactions between vegetation-induced bottom-up control processes and soil-induced bottom-up control processes are thought to occur at different spatial scales. Quantifying these interactive effects on the beetle communities' structures can help to reveal the assembly rules of beetle communities, and to predict the consequences of vegetation and soil changes on beetle community structure.

The SEM results revealed the complex mechanisms through which vegetation and soil variables interact, both directly and indirectly, in their effects on the beetle abundance and diversity patterns per functional group. Conventional regression models are unable to reveal these mechanisms (Van den Berg et al., 2011). Our data showed that the relative strength and direction of the direct and indirect effects of vegetation and soil variables differed among functional groups of ground beetles, as well as their performance measures (abundance and diversity). For example, the changes in detritivore activity abundance were jointly shaped by the direct effects of HSR, SC, and EC, along with the indirect effects of SH, HPB, and pH, through their impacts on other explanatory variables. The changes in herbivore activity abundance were jointly shaped by the direct effects of HSR, SH, and HPB, along with the indirect effects of HPB, through the impacts of HPB on other explanatory variables. The changes in predator activity abundance were mostly driven by the direct effects of SC and HPB, as well as the indirect effects of HPB, SH, and EC, through their impacts on other explanatory variables. Overall, shrub cover, herbaceous species richness, and soil electrical conductivity were the most important direct drivers of the activity abundance of the detritivorous beetle assemblage. For the herbivorous beetle assemblage, herbaceous species richness, herbaceous plant biomass, and shrub height were the most important direct drivers of the activity abundance. Finally, shrub cover and herbaceous plant biomass were the key direct drivers of the activity abundance of the predatory beetles.

Table 3
Variation partitioning to quantify the relative contributions of the seven explanatory variables to the variation in species composition of the three carabid and tenebrionid beetle functional groups (inertia is the measure of variation). The explanatory variables consisted of shrub cover (SC), shrub height (SH), herbaceous plant biomass (HPB), herbaceous species richness (HSR), soil pH (pH), soil sand content (SSC), and soil electrical conductivity (EC). Significant effects ($P < 0.05$) are shown in bold.

Explanatory variables	Inertia (adj)	% Of all variation	*F*	*P*
Detritivores (all variation = 0.912)				
SC	0.604	66.23	89.3	**0.001**
SH	0.003	0.33	0.9	0.402
HPB	0.013	1.43	4.9	**0.014**
HSR	0.100	10.96	25.3	**0.001**
pH	0.004	0.44	1.7	0.180
SSC	0.013	1.43	4.6	**0.022**
EC	0.025	2.74	7.6	**0.006**
Residual	0.072	7.89	16.2	**0.001**
Total inertia	0.834	91.45	42.2	**0.001**
Herbivores (all variation = 0.670)				
SC	0.189	28.21	24.7	**0.001**
SH	0.031	4.63	5.7	**0.001**
HPB	0.001	0.15	0.2	0.918
HSR	0.051	7.61	8	**0.001**
pH	0.010	1.49	2.1	0.113
SSC	0.017	2.54	3.4	**0.022**
EC	0.001	0.15	0.1	0.998
Residual	0.148	22.09	19.3	**0.001**
Total inertia	0.448	66.87	8.1	**0.001**
Predators (all variation = 0.749)				
SC	0.076	10.15	15.2	**0.001**
SH	0.264	35.25	30.3	**0.001**
HPB	0.012	1.60	2.7	0.078
HSR	0.063	8.41	8.8	**0.004**
pH	0.003	0.40	0.7	0.538
SSC	0.001	0.13	0.2	0.840
EC	0.001	0.13	0.1	0.907
Residual	0.141	18.82	28.2	**0.001**
Total inertia	0.561	74.90	11.9	**0.001**

4.3. *Effects of plant diversity on beetle community assembly*

The diversity of herbaceous plant species had a positive direct and positive net effect, in spite of negative indirect effects, on the activity abundance and species richness of detritivorous beetles. Thus, detritivore abundance and diversity increased with higher herbaceous plant diversity. Similarly, the diversity of herbaceous plant species had a positive direct effect, as well as a positive net effect, on the activity abundance of herbivorous beetles. This confirmed the theory that higher herbaceous plant diversity can support a higher activity abundance of herbivores. However, contrary to what we expected, herbaceous plant diversity had a small, but significant, negative direct and negative net effect on the activity abundance of predatory beetles. We also found a very weak positive direct effect, and a weak negative net effect, of herbaceous plant diversity on species richness of predatory beetles, suggesting that predator diversity was largely unaffected by herbaceous plant diversity. This result is consistent with that of a study in the North China Plain, which reported that the activity abundance of small and omnivorous carabid beetles in agricultural landscapes was significantly and positively correlated with plant species diversity (Liu et al., 2015). However, for predatory carabid activity abundance, their study found no significant relationship with plant species diversity. The observed negative relationship between predatory beetle activity abundance and herbaceous plant diversity is also in accordance with the results of Koricheva et al. (2000). In their grassland ecosystem study, a negative relationship between herbaceous plant diversity and predatory arthropod activity abundance was also reported.

Our observed negative correlation between herbaceous plant diversity and predatory beetle abundance and diversity does not support the Enemies Hypothesis. This hypothesis states that plant species diversity is positively associated with predatory arthropod abundance (Root, 1973; Russell, 1989). Nevertheless, the positive correlations of vegetation diversity with the other two functional groups, the detritivorous and herbivorous beetles, do support this

Fig. 2. Structural equation models (SEM) displaying the magnitude and direction of direct and indirect effects of the seven explanatory variables on the activity abundance and species richness of the sampled carabid and tenebrionid beetle functional groups (detritivores, herbivores, and predators). The explanatory variables included shrub cover (SC), shrub height (SH), herbaceous plant biomass (HPB), herbaceous species richness (HSR), soil pH (pH), soil sand content (SSC), and soil electrical conductivity (EC). The width of solid arrow lines is proportional to the standardized direct path coefficients (see legend for scale). Significant direct effects are marked with * ($P < 0.05$). Dashed arrow lines indicate all significant indirect effects ($P < 0.05$) of the seven explanatory variables on the response variables, and the width of the dashed lines is proportional to their standardized indirect path coefficients (also see legend for scale).

Table 4
Variation partitioning to quantify the relative contribution of vegetation, soil and their interaction to the variation in species composition of the sampled three carabid and tenebrionid beetle functional groups (inertia is the measure of variation). Significant effects ($P < 0.05$) are shown in bold.

Fraction	Inertia (adj)	% Of variation explained	% Of all variation	df	MS	F	P
Detritivores							
Vegetation	0.337	37.8	33.7	4	0.080	26.1	**0.001**
Soil	0.038	4.3	3.8	3	0.014	4.7	**0.004**
Interaction between vegetation and soil	0.516	57.9	51.6			42.2	**0.001**
Total inertia	0.892	100	89.2	7	0.131		
All variation	1.000	–	100	35			
Herbivores							
Vegetation	0.209	35.6	20.9	4	0.060	5.1	**0.001**
Soil	0.011	1.9	1.1	3	0.015	1.3	0.279
Interaction between vegetation and soil	0.367	62.5	36.7			8.1	**0.001**
Total inertia	0.587	100	58.7	7	0.096		
All variation	1.000	–	100	35			
Predators							
Vegetation	0.270	39.4	27.0	4	0.070	7.9	**0.001**
Soil	0.020	2.9	2.0	3	0.003	0.3	0.937
Interaction between vegetation and soil	0.436	63.6	43.6			11.9	**0.001**
Total inertia	0.686	100	68.6	7	0.107		
All variation	1.000	–	100	35			

hypothesis.

Overall, the lack of a significant positive correlation between predatory beetle abundance and diversity and herbaceous plant diversity may be explained by the poor habitat quality of our studied ecosystem. A resource-poor habitat like a desert is unable to support enough herbivores and detritivores as food resources to sustain predator populations (Liu et al., 2015). Thus, the effects of plant diversity on predatory beetle diversity are masked (Scherber et al., 2010; Zhang and Adams, 2011). Another possible explanation is that higher plant diversity can potentially support a higher density of herbivorous arthropods in natural ecosystems, which might also reduce the predators' overall foraging time and, hence, their recorded activity abundance (Schuldt et al., 2011). Our study highlights the existence of the complex interactions between herbaceous plants, detritivorous beetles, herbivorous beetles, and predatory beetles inhabiting this simple desert ecosystem. We therefore suggest that future research should explore these relationships with a manipulative approach.

5. Conclusions

The present study substantially contributes to our understanding of the underlying impacts of land-use change induced alterations of vegetation and soil conditions on the composition and diversity of different beetle functional groups. The vegetation and soil variables that we examined played contrasting roles in structuring the local communities of detritivorous, herbivorous, and predatory beetles. Altered vegetation conditions had stronger bottom-up effects on beetle species composition than altered soil conditions. Moreover, the interactive effects of vegetation and soil variables accounted for most of the observed variation in beetle functional group composition. Shrub cover and herbaceous plant diversity were the best predictors of species composition of detritivorous and herbivorous beetle assemblages, whereas for the predatory beetles, shrub height and cover were the best. Bottom-up effects of vegetation and soil on beetle activity abundance and diversity were initiated via both direct and indirect effects. The strength of these effects differed among the three functional groups. Overall, the findings of this study can help reveal the assembly rules of natural beetle communities, and may be used to design an effective strategy for conserving beetle biodiversity and their ecological functions.

Author Contributions

FRL and JLL designed and performed the experiments. JLL collected the beetle data. TSS, LFM, LLL, and KY collected the vegetation and soil data. FRL and TSS performed statistical analyses. FRL wrote the manuscript.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at http://dx.doi.org/10.1016/j.jaridenv.2016.01.009.

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